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The human remains from Axlor (Dima, Biscay, Northern Iberian Peninsula)

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Abstract

Objectives: We provide the description and comparative analysis of all the human fossil remains found at Axlor during the excavations carried out by J.M. Barandiarán from 1967 to 1974: a cranial vault fragment and eight teeth, five of which likely belonged to the same individual, although two are currently lost. Our goal is to describe in detail all these human remains and discuss both their taxonomic attribution and their stratigraphic context.

Materials and methods: We describe external and internal anatomy, and use classic and geometric morphometrics. The teeth from Axlor are compared to Neandertals, Upper Paleolithic and recent modern humans.

Results: Three teeth (a left dm^2 , a left di^1 , and a right I_1) and the parietal fragment show morphological features consistent with a Neanderthal classification, and were found in an undisturbed Mousterian context. The remaining three teeth (plus the two lost ones), initially classified as Neandertals, show morphological features and a general size that are more compatible with their classification as modern humans.

Discussion: The combined anatomical and stratigraphic study suggest that the remains of two different adult Neandertals have been recovered during the old excavations performed by Barandiarán: a left parietal fragment (level VIII) and a right I_1 (level V). Additionally, two different Neanderthal children lost deciduous teeth during the formations of levels V (left di^1) and IV (right dm^2). In addition, a modern human individual is represented by five remains (two currently lost) from a complex stratigraphic setting. Some of the morphological features of these remains suggest that they may represent one of the scarce examples of Upper Paleolithic modern human remains in the northern Iberian Peninsula, which should be confirmed by further testing.

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KEYWORDS

Neandertal, anatomically modern humans, enamel-dentine junction, geometric morphometrics,
Paleolithic

1-Introduction

The rock-shelter of Axlor is located in the mountainous region included in the national park of Urkiola (Biscay, Basque Country) and preserves one of the most important Middle Paleolithic sequences in the northern Iberian Peninsula (Figure 1). Axlor was discovered in 1932 by the Basque prehistorian J. M. Barandiarán. The first archaeological excavations took place in 1967, and encompassed a total of eight field seasons until 1974 (Barandiarán, 1980). These excavations revealed a sequence of nine layers (I-IX), in which Middle Paleolithic lithic assemblages were found in levels III to VIII. Recent excavations (2000-2008) directed by González-Urquijo, Ibáñez and Rios-Garaizar, provide a new stratigraphic sequence, roughly equivalent to the previous one, but with additional levels, not previously identified or excavated by Barandiarán. Some of these levels were deposited before level VIII, but their chronology remains uncertain (González-Urquijo, Ibáñez, Lazuén & Mozota, 2014; Rios-Garaizar, 2017). Additionally, an early Upper Paleolithic occupation has been recognized (level A of the new excavations, equivalent to the base of Barandiarán's level II, previously considered sterile; González-Urquijo et al., 2014). Ultra-filtered dates obtained from red deer with anthropogenic marks from level IV have yielded results that go beyond the radiocarbon limit, correcting previous dating which situated this level at the very end of regional Middle Paleolithic (Marín-Arroyo et al., 2018). Across the sequence, there are clear differences in terms of the technological characteristics, percentage of ungulate taxa consumed, and type of occupation of the cave between the upper (III-VI) and lower levels (VII-VIII) of the Mousterian sequence, which has been confirmed during the recent excavations (Altuna, 1989; Castaños, 2005; González-Urquijo et al., 2014; Rios-Garaizar, 2017). Recent reassessment of the Barandiarán collection has identified the presence of bird and carnivore exploitation for the first time during the Middle Paleolithic of the Cantabrian region: at least a golden eagle and a lynx where exploited for dietary purposes (Gómez-Olivencia et al., 2018a).

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2 [INSERT FIGURE 1 HERE]
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7 The current human fossil record published for Axlor is limited to five upper left dental
8 remains (C, P⁴-M³) with a maxilla fragment, likely belonging to the same individual (a young
9 adult), which were found in 1967 from a level with Quina Mousterian lithics and faunal remains of
10 red deer, reindeer, and steppe bison (Basabe, 1973; [Figure 2](#)). Basabe (1973) seems to be cautious
11 in the taxonomic assessment of these remains. While he considers that the morphology of these
12 dental remains is compatible with that found in similar (Mousterian) archaeological contexts, he
13 nonetheless considers these remains as “evolved”, with “intermediate” size and traits, including the
14 “unclear” taurodontism in M1-M2 (Basabe, 1973). Currently, only three (P⁴, M¹, M³) of these
15 remains are curated at the Arkeologi Museoa (Bilbao), whereas the location of the other teeth is
16 unknown. A more recent reassessment of these teeth supported a Neandertal classification based on
17 their size and the alleged presence of taurodontism in the molars (Rostro-Carmona, 2013).
18 However, a visual inspection of the morphology of the M¹ shows that it does not present the typical
19 Neandertal morphology for this tooth (e.g., Bailey, 2004; Gómez-Robles et al., 2007). Moreover, no
20 study of the internal anatomy of the teeth based on virtual anthropology techniques has been
21 performed, which could provide a more accurate taxonomic assessment. In 2005, the re-assessment
22 of the whole Barandiarán collection (coordinated by J.E. González Urquijo) resulted in the
23 recognition of three additional human remains: two teeth and a cranial fragment. More recently, the
24 reassessment of the faunal collection from Barandiarán's excavation has resulted in the
25 identification of an additional human remain among the faunal remains: an upper deciduous molar.
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52 [INSERT FIGURE 2 HERE]
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57 Here we provide a detailed description and comparative analysis of all the human fossil
58 remains from Axlor found during J.M. Barandiarán's excavations, including a taphonomic analysis
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1
2 of the cranial fragment. This study also reassess the taxonomic affinities of the remains published
3
4 by Basabe (1973) and Rostro-Carmona (2013), and discusses the archaeological context of all the
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6 human remains from this collection. In fact, the revision of the archaeological context from the
7
8 field-notes taken by J.M. de Barandiarán at the site casts doubts on the stratigraphic position of all
9
10 the teeth studied by Basabe (1973) and Rostro-Carmona (2013), while in the rest of the cases the
11
12 association of these human remains to Mousterian contexts seems secure ([Supplementary](#)
13
14 [Information Text S1](#)).
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22 **2-Materials and Methods**

23 *2.1-Materials*

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The current collection of human remains from the Barandiarán excavations includes an upper fourth premolar, an upper first molar and an upper third molar from the same (young adult) individual (Basabe, 1973), a cranial fragment, a lower right central incisor, an upper left first deciduous incisor and a left upper deciduous second molar ([Table 1](#)). Their spatial location, according to the available information is shown in [Figure 2](#). Access to these materials was granted by the Arkeologi Museoa (Bilbao). The CT scans of these fossils, ~~and~~ the derived segmentation files, and 3D volumes are [freely accessible](#)~~accessible via XXX~~.

[Note to the Editor and the reviewers: All the original micro-CTs and the derived segmentation files and 3D volumes will be made accessible in a public repository (e.g., morphosource or figshare) and the corresponding DOIs will be included in the next version of this manuscript.]

[INSERT TABLE 1 HERE]

2.2-Micro-CT scanning

All the Axlor human remains were micro-CT scanned at the Spanish National Research Center for Human Evolution (CENIEH) using a Phoenix v/tome/x s (GE Measurement & Control). The resolution was maximized depending on the size of the different fossil remains (teeth: 18.99 μ m; cranial fragment: 33 μ m).

2.3-Anatomical descriptions

Standard methods were used to describe and analyze the external and internal anatomy of the cranial fragment. Previous knowledge of the anatomy and relative variation of exo and endocranial surfaces was used to identify the anatomical position and diagnostic features of the cranial fragment (e.g., Balzeau, 2013; Balzeau, Grimaud-Hervé & Gilissen, 2011; Balzeau et al., 2017). The teeth were described following ~~established~~ anatomical dental terms (Carlsen, 1987). In addition, we scored several non-metric traits following both the Arizona State University Dental Anthropology System (ASUDAS) (Turner, Nichol & Scott, 1991) and some complementary traits described by Bailey (2002), which were compared to Neandertals, Upper Paleolithic modern humans (UPMH) and recent humans (Martínón-Torres, Bermúdez de Castro, Gómez-Robles, Prado-Simón, & Arsuaga, 2012). Some of these traits were also scored in the EDJ surface and completed by the traits described by Martin, Hublin, Gunz, & Skinner (2017) for the molars. The roots of the incisors were measured following the method described by Le Cabec, Gunz, Kupczik, Braga & Hublin (2013): Root Length (RL), Root Volume (RV), Root Pulp Volume (RPV), Crown Pulp Volume (CrPV) and different ratios between these measurements. Dental wear assessment was based on Molnar (1971).

2.4-Bone thickness mapping (cranial fragment) and volume segmentation (teeth)

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2 The 3D variation of the total bone thickness of the cranial fragment was evaluated using the
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The 3D variation of the total bone thickness of the cranial fragment was evaluated using the
exo- and endocranial surfaces using the module Surface-Distance of Avizo 7. The results of this
analysis were illustrated using a chromatic scale and compared to previous studies (Balzeau, 2013)
in order to gain insights on the potential taxonomic significance of the thickness distribution
pattern.

In the case of the teeth, before their segmentation, the CT image volumes were pre-
processed using Fiji (Schindelin et al., 2012) by first converting them to 8-bit and then re-sampling
them in the Z direction by a factor of 2 (final volume resolution: 0.019 x 0.019 x 0.038 microns per
voxel). Next, the volumes were segmented using an interactive learning approach (Arganda-
Carreras et al., 2017) that classified each voxel as belonging to one of the following classes: bone,
dentine, enamel, or background. The pulp chamber was afterwards labeled by semi-automatic
filling of the cavity inside the other teeth labels. The output label images were cleaned up by
removing small artifacts and noise by means of morphological operations (Legland, Arganda-
Carreras & Andrey, 2016). Finally, we performed manual correction of the segmented images using
AvizoLite software due to the presence of cracks in some teeth, and lower density zones in the
enamel some of the teeth.

2.5-Taphonomic analysis

The cranial bone was macroscopically and microscopically examined using a hand lens and a
stereoscopic zoom microscope (Olympus SZX10) to examine surface modifications. For the
analysis of striae regarding the differentiation between cut marks and trampling marks we have used
the protocol proposed by Domínguez-Rodrigo, de Juana, Galán & Rodríguez (2009). The cranial
breakage pattern was analyzed following the criteria developed by Sala, Pantoja-Pérez, Arsuaga,
Pablos & Martínez (2016) to assess the presence/absence of perimortem (fresh bone) and
postmortem (dry bone) fractures. Four parameters were recorded: fracture outline (linear, depressed,

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2 stellate); fracture angle (right or oblique); fracture edge (smooth or jagged); presence/absence of
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4 cortical delamination.
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6 7 8 9 *2.6-Geometric morphometrics*

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11 Geometric morphometric analyses of the occlusal surface of the premolar and molar crowns
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13 were used to compare the Axlor posterior permanent teeth with the Neandertal and modern human
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15 samples used in Gomez-Robles et al. (2007), Gómez-Robles, Bermúdez de Castro, Martínón-
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17 Torres, Prado-Simón, & Arsuaga (2012), and Gómez-Robles, Martínón-Torres, Bermúdez de
18
19 Castro, Prado-Simón, & Arsuaga (2011). Modern human samples included both fossil and recent
20
21 modern humans. Occlusal photographs were used to place 2D configurations of landmarks and
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23 semilandmarks. For the M¹, analyses were repeated on the original photographs and on an occlusal
24
25 projection of the occlusal surface obtained after virtually correcting enamel cracks. Because the
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27 Axlor M¹ is heavily worn, the location of anatomical landmarks on cusp apices cannot be
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29 unequivocally determined. Therefore, M¹ analyses were repeated twice, using the original
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31 configuration of landmarks and semilandmarks as described in Gómez-Robles et al. (2007) and only
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33 the configuration of outline semilandmarks (after removing the four anatomical landmarks). The
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35 second analysis, therefore, focuses on the ability of the M¹ occlusal outline to differentiate
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37 Neandertal from modern human molars. The Axlor P⁴ and M³ are substantially less worn than the
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39 M¹, so only the complete configuration of landmarks and semilandmarks was evaluated for them.
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41 For all the posterior teeth, geometric morphometric analyses were performed that included and
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43 excluded size variation (in form and shape space, respectively). A discriminant analysis based on
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45 the first ten principal components of shape variation was carried out to evaluate the species that
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47 Axlor teeth are assigned to.
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3-Metric, morphological and taphonomic description

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4 The cranial and the dental remains are described here. The comparison of the external crown
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6 metric data between Axlor teeth and different comparative samples are shown in [Table 2](#). Only
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8 taxonomically useful metric traits are discussed below.
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13 [INSERT TABLE 2 HERE]
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18 *3.1-Cranial ~~fragment~~remain*

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20 AX.11B.415.400 is a fragment (56 × 41 mm) of a left parietal bone, which preserves 54 mm
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22 of the sagittal suture ([Figure 3](#)). The suture is not fused, and this left fragment has been separated
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24 from the right parietal bone without any breakage of the indentations. Bone thickness for the
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26 analyzed area is only slightly smaller than in La Ferrassie 1 (Balzeau, 2013) and thus incompatible
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28 with a young immature status. Thus, the fragment is not from a child, but may belong to a young
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30 adult or adult. The antero-posterior curvature of this fragment is not very pronounced.
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36 [INSERT FIGURE 3 HERE]
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41 Bone thickness distribution was quantified on nearly the whole preserved area of this
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43 fragment. Thickness varies between 3.4 mm and 10.5 mm. ~~The mean~~Mean thickness of the
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45 fragment is 5.4 mm. Thickness is evenly distributed along the surface of the fragment, there is no
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47 clear increase or decrease related to bone thickness variation. The only exception concerns the
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49 blood vessels on the endocranial surface of the anterior border of the fragment, which are associated
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51 with a clear thinning of the bone (the area with white dots at the anterior border of the bone, noted
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53 V on [Figure 3](#)). Moreover, the infero-anterior corner of the fragment shows a slight increase in bone
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55 thickness (represented by the purple area, noted PC on [Figure 3](#)) which continues posteriorly and
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57 obliquely. It corresponds to the postcentral sulcus.
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4 Some clear endocranial features are visible. Some branches of the meningeal system are
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6 noticeable. They probably all belong to the anterior ramus, one being the anterior branch (noted A
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8 on [Figure 3](#)), the second corresponding to the obelic branch (noted O on Fig. 3). The anterior branch
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10 splits in two simple veins that are quite large. The obelic branch splits into two smaller and long
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12 veins. Concerning the gyral pattern visible on this endocranial surface, two sulci are clear. The
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14 course of the postcentral sulcus (noted PC on [Figure 3](#)) goes from the antero-inferior corner of the
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16 fragment to the center of the medial border of the fragment. This sulcus is well printed and shows a
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18 clear course. Anteriorly, the central sulcus (noted C on [Figure 3](#)) seems to run along the course of
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20 the most anterior vein of the anterior ramus. Those two sulci have a parallel course, delimiting a
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22 post-central gyrus that has a regular width on its preserved extension.
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30 Both bone thickness distribution pattern and endocranial anatomy ~~provide~~
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32 information that helps to propose a taxonomic attribution for this fragment. Bone thickness shows
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34 little variation. In modern humans, there is a clear decrease in bone thickness in the area of the
35
36 superior parietal gyrus. The pattern observed on this fragment resembles what has been described
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38 for Neandertals (Balzeau, 2013). The position and size of the anterior branch of the meningeal
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40 system on this fragment, as well as its subsequent bone thickness variation, fits with the anatomy
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42 observed in Neandertals. The meningeal system in this area has more anastomoses than in modern
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44 humans, and blood vessels are thinner and more numerous (Grimaud-Hervé, 1997). In summary the
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46 anatomical features preserved in this parietal fragment are consistent with a Neandertal
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48 classification.
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55 The bone surface of the cranial ~~fragment~~~~remain~~ is well preserved and does not show
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57 weathering (sensu Behrensmeyer, 1978). No direct carnivore activity (i.e., tooth marks) was
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59 documented, nor any sign of burning. Similarly, no other biological modifications, such as rodent
60

1 activity or root etching, was observed. This cranial fragment shows several striations in the outer
2 table in five different areas (Figure 4). In some cases, the grooves are close “V” shaped, but
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4 microstriations were not evident. On the other hand, the trajectories of the grooves are usually
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6 sinuous and most of the bone surface is covered by very shallow striae. In some cases, the color of
7
8 the striations is lighter compared with the bone surface suggesting that they have occurred after its
9
10 deposition. These observations are compatible with trampling marks following the protocol
11
12 described by Domínguez-Rodrigo et al. (2009). Regarding the fracture analysis, this remain
13
14 displays three linear fractures, one of them parallel and two perpendicular to the cranial suture. The
15
16 two fractures perpendicular to the suture have right angled edges, jagged surfaces and absence of
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18 cortical delamination. These characteristics are typical of fracturing in dry bone (Sala et al., 2016).
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20 However, the fracture that is parallel to the suture displays an oblique angle, smooth surface and
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22 presence of cortical delamination (0.75 cm) on the inner table. The combination of these fracture
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24 attributes is usually considered representative of perimortem fractures (Sala et al., 2016).
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34 [INSERT FIGURE 4 HERE]
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39 *3.2-Upper left fourth premolar, maxillary fragment with upper first molar and upper third molar*
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41 *belonging to the same individual*
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46 Descriptions and analyses are provided for the three dental remains belonging to the same
47 individual. These remains are shown in Figure 5 and are morphologically compared in Tables 3-5.
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52 Ax.13F.265.1 (AX.13E/13F.265-270.1 according to the museum records) is a complete
53 premolar, although its root is damaged and presents longitudinal cracks on both sides and some
54 smaller transversal cracks. In addition, there is a small pitting on the vestibular side of the buccal
55 cusp, and erosion on the tip of this cusp (Figure 5). Also, in the areas with the highest enamel
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1
2 thickness of the crown (the buccal and lingual sides) there is a part of the enamel that shows lower
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4 density in the CT images ([Supplementary information Figure S12](#)). The similarity in height between
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6 the lingual and buccal cusps and the two long inter-proximal facets suggest it is a P⁴. In addition,
7
8 the distal interproximal wear facet matches well the mesial counterpart of the Axlor M¹ ([Figure 5](#)),
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10 further supporting that this is a P⁴, and indicating that they both belonged to the same individual
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12 (see below).
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18 [INSERT FIGURE 5 HERE]
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23 The occlusal surface is moderately worn (stage 3; Molnar, 1971), and the dentine is exposed
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25 on the lingual cusp. Yet, the inter-proximal wear facets are visible to the naked eye, and the distal
26
27 one is larger. This premolar shows a distal accessory marginal tubercle, a bifurcated buccal essential
28
29 crest (grade 2 from Bailey, 2002) and a distal accessory ridge on the buccal cusp ([Table 3](#)).
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34 [INSERT TABLE 3 HERE]
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39 At the EDJ level, two major cusps are observed: buccal and lingual. The essential crest of
40
41 both the lingual and buccal cusps are bifurcated (Grade 2; [Table 3](#)), which are features typically
42
43 observed on Neandertals (92.3% and 61.5% respectively). On the mesial side it presents a
44
45 continuous transverse crest that does not connect with the horn tip of the lingual cusp, also typical
46
47 in Neandertals (69.2%). In addition, there is an intermediate accessory marginal tubercle distal to
48
49 the buccal cusp. The coronal pulp cavity is conformed by the two horns corresponding to the main
50
51 cusps, where the buccal horn is almost two times larger than the lingual one.
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56
57 This premolar shows a single, mediolaterally flat root. This root runs wide and straight in
58
59 the most cervical half, while the apical third is narrower. Both the mesial and distal sides present
60

1 longitudinal grooves, of which the distal is more pronounced. The analysis of the root canal based
2 on the μ CT images shows that this is a single canal (Type 1R₁) which is only found in 12.5% of
3
4 Neandertals (Pan & Zanolli, 2019; [Table 3](#)).
5
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8
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10
11 Geometric morphometric analyses show that Neandertals and recent modern humans are
12 almost completely separated along the P⁴ morphospace, with Neandertals showing a lingually
13 expanded and asymmetric morphology and modern humans showing a symmetric and lingually
14 reduced configuration, where the interfoveal distance is strongly reduced ([Figure 6](#); Gómez-Robles
15 et al., 2011). Interestingly, fossil modern humans completely overlap with Neandertals, showing a
16 premolar configuration that is much more similar to that of Neandertals than to that of recent
17 modern humans. The Axlor P⁴ plots right on the imaginary line that separates the areas of
18 distribution of Neandertals and recent modern humans, but outside the range of distribution of both
19 groups. The Axlor P⁴ plots on this intermediate position because it shares a generally asymmetric
20 morphology with Neandertals, but a moderately reduced distal cusp and a shortened interfoveal
21 distance with modern humans. Based on these traits, a discriminant analysis classifies the Axlor P⁴
22 as a modern human, but with a low probability of only 56%. When adding size information, the
23 Axlor P⁴ plots again in an intermediate position between Neandertals and recent modern humans.
24 Interestingly, it also plots on the lower extreme of the size variation found in fossil modern humans,
25 indicating that the Axlor P⁴ is larger than most recent modern humans, but smaller than most
26 Neandertals and fossil modern humans.
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50 [INSERT FIGURE 6 HERE]
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57 Ax.13F.265.3 (AX.13E/13F.265-270.3 according to the museum records) represents a left
58 maxilla fragment, preserving both the external surface (ca. 13.3 × 9.2 mm), and the internal surface
59
60

1
2 (13.4 × 9.8 mm), with the left M¹ placed in its alveolus. This tooth is fragmented due to longitudinal
3
4 and transversal cracks that affect the crown and roots (Figure 5). Inter-proximal wear facets are
5
6 clear in both sides and the mesial one shows clear grooves on it. This mesial facet shows two
7
8 chippings in its occlusal border. Also, the occlusal surface of the tooth is heavily worn (stage 4-5;
9
10 Molnar, 1971) and the dentine is exposed in all four main cusps, which interferes with the
11
12 observation of several morphological traits.
13
14
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16
17

18 The metacone and the hypocone of this molar are well developed (grade 4 ASUDAS), and
19
20 there is no cusp 5 (Table 4). The hypocone is not distolingually projected, but it is aligned with the
21
22 protocone on the lingual side and with the metacone on the distal side. Due to the heavy occlusal
23
24 wear, it is not possible to score the presence of Carabelli's tubercle or the mesial marginal accessory
25
26 tubercle. The EDJ reveals the presence of an intermediate post-paracone tubercle and no sign of
27
28 fifth cusp (Table 4). Moreover, there is a type II *crista obliqua*, continuously connecting the
29
30 metacone to the protocone, which is centrally positioned. The occlusal wear also affects the dentine
31
32 to a large extent, which may influence trait assessments, but a Carabelli's tubercle does not seem to
33
34 be present. The horn tip of the hypocone pulp cavity is small and not projected, in contrast with the
35
36 typical Neandertal morphology (Supplementary Information Figure S14).
37
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43 [INSERT TABLE 4 HERE]
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48 The three roots are separated, all the radicular canals are divergent and the body is relatively
49
50 short. The canal corresponding to the mesio-buccal root is the widest one, being mesiodistally flat.
51
52 Moreover, the cervical third of this root canal is elongated, presenting a wide morphology, and the
53
54 apical end is bifurcated. This root morphology contrasts with the typical Neandertal taurodont
55
56 configuration.
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1
2 Analyses of shape variation show a generally clear separation between Neandertals and
3
4 modern humans, with Neandertals showing a skewed M¹ configuration and modern humans
5
6 showing a squared configuration ([Figure 6](#); Bailey, 2004; Gómez-Robles et al., 2007). Both groups
7
8 show a minor overlapping area where many fossil modern humans, as well as the Axlor M¹, are
9
10 found. Based on shape data, Axlor M¹ is classified as a modern human with a probability of 88.8%
11
12 or 98.6% (before and after correcting the enamel cracks, respectively). Because of the small size of
13
14 the Axlor M¹, adding size information to the PCA makes this specimen plot comfortably within the
15
16 modern human range of distribution.
17
18
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22
23 When assessing only the M¹ outline as defined by curve semilandmarks ([Supplementary](#)
24
25 [Information Figure S15](#)), the differentiation between Neandertals and modern humans is less clear.
26
27 There is still an area of the morphospace occupied only for Neandertals and another one occupied
28
29 only by modern humans on the grounds of their skewed or squared outline configurations,
30
31 respectively. However, the overlapping area between both species is larger in this case.
32
33 Irrespectively of whether enamel cracks are corrected or not, the Axlor M¹ plots again in the area of
34
35 overlapping of both species. Outline shape data also classify the Axlor M¹ as a modern human with
36
37 a very high probability of more than 99% (with and without enamel crack corrections). Form
38
39 analyses (including size information) also make Axlor M¹ plot comfortably within the range of
40
41 variation of modern humans.
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50 Ax.13F.265.2 (AX.13E/13F.265-270.2 according to museum records) This tooth is well
51
52 preserved upper left M³. The crown is complete, but the lingual root is broken, and it is possible to
53
54 observe longitudinal cracks on both sides of the preserved root fragment. In addition, it shows
55
56 moderate wear on the buccal cusp tips but there is no exposed dentine on them (stage 2; Molnar,
57
58 1971).
59
60

1
2
3
4 There is a well-developed metacone but the hypocone is absent (Table 5). Nevertheless,
5
6 there is a small fifth cusp, that is positioned distally to a lingual tubercle. On the EDJ it can be
7
8 observed that there is no crista obliqua, and that the post-paracone tubercle is intermediate (Table
9
10 5). Dentine horn tips of the major cusps are not centrally compressed. The preserved part of the root
11
12 corresponds to the two buccal roots, with both apical tips completely closed. These two roots are
13
14 fused, but the root canals run independently along most of the root, except in the most apical tip
15
16 where they meet again.
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22 [INSERT TABLE 5 HERE]
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27 Shape analyses show that the separation between Neandertal and modern human M³s is far
28
29 from clear (Figure 6; Gómez-Robles et al., 2012). Both species overlap completely along PC1, and
30
31 they show certain morphological trends only along PC2, with Neandertals tending to show positive
32
33 values associated with a more expanded hypocone, and modern humans tending to show negative
34
35 values associated with a strongly reduced hypocone that may be absent altogether. As with the other
36
37 adult posterior teeth, the M³ from Axlor plots on the area of the morphospace where Neandertals
38
39 and modern humans overlap. Shape data classify this M³ as a modern human with a probability of
40
41 78.4%, but it should be noted that the percentage of correct classification for Neandertals is very
42
43 low. The inclusion of size information makes this molar plot far outside the range of variation of
44
45 Neandertals on the grounds of its small size.
46
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52 In summary, based on both morphological and size characteristics, this individual shows
53
54 stronger affinities with modern humans than with Neandertals.
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3.3-Additional dental remains

AX.5B.299.16 This is a well-preserved lower right first incisor, although it shows heavy wear on the incisal edge, having lost between the 20-50% of the crown (roughly equivalent to Grade 4; Molnar, 1971; [Figure 7](#)). The degree of shoveling, labial convexity and the interproximal facets cannot be assessed due to the heavy incisal wear. The bucco-lingual diameter (7.7 mm) is larger than the one observed in modern humans and it fits well within the Neandertal range of variation. In contrast, the mesio-distal diameter is slightly smaller than the Neandertal minimum and falls within the modern human distribution ([Table 2](#)). Nonetheless, this mesio-distal measure is most probably affected by the wear of the crown. The cingular region is bulky, although there is no tuberculum dentale. The heavy wear also affects the observation of the degree of shoveling at the EDJ level, where no tuberculum dentale is observed. The root length of this incisor is 20.86 mm, equal to the maximum value reported in Neandertals (13.8-20.86 mm), and longer than the currently known values for Upper Palaeolithic (11.84-14.20 mm) and recent modern humans (13.18-19.22 mm) (comparative samples from Le Cabec et al., 2013). In addition, the root volume is higher than any reported value for Neandertals or anatomically modern humans (458.33 mm³). On the other hand, the volume of the crown pulp (CrPV) and the radicular canal (RpV) are in the low end of the variability of Neandertals, 6.61 mm³ and 2.65 mm³, respectively. The ratio between the volume of these two values is 0.4, which is situated in the highest half of the Neandertal variability, indicating a proportionally bigger crown pulp segment compared to the root (comparative samples from Le Cabec et al., 2013). In sum, the features observed on this tooth (in particular, its crown and root length size) align it with Neandertals.

[INSERT FIGURE 7 HERE]

1
2 AX.5B.299.31.64.17 This is an upper left first deciduous incisor with a well-preserved crown, but
3
4 the root is not complete (Figure 7). The smooth and twisted aspect of the fracture line of the root
5
6 has been interpreted in other individuals as the result of root resorption, corresponding to a 6-8-
7
8 years-old individual based on modern standards (AlQahtani, Hector, & Liversidge, 2010). Despite
9
10 the heavy wear (Grade 5, Molnar, 1971), a marked shovel shape is observable on the enamel
11
12 surface (>3 ASUDAS). The mesio-distal diameter of this incisor falls within the metric variation of
13
14 both Neandertals and modern humans, but the bucco-lingual diameter is larger than the maximum
15
16 value for the latter group (Table 2). There is no tuberculum dentale, and it is not possible to evaluate
17
18 the labial convexity on the enamel. The EDJ shows a strong and asymmetric labial convexity, more
19
20 marked on the mesial side than on the distal. Moreover, there is no tuberculum dentale observed at
21
22 the EDJ level, and it shows a well-developed shovel shape (>3 ASUDAS). In sum, the features
23
24 observed on this tooth (in particular, its strong and asymmetric labial convexity, its well-developed
25
26 shovel shape) and its size align it with Neandertals.
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36 AX.9E.283.103 This tooth is an upper left second deciduous molar that preserves a nearly complete
37
38 crown. The tooth is heavily worn exhibiting dentine in all four cusps, and the mesial inter-proximal
39
40 side of the enamel is missing. This tooth does not preserve the root, likely resorpted and/or
41
42 subsequently broken, and would have belonged to a 10-11-years-old individual based on modern
43
44 standards (AlQahtani et al., 2010). The size of the crown of this specimen does not provide
45
46 taxonomic information due to the large overlap between Neandertals and modern humans (Table 2).
47
48 Both the metacone and the hypocone are well developed (grade 4 ASUDAS). Despite the heavy
49
50 wear, it is possible to observe a big Carabelli's trait (Grade > 2 ASUDAS), but it is not possible to
51
52 assess the presence of any other accessory tubercles. The EDJ presents a big Carabelli's trait that is
53
54 affected by the fracture of the mesial interproximal side of the tooth, which does not allow locating
55
56 the dentine horn. Moreover, the crista obliqua is continuous, and of type II, with a centered placed
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1
2 protocone, which is a typical Neandertal trait (Becam et al., 2015; Becam & Chevalier, 2019). A
3
4 quantitative analysis of this molar has not been carried out, but qualitative observation shows that
5
6 the skewed morphology typical of Neandertal dm²s is not present (Bailey et al., 2014). A generally
7
8 squared outline morphology is present in this specimen instead. This squared morphology may
9
10 result from the presence of a well-developed Carabelli's trait, which is reported to give Neandertal
11
12 dm²s a less skewed appearance (Bailey et al., 2014). In sum, most features observed on this tooth
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14 align it with Neandertals.
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20 **Discussion**

21 *Taxonomic assessment of the Axlør fossil remains*

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29 The human remains from Axlør can be divided into two different groups. The first group includes a
30
31 series of published dental remains, traditionally regarded as belonging to a single Neandertal
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33 individual (Basabe, 1973), which our results better classify as belonging to a modern human.
34
35 Indeed, a detailed evaluation of the field notes of J.M. Barandiarán and our own assessment of the
36
37 stratigraphy at the place where these remains were found cast doubts regarding their belonging to
38
39 the Middle Paleolithic layers ([Supplementary Information Text S1](#)). The second group of human
40
41 remains includes three dental remains and a cranial fragment, described here for the first time,
42
43 which show clear Neandertal affinities and whose attribution to Mousterian layers seems secure
44
45 based on our assessment of the J.M. Barandiarán field notes.
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51
52 The first group includes three teeth, P⁴, M¹ and M³ (plus two additional lost specimens),
53
54 likely belonging to the same individual as already stated by Basabe (1973). The (moderate) wear
55
56 stage and the fact that the apical tip of the M³ root is closed indicates that they belonged to a young
57
58 adult. Several features, mainly related to the M¹ morphology, question the previous taxonomic
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60

1
2 assignment of these teeth. First, the hypocone of the M¹ is not bulky and projected disto-lingually
3
4 (Figures 5-6; Supplementary Information Figures S14-S15), the tips of the dentine horns, as far as it
5
6 can be inferred given the heavy wear of the molar, are not centrally placed, and the molar is not
7
8 taurodont. In summary, this molar lacks all the traits that are typically associated with Neandertal
9
10 M¹s. Second, the P⁴ shows a single root channel (an infrequent trait in Neandertals; Pan & Zanolli,
11
12 2019), a reduced lingual cusp and a shortened interfoveal distance (typically observed in modern
13
14 humans). However, other traits in this individual seem to be more frequent in Neandertals. First, the
15
16 bifurcated buccal and lingual essential crests on the P⁴ EDJ and the continuous transverse crest are
17
18 typically Neandertal features (Becam et al., 2019), as it is a generally asymmetric P⁴ crown
19
20 (Gómez-Robles et al., 2011). Second, the presence of crista obliqua is a Neandertal M³ common
21
22 feature (Martin et al., 2017), but the Axlör specimen does not present it in any typology. Moreover,
23
24 in this M³ only the metacone dentine horn tip is slightly centrally placed, while the rest of the cusps
25
26 show the typical morphology of *Homo sapiens*. However, it should be noted that variation of
27
28 UPMH in many of these traits is not completely understood (e.g., for the P⁴, there is only
29
30 information from one UPMH; Becam et al., 2019). Moreover, the discovery of UPMH with
31
32 evidence of recent Neandertal admixture (Fu et al., 2015) and the mounting evidence that
33
34 Neandertal-modern human hybridization may have been common could partially explain the
35
36 differences found between the dental morphology of the UPMH and Holocene populations.
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45 In addition, a qualitative assessment of the teeth that are now lost from the collection (C*
46
47 and M²), based on the information and figures provided by Basabe (1973), indicates that they likely
48
49 belonged to the same individual due to the overall morphology and wear degree compatibility.
50
51 Moreover, the M³ presents a small interproximal facet, compatible with the M² with reduced
52
53 hypocone presented by Basabe (1973). Regarding the morphology of these two lost teeth, it is
54
55 possible to observe on the original publication that the upper canine has some archaic features: a
56
57 bulky tuberculum linguale (ASUDAS grade >3) and well developed mesial ridge (grade 2), more
58
59
60

1
2 common in Neandertals (100% and 42.1%, respectively) and UPMHs (40% and 11.1%,
3
4 respectively) than in recent *Homo sapiens* (8% and 5.3%, respectively) (Martín-Torres et al.,
5
6 2012). On the other hand, the M² presents a large metacone (ASUDAS grade 3-4), a reduced
7
8 hypocone (ASUDAS grade 0-2), and absence of Carabelli's tubercle (ASUDAS grades 0-1).
9
10 Reduced hypocones are more common in UPMHs (50%) than in Neandertals (24.9%) (Martín-
11
12 Torres et al., 2012).
13
14

15
16 Based on this morphological information, the absence of Holocene recent prehistory remains
17
18 from the Axlor sequence, the presence of an early Upper Paleolithic occupation in the site
19
20 (González-Urquijo et al., 2014), and the unclear previous ascription to the Mousterian level III due
21
22 to their finding in loose sediment close to the rock-shelter wall (see [Supplementary information](#)),
23
24 we hypothesize that these human remains could belong to an UPMH, which should be tested in the
25
26 near future using direct C14 datings. Currently, except for a few skeletons (Lagar Velho, Mirón;
27
28 Duarte et al., 1999; Carretero et al., 2015) most of the Upper Paleolithic remains from the Iberian
29
30 Peninsula consist of isolated teeth or cranial remains (Pérez Iglesias, 2007, and references therein).
31
32
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34
35 We consider that the stratigraphic ascription of these teeth, rather than their morphology *per*
36
37 *se*, have contributed to incorrectly classify the published teeth from Axlor as belonging to
38
39 Neandertals. While Basabe (1973) considers that their general morphology resembles that of other
40
41 individuals found in Mousterian contexts, he still underlines their “evolved” status with the
42
43 presence of “intermediary characters” (Basabe, 1973:200), especially referring to the low degree of
44
45 taurodontism in the M¹ and the M². The same author did classify the M¹ from Lezetxiki, which
46
47 shows the typical Neandertal occlusal morphology and a clear taurodontism (Basabe, 1970), as
48
49 belonging to a Neandertal individual.
50
51

52
53 The second study that classified the Axlor teeth as Neandertals compared them with Sima de
54
55 los Huesos, Neandertals and modern humans both morphologically (using the data by Martín-
56
57 Torres et al., 2012) and metrically (using the data by Rodríguez-Cuenca (2003) and García-Bour,
58
59 Pérez-Pérez, & Chimenos (1997). However, most traits included in that study (Rostro-Carmona,
60

1
2 2013) are not taxonomically distinctive and, for those which are, the Axlör teeth show modern
3
4 human affinities. In terms of size, and using the data provided by Rostro-Carmona (2013), only the
5
6 canine would show a size closer to the Neandertal mean, the P⁴ and M¹ would show intermediate
7
8 affinities while the size of the M² and M³ would be more similar to modern humans. Our study
9
10 shows that, after including UPMHs in the comparative samples, and despite the overlap between
11
12 modern humans and Neandertals, the general size of the Axlör teeth is either non-determinant or
13
14 more similar to modern humans. Finally, Rostro-Carmona (2013) used the presence of taurodontism
15
16 in the Axlör teeth to classify them as belonging to Neandertals, but our assessment indicates that the
17
18 Axlör teeth show a very limited degree of taurodontism, particularly when compared with classic
19
20 Neandertal molars.
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24
25 The second group would encompass the cranial fragment and three additional tooth remains
26
27 that have clear Neandertal affinities and their stratigraphic position is secure within the Mousterian
28
29 levels. The bone thickness distribution pattern and endocranial anatomy of the cranial
30
31 fragment remain are consistent with Neandertal anatomy. Additionally, both incisors and the dm²
32
33 present characteristics that allow us to ascribe them to Neandertals. Although heavily worn, the I₁
34
35 shows Neandertal affinities in its root configuration and proportions. Nevertheless, the CrPV and
36
37 RpV values are lower than the Neandertal values reported to date (Le Cabec et al., 2013; Becam &
38
39 Chevalier, 2019). This might be related to an advanced age for the individual, as aging related
40
41 deposition of secondary dentine causes the reduction of the pulp channel (Aboshi, Takahashi, &
42
43 Komuro, 2010; Solheim, 1992). This would be consistent with the heavy wear present in this tooth.
44
45 Second, both the OES and EDJ of the deciduous upper incisor from Axlör present a set of
46
47 characteristics observed in other Neandertal specimens such as Portel-Ouest, La Ferrassie 8 (strong
48
49 mesial and distal marginal ridges, pronounced and asymmetric labial convexity) (Becam &
50
51 Chevalier, 2019). Third, although the dm² does not show the typical Neanderthal skewed
52
53 configuration, it does show a notable development of the hypocone in relation to the metacone, the
54
55 presence of the crista obliqua, and a large Carabelli's tubercle at the OES and EDJ. These are
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1
2 common features to other Neandertal dm²s, such as Arrillor, La Ferrassie 8 or Portel-Ouest (Becam
3 & Chevalier, 2019; Bermúdez de Castro & Saenz de Buruaga, 1999). These new remains confirm
4 the presence of Neandertal fossil remains in Axlor, thus increasing the Neandertal hypodigm
5 recovered in the Eastern Cantabrian Region.
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10 11 12 13 14 15 16 *Origin of the accumulation of the human fossil remains* 17 18 19

20 Taphonomic and forensic analyses on hominin fossils are important to determine the origin of
21 bone deposition and reconstruct the processes occurred during the fossil-diagenetic processes even
22 for isolated fossils (Sanz et al., 2018). In some cases, it is even possible to determine causes of
23 death (Sala et al., 2015) or drawing inferences about the mortuary practices of hominin groups, such
24 as cannibalism (Rougier et al., 2016; Sala & Conard, 2016; Saladié et al., 2012; Saladié &
25 Rodríguez-Hidalgo, 2017) or funerary activities (Gómez-Olivencia et al., 2018b).
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36 In the case of the two deciduous teeth, they were lost by two different Neandertal individuals
37 during the formation of levels V (left di¹) and IV (right dm²). The presence of isolated deciduous
38 teeth is not rare in Middle Paleolithic layers, and the closest example is found less than 25 km south
39 from Axlor, in Arrillor (Figure 1; Bermúdez de Castro & Saénz de Buruaga, 1999; Iriarte-
40 Chiapusso, Wood, & Sáenz de Buruaga, 2019), with other example from Le Portel Ouest (Becam &
41 Chevalier, 2019). The cranial fragment from Axlor displays evidence of postmortem and
42 perimortem fractures, but the absence of traces that could indicate the causes of such fractures
43 makes it difficult to interpret its origin. Although we cannot rule out intentional causes for the
44 perimortem fractures, the lack of clear anthropic cut marks or signs of anthropic manipulation does
45 not allow us to go further in our interpretation. The absence of weathering could be interpreted as a
46 non-aerial (or short-term) exposure of the fossils in the biostratigraphic phase. On the other hand,
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1
2 trampling has been documented on the cranial fragment suggesting certain displacement of the
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4 fossils which could be one of the explanations of the scarcity of human remains at the site.
5
6 Additionally, the Barandiarán collection shows some significant bias in comparison with the
7
8 richness in fossil remains that we have observed at the site during recent excavations (Gómez-
9
10 Olivencia et al., 2018a), in which smaller shaft fragments are absent. This bias could be a secondary
11
12 reason of this scarcity. In this context, the recovery of additional human fossils in the Axlor site
13
14 would help elucidate the nature of these isolated remains found in a human occupation context.
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20 **Conclusions**

21
22 Axlor (Dima, Biscay) is one of the most important Middle Paleolithic sites in the Cantabrian
23
24 region (northern Iberian Peninsula). The excavations performed by J.M. Barandiarán at the Axlor
25
26 site 50 years ago yielded a cranial vault fragment and eight teeth, five of which likely belonged to
27
28 the same individual, although two are currently lost. Three teeth (a left dm^2 , a left di^1 , and a right I_1)
29
30 and the cranial fragment show morphological features consistent with their classification as
31
32 Neandertals, and were found in undisturbed Mousterian context. However, the remaining three teeth
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34 (plus two that have been lost since the initial finding), traditionally classified as Neandertals
35
36 (Basabe, 1973; Rostro Carmona, 2013), show morphological features and a general size more
37
38 compatible with their classification as modern humans. Moreover, the review of the original notes
39
40 by J.M. Barandiarán and our own observations during the recent excavations at the site suggest that
41
42 the archaeological context of these remains should be carefully reconsidered. We hypothesize that
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44 these teeth may constitute one of the scarce examples of Upper Paleolithic remains in the Iberian
45
46 Peninsula, a hypothesis that would require a direct C14 dating to be tested, which currently is not
47
48 possible due to access limitations.
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The original micro-ct scans, the derived segmentation files, and 3D volumes are available in
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Figure legends

FIGURE 1 Location of Axlor (red star) and other Paleolithic sites with human remains in the Center and East of the Cantabrian Region (northern Iberian Peninsula and southwestern France). 1: La Pasiega (González Echegaray & Ripoll Perelló, 1954); 2: Castillo (N; HS; Garralda, 2005; Garralda, Maíllo-Fernández, Higham, Neira, & Bernaldo de Quirós, in press; Obermaier, 1925; Tejero et al., 2010; Vallois & Delmas, 1976; 3 Covalejos (N, HS; Sanguino González & Montes Barquín, 2005); 4: Pendo (Basabe, 1982); 5: Morín (HS; González Echegaray & Freeman, 1973; Obermaier, 1925); 6: Rascaño (Guerrero Sala & Lorenzo Lizalde, 1981); 7: La Chora (González Echegaray, García Guinea, Begines Ramírez & Madariaga de la Campa, 1963); 8: Mirón (HS; Carretero et al., 2015); 9: Arrillor (N, Bermúdez de Castro & Sáenz de Buruaga, 1999); 10: Axlor (N; HS; this work); 11: Lezetxiki (N; Basabe, 1970); 12: Santa Catalina (HS; Albisu Andrade, Etxeberria Gabilondo, & Herrasti Erlogorri, 2014); 13: Aitzbitarte III (HS; de la Rúa & Hervella, 2011); 14: Alkerdi (Barandiarán & Cava, 2008); 15: Isturitz (HS; Henry-Gambier, Normand, & Pétilion, 2013); 16: Duruthy (HS; ~~Henry-Gambier, 2006~~~~Arambourou & Genet-Varein, 1965~~). N=Neandertal; HS=*Homo sapiens*. Base map made with QGIS 2.18.17 (QGIS Development Team, 2009) with data by Jarvis, Reuter, Nelson, & Guevara (2008).

FIGURE 2 Excavation plan (a) and stratigraphic column (b) of Axlor cave (modified from Gómez-Olivencia et al., 2018a). (a) In the excavation plan the grid system used by J.M. Barandiarán (black square and white numbers) and the excavation area is shadowed in gray. The grid system used by the recent excavations is marked using black letters and numbers and the excavation area is outlined using a thick black line. The dotted line represents the rock-shelter wall when the site was first excavated, during the excavation this wall went back, revealing a possible cave infilling. The colors correspond to the levels to which these remains were attributed based on the notes by

1
2 Barandiarán. (b) Synthetic section of the 1967–1974 excavation stratigraphy, drawn from the
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4 description of the layers by J. M. Barandiarán (1980). Different levels are marked with different
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6 colors, and the human remains are marked by silhouettes.
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11 **FIGURE 3** Ax.11B.415.400 left parietal fragment. The original fossil and the 3D model are
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13 shown on different views. On the lower row, the approximate location of this fragment is shown on
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15 the La Ferrassie 1 Neandertal cranium (left), a thickness map (from 2 to 12 mm) is shown (middle)
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17 with PC that correspond to thicker bone where is located the postcentral sulcus and V to a relative
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19 thinning produced by the anterior ramus of the meningeal system; and the anatomical features on
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21 the endocranial surface (right): including meningeal veins, A = anterior branch, O = obelisc branch,
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23 and sulcal imprints C = central sulcus, PC = postcentral sulcus.
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30 **FIGURE 4** Ectocranial view of the specimen Ax.11B.415.400 with the location of zones a-d,
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32 and detailed images of these zones, where striations are located. In some cases, the grooves show a
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34 close “V” shape but do not show microstriations. The general morphology of these grooves (see
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36 text) make them compatible with trampling marks.
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42 **FIGURE 5** Dental remains previously studied by Basabe (1973) and Rostro-Carmona (2013),
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44 and likely belonging to the same individual. The teeth are shown in mesial, buccal, distal, lingual
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46 (top) and occlusal (bottom) views, together with the results of the enamel segmentation and the EDJ
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48 surface morphology. Pulp chamber volumes (in blue) are shown in mesial (P⁴, M¹) and lingual (M²)
49
50 views. A virtual reconstruction of the teeth in buccal and occlusal views is also provided. Scale bars
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52 = 1 cm.
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58 **FIGURE 6** Principal components analysis of shape (left column) and form variation (right
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60 column), corresponding to the teeth previously studied by Basabe (1973) and Rostro-Carmona

1
2 (2013), and likely belonging to the same individual. The Axlor remains have been compared to
3
4 Neandertals (NEA), fossil *Homo sapiens* (FSAP) and recent *Homo sapiens* (RSAP). In both form
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6 and shape space, the Axlor remains align more closely with modern humans. TPS-grids show
7
8 anatomical variation corresponding to the positive and negative extreme of each PC when all the
9
10 other PCs are held equal to 0. For M¹ variation, the two data points correspond to Axlor's variation
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12 before (darker red) and after (lighter red) correcting the enamel cracks ([Supplementary information](#)
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14 [Figure S13](#)).
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20 **FIGURE 7** New dental remains from the Barandiarán collection of Axlor. AX.5B.299.16 (right
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22 permanent first lower incisor, I₁): root canal morphology (blue) in mesial view; mesial, buccal,
23
24 distal, lingual and occlusal views. AX.5B.299.31.64.17 (upper left first deciduous incisor, dI¹): top,
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26 mesial, buccal, distal, lingual and occlusal views. AX.9E.283.103 (left dM²): top, mesial, buccal,
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28 distal, lingual and occlusal views. In the virtual reconstructions, enamel is represented in white and
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30 dentine in brown. Scale bars = 1 cm
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2 The human remains from Axlor (Dima, Biscay, Northern Iberian Peninsula)
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Abstract

Objectives: We provide the description and comparative analysis of all the human fossil remains found at Axlor during the excavations carried out by J.M. Barandiarán from 1967 to 1974: a cranial vault fragment and eight teeth, five of which likely belonged to the same individual, although two are currently lost. Our goal is to describe in detail all these human remains and discuss both their taxonomic attribution and their stratigraphic context.

Materials and methods: We describe external and internal anatomy, and use classic and geometric morphometrics. The teeth from Axlor are compared to Neandertals, Upper Paleolithic and recent modern humans.

Results: Three teeth (a left dm^2 , a left di^1 , and a right I_1) and the parietal fragment show morphological features consistent with a Neanderthal classification, and were found in an undisturbed Mousterian context. The remaining three teeth (plus the two lost ones), initially classified as Neandertals, show morphological features and a general size that are more compatible with their classification as modern humans.

Discussion: The combined anatomical and stratigraphic study suggest that the remains of two different adult Neandertals have been recovered during the old excavations performed by Barandiarán: a left parietal fragment (level VIII) and a right I_1 (level V). Additionally, two different Neanderthal children lost deciduous teeth during the formations of levels V (left di^1) and IV (right dm^2). In addition, a modern human individual is represented by five remains (two currently lost) from a complex stratigraphic setting. Some of the morphological features of these remains suggest that they may represent one of the scarce examples of Upper Paleolithic modern human remains in the northern Iberian Peninsula, which should be confirmed by further testing.

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KEYWORDS

Neandertal, anatomically modern humans, enamel-dentine junction, geometric morphometrics,
Paleolithic

1-Introduction

The rock-shelter of Axlor is located in the mountainous region included in the national park of Urkiola (Biscay, Basque Country) and preserves one of the most important Middle Paleolithic sequences in the northern Iberian Peninsula (Figure 1). Axlor was discovered in 1932 by the Basque prehistorian J. M. Barandiarán. The first archaeological excavations took place in 1967, and encompassed a total of eight field seasons until 1974 (Barandiarán, 1980). These excavations revealed a sequence of nine layers (I-IX), in which Middle Paleolithic lithic assemblages were found in levels III to VIII. Recent excavations (2000-2008) directed by González-Urquijo, Ibáñez and Rios-Garaizar, provide a new stratigraphic sequence, roughly equivalent to the previous one, but with additional levels, not previously identified or excavated by Barandiarán. Some of these levels were deposited before level VIII, but their chronology remains uncertain (González-Urquijo, Ibáñez, Lazuén & Mozota, 2014; Rios-Garaizar, 2017). Additionally, an early Upper Paleolithic occupation has been recognized (level A of the new excavations, equivalent to the base of Barandiarán's level II, previously considered sterile; González-Urquijo et al., 2014). Ultra-filtered dates obtained from red deer with anthropogenic marks from level IV have yielded results that go beyond the radiocarbon limit, correcting previous dating which situated this level at the very end of regional Middle Paleolithic (Marín-Arroyo et al., 2018). Across the sequence, there are clear differences in terms of the technological characteristics, percentage of ungulate taxa consumed, and type of occupation of the cave between the upper (III-VI) and lower levels (VII-VIII) of the Mousterian sequence, which has been confirmed during the recent excavations (Altuna, 1989; Castaños, 2005; González-Urquijo et al., 2014; Rios-Garaizar, 2017). Recent reassessment of the Barandiarán collection has identified the presence of bird and carnivore exploitation for the first time during the Middle Paleolithic of the Cantabrian region: at least a golden eagle and a lynx where exploited for dietary purposes (Gómez-Olivencia et al., 2018a).

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2 [INSERT FIGURE 1 HERE]
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7 The current human fossil record published for Axlor is limited to five upper left dental
8 remains (C, P⁴-M³) with a maxilla fragment, likely belonging to the same individual (a young
9 adult), which were found in 1967 from a level with Quina Mousterian lithics and faunal remains of
10 red deer, reindeer, and steppe bison (Basabe, 1973; [Figure 2](#)). Basabe (1973) seems to be cautious
11 in the taxonomic assessment of these remains. While he considers that the morphology of these
12 dental remains is compatible with that found in similar (Mousterian) archaeological contexts, he
13 nonetheless considers these remains as “evolved”, with “intermediate” size and traits, including the
14 “unclear” taurodontism in M1-M2 (Basabe, 1973). Currently, only three (P⁴, M¹, M³) of these
15 remains are curated at the Arkeologi Museoa (Bilbao), whereas the location of the other teeth is
16 unknown. A more recent reassessment of these teeth supported a Neandertal classification based on
17 their size and the alleged presence of taurodontism in the molars (Rostro-Carmona, 2013).
18 However, a visual inspection of the morphology of the M¹ shows that it does not present the typical
19 Neandertal morphology for this tooth (e.g., Bailey, 2004; Gómez-Robles et al., 2007). Moreover, no
20 study of the internal anatomy of the teeth based on virtual anthropology techniques has been
21 performed, which could provide a more accurate taxonomic assessment. In 2005, the re-assessment
22 of the whole Barandiarán collection (coordinated by J.E. González Urquijo) resulted in the
23 recognition of three additional human remains: two teeth and a cranial fragment. More recently, the
24 reassessment of the faunal collection from Barandiarán's excavation has resulted in the
25 identification of an additional human remain among the faunal remains: an upper deciduous molar.
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52 [INSERT FIGURE 2 HERE]
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57 Here we provide a detailed description and comparative analysis of all the human fossil
58 remains from Axlor found during J.M. Barandiarán's excavations, including a taphonomic analysis
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2 of the cranial fragment. This study also reassess the taxonomic affinities of the remains published
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4 by Basabe (1973) and Rostro-Carmona (2013), and discusses the archaeological context of all the
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6 human remains from this collection. In fact, the revision of the archaeological context from the
7
8 field-notes taken by J.M. de Barandiarán at the site casts doubts on the stratigraphic position of all
9
10 the teeth studied by Basabe (1973) and Rostro-Carmona (2013), while in the rest of the cases the
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12 association of these human remains to Mousterian contexts seems secure ([Supplementary](#)
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14 [Information Text S1](#)).
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22 **2-Materials and Methods**

23 *2.1-Materials*

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The current collection of human remains from the Barandiarán excavations includes an upper fourth premolar, an upper first molar and an upper third molar from the same (young adult) individual (Basabe, 1973), a cranial fragment, a lower right central incisor, an upper left first deciduous incisor and a left upper deciduous second molar ([Table 1](#)). Their spatial location, according to the available information is shown in [Figure 2](#). Access to these materials was granted by the Arkeologi Museoa (Bilbao). The CT scans of these fossils, the derived segmentation files, and 3D volumes are freely accessible.

[INSERT TABLE 1 HERE]

55 *2.2-Micro-CT scanning*

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All the Axlor human remains were micro-CT scanned at the Spanish National Research Center for Human Evolution (CENIEH) using a Phoenix v/tome/x s (GE Measurement & Control).

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2 The resolution was maximized depending on the size of the different fossil remains (teeth:
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4 18.99 μm ; cranial fragment: 33 μm).
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9 *2.3-Anatomical descriptions*

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11 Standard methods were used to describe and analyze the external and internal anatomy of
12
13 the cranial fragment. Previous knowledge of the anatomy and relative variation of exo and
14
15 endocranial surfaces was used to identify the anatomical position and diagnostic features of the
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17 cranial fragment (e.g., Balzeau, 2013; Balzeau, Grimaud-Hervé & Gilissen, 2011; Balzeau et al.,
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19 2017). The teeth were described following established anatomical dental terms (Carlsen, 1987). In
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21 addition, we scored several non-metric traits following both the Arizona State University Dental
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23 Anthropology System (ASUDAS) (Turner, Nichol & Scott, 1991) and some complementary traits
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25 described by Bailey (2002), which were compared to Neandertals, Upper Paleolithic modern
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27 humans (UPMH) and recent humans (Martinón-Torres, Bermúdez de Castro, Gómez-Robles,
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29 Prado-Simón, & Arsuaga, 2012). Some of these traits were also scored in the EDJ surface and
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31 completed by the traits described by Martin, Hublin, Gunz, & Skinner (2017) for the molars. The
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33 roots of the incisors were measured following the method described by Le Cabec, Gunz, Kupczik,
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35 Braga & Hublin (2013): Root Length (RL), Root Volume (RV), Root Pulp Volume (RPV), Crown
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37 Pulp Volume (CrPV) and different ratios between these measurements. Dental wear assessment was
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39 based on Molnar (1971).
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48 *2.4-Bone thickness mapping (cranial fragment) and volume segmentation (teeth)*

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50 The 3D variation of the total bone thickness of the cranial fragment was evaluated using the
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52 exo- and endocranial surfaces using the module Surface-Distance of Avizo 7. The results of this
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54 analysis were illustrated using a chromatic scale and compared to previous studies (Balzeau, 2013)
55
56 in order to gain insights on the potential taxonomic significance of the thickness distribution
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58 pattern.
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2 In the case of the teeth, before their segmentation, the CT image volumes were pre-
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4 processed using Fiji (Schindelin et al., 2012) by first converting them to 8-bit and then re-sampling
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6 them in the Z direction by a factor of 2 (final volume resolution: 0.019 x 0.019 x 0.038 microns per
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8 voxel). Next, the volumes were segmented using an interactive learning approach (Arganda-
9
10 Carreras et al., 2017) that classified each voxel as belonging to one of the following classes: bone,
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12 dentine, enamel, or background. The pulp chamber was afterwards labeled by semi-automatic
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14 filling of the cavity inside the other teeth labels. The output label images were cleaned up by
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16 removing small artifacts and noise by means of morphological operations (Legland, Arganda-
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18 Carreras & Andrey, 2016). Finally, we performed manual correction of the segmented images using
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20 AvizoLite software due to the presence of cracks in some teeth, and lower density zones in the
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22 enamel some of the teeth.
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29 *2.5-Taphonomic analysis*

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32 The cranial bone was macroscopically and microscopically examined using a hand lens and a
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34 stereoscopic zoom microscope (Olympus SZX10) to examine surface modifications. For the
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36 analysis of striae regarding the differentiation between cut marks and trampling marks we have used
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38 the protocol proposed by Domínguez-Rodrigo, de Juana, Galán & Rodríguez (2009). The cranial
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40 breakage pattern was analyzed following the criteria developed by Sala, Pantoja-Pérez, Arsuaga,
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42 Pablos & Martínez (2016) to assess the presence/absence of perimortem (fresh bone) and
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44 postmortem (dry bone) fractures. Four parameters were recorded: fracture outline (linear, depressed,
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46 stellate); fracture angle (right or oblique); fracture edge (smooth or jagged); presence/absence of
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48 cortical delamination.
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54 *2.6-Geometric morphometrics*

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57 Geometric morphometric analyses of the occlusal surface of the premolar and molar crowns
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59 were used to compare the Axlor posterior permanent teeth with the Neandertal and modern human
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2 samples used in Gomez-Robles et al. (2007), Gómez-Robles, Bermúdez de Castro, Martínón-
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4 Torres, Prado-Simón, & Arsuaga (2012), and Gómez-Robles, Martínón-Torres, Bermúdez de
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6 Castro, Prado-Simón, & Arsuaga (2011). Modern human samples included both fossil and recent
7
8 modern humans. Occlusal photographs were used to place 2D configurations of landmarks and
9
10 semilandmarks. For the M¹, analyses were repeated on the original photographs and on an occlusal
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12 projection of the occlusal surface obtained after virtually correcting enamel cracks. Because the
13
14 Axlor M¹ is heavily worn, the location of anatomical landmarks on cusp apices cannot be
15
16 unequivocally determined. Therefore, M¹ analyses were repeated twice, using the original
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18 configuration of landmarks and semilandmarks as described in Gómez-Robles et al. (2007) and only
19
20 the configuration of outline semilandmarks (after removing the four anatomical landmarks). The
21
22 second analysis, therefore, focuses on the ability of the M¹ occlusal outline to differentiate
23
24 Neandertal from modern human molars. The Axlor P⁴ and M³ are substantially less worn than the
25
26 M¹, so only the complete configuration of landmarks and semilandmarks was evaluated for them.
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28 For all the posterior teeth, geometric morphometric analyses were performed that included and
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30 excluded size variation (in form and shape space, respectively). A discriminant analysis based on
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32 the first ten principal components of shape variation was carried out to evaluate the species that
33
34 Axlor teeth are assigned to.
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45 **3-Metric, morphological and taphonomic description**

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50 The cranial and the dental remains are described here. The comparison of the external crown
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52 metric data between Axlor teeth and different comparative samples are shown in [Table 2](#). Only
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54 taxonomically useful metric traits are discussed below.
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59 [INSERT TABLE 2 HERE]
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3.1-Cranial fragment

AX.11B.415.400 is a fragment (56 × 41 mm) of a left parietal bone, which preserves 54 mm of the sagittal suture (Figure 3). The suture is not fused, and this left fragment has been separated from the right parietal bone without any breakage of the indentations. Bone thickness for the analyzed area is only slightly smaller than in La Ferrassie 1 (Balzeau, 2013) and thus incompatible with a young immature status. Thus, the fragment is not from a child, but may belong to a young adult or adult. The antero-posterior curvature of this fragment is not very pronounced.

[INSERT FIGURE 3 HERE]

Bone thickness distribution was quantified on nearly the whole preserved area of this fragment. Thickness varies between 3.4 mm and 10.5 mm. The mean thickness of the fragment is 5.4 mm. Thickness is evenly distributed along the surface of the fragment, there is no clear increase or decrease related to bone thickness variation. The only exception concerns the blood vessels on the endocranial surface of the anterior border of the fragment, which are associated with a clear thinning of the bone (the area with white dots at the anterior border of the bone, noted V on Figure 3). Moreover, the infero-anterior corner of the fragment shows a slight increase in bone thickness (represented by the purple area, noted PC on Figure 3) which continues posteriorly and obliquely. It corresponds to the postcentral sulcus.

Some clear endocranial features are visible. Some branches of the meningeal system are noticeable. They probably all belong to the anterior ramus, one being the anterior branch (noted A on Figure 3), the second corresponding to the obelic branch (noted O on Fig. 3). The anterior branch splits in two simple veins that are quite large. The obelic branch splits into two smaller and long veins. Concerning the gyral pattern visible on this endocranial surface, two sulci are clear. The

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2 course of the postcentral sulcus (noted PC on [Figure 3](#)) goes from the antero-inferior corner of the
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4 fragment to the center of the medial border of the fragment. This sulcus is well printed and shows a
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6 clear course. Anteriorly, the central sulcus (noted C on [Figure 3](#)) seems to run along the course of
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8 the most anterior vein of the anterior ramus. Those two sulci have a parallel course, delimiting a
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10 post-central gyrus that has a regular width on its preserved extension.
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16 Both bone thickness distribution pattern and endocranial anatomy provide information that
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18 helps to propose a taxonomic attribution for this fragment. Bone thickness shows little variation. In
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20 modern humans, there is a clear decrease in bone thickness in the area of the superior parietal gyrus.
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22 The pattern observed on this fragment resembles what has been described for Neandertals (Balzeau,
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24 2013). The position and size of the anterior branch of the meningeal system on this fragment, as
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26 well as its subsequent bone thickness variation, fits with the anatomy observed in Neandertals. The
27
28 meningeal system in this area has more anastomoses than in modern humans, and blood vessels are
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30 thinner and more numerous (Grimaud-Hervé, 1997). In summary the anatomical features preserved
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32 in this parietal fragment are consistent with a Neandertal classification.
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39 The bone surface of the cranial fragment is well preserved and does not show weathering
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41 (sensu Behrensmeyer, 1978). No direct carnivore activity (i.e., tooth marks) was documented, nor
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43 any sign of burning. Similarly, no other biological modifications, such as rodent activity or root
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45 etching, was observed. This cranial fragment shows several striations in the outer table in five
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47 different areas ([Figure 4](#)). In some cases, the grooves are close “V” shaped, but microstriations were
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49 not evident. On the other hand, the trajectories of the grooves are usually sinuous and most of the
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51 bone surface is covered by very shallow striae. In some cases, the color of the striations is lighter
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53 compared with the bone surface suggesting that they have occurred after its deposition. These
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55 observations are compatible with trampling marks following the protocol described by Domínguez-
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57 Rodrigo et al. (2009). Regarding the fracture analysis, this remain displays three linear fractures,
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2 one of them parallel and two perpendicular to the cranial suture. The two fractures perpendicular to
3
4 the suture have right angled edges, jagged surfaces and absence of cortical delamination. These
5
6 characteristics are typical of fracturing in dry bone (Sala et al., 2016). However, the fracture that is
7
8 parallel to the suture displays an oblique angle, smooth surface and presence of cortical
9
10 delamination (0.75 cm) on the inner table. The combination of these fracture attributes is usually
11
12 considered representative of perimortem fractures (Sala et al., 2016).
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18 [INSERT FIGURE 4 HERE]
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22

23 *3.2-Upper left fourth premolar, maxillary fragment with upper first molar and upper third molar*
24
25 *belonging to the same individual*
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30 Descriptions and analyses are provided for the three dental remains belonging to the same
31
32 individual. These remains are shown in Figure 5 and are morphologically compared in Tables 3-5.
33
34
35

36 Ax.13F.265.1 (AX.13E/13F.265-270.1 according to the museum records) is a complete
37
38 premolar, although its root is damaged and presents longitudinal cracks on both sides and some
39
40 smaller transversal cracks. In addition, there is a small pitting on the vestibular side of the buccal
41
42 cusp, and erosion on the tip of this cusp (Figure 5). Also, in the areas with the highest enamel
43
44 thickness of the crown (the buccal and lingual sides) there is a part of the enamel that shows lower
45
46 density in the CT images (Supplementary information Figure S12). The similarity in height between
47
48 the lingual and buccal cusps and the two long inter-proximal facets suggest it is a P⁴. In addition,
49
50 the distal interproximal wear facet matches well the mesial counterpart of the Axlor M¹ (Figure 5),
51
52 further supporting that this is a P⁴, and indicating that they both belonged to the same individual
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55
56
57 (see below).
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60

1
2 [INSERT FIGURE 5 HERE]
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5

6 The occlusal surface is moderately worn (stage 3; Molnar, 1971), and the dentine is exposed
7 on the lingual cusp. Yet, the inter-proximal wear facets are visible to the naked eye, and the distal
8 one is larger. This premolar shows a distal accessory marginal tubercle, a bifurcated buccal essential
9 crest (grade 2 from Bailey, 2002) and a distal accessory ridge on the buccal cusp (Table 3).
10
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18 [INSERT TABLE 3 HERE]
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22

23 At the EDJ level, two major cusps are observed: buccal and lingual. The essential crest of
24 both the lingual and buccal cusps are bifurcated (Grade 2; Table 3), which are features typically
25 observed on Neandertals (92.3% and 61.5% respectively). On the mesial side it presents a
26 continuous transverse crest that does not connect with the horn tip of the lingual cusp, also typical
27 in Neandertals (69.2%). In addition, there is an intermediate accessory marginal tubercle distal to
28 the buccal cusp. The coronal pulp cavity is conformed by the two horns corresponding to the main
29 cusps, where the buccal horn is almost two times larger than the lingual one.
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41 This premolar shows a single, mediolaterally flat root. This root runs wide and straight in
42 the most cervical half, while the apical third is narrower. Both the mesial and distal sides present
43 longitudinal grooves, of which the distal is more pronounced. The analysis of the root canal based
44 on the μ CT images shows that this is a single canal (Type 1R₁) which is only found in 12.5% of
45 Neandertals (Pan & Zanolli, 2019; Table 3).
46
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54

55 Geometric morphometric analyses show that Neandertals and recent modern humans are
56 almost completely separated along the P⁴ morphospace, with Neandertals showing a lingually
57 expanded and asymmetric morphology and modern humans showing a symmetric and lingually
58
59
60

1
2 reduced configuration, where the interfoveal distance is strongly reduced (Figure 6; Gómez-Robles
3
4 et al., 2011). Interestingly, fossil modern humans completely overlap with Neandertals, showing a
5
6 premolar configuration that is much more similar to that of Neandertals than to that of recent
7
8 modern humans. The Axlor P⁴ plots right on the imaginary line that separates the areas of
9
10 distribution of Neandertals and recent modern humans, but outside the range of distribution of both
11
12 groups. The Axlor P⁴ plots on this intermediate position because it shares a generally asymmetric
13
14 morphology with Neandertals, but a moderately reduced distal cusp and a shortened interfoveal
15
16 distance with modern humans. Based on these traits, a discriminant analysis classifies the Axlor P⁴
17
18 as a modern human, but with a low probability of only 56%. When adding size information, the
19
20 Axlor P⁴ plots again in an intermediate position between Neandertals and recent modern humans.
21
22 Interestingly, it also plots on the lower extreme of the size variation found in fossil modern humans,
23
24 indicating that the Axlor P⁴ is larger than most recent modern humans, but smaller than most
25
26 Neandertals and fossil modern humans.
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34 [INSERT FIGURE 6 HERE]
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41 Ax.13F.265.3 (AX.13E/13F.265-270.3 according to the museum records) represents a left
42
43 maxilla fragment, preserving both the external surface (ca. 13.3 × 9.2 mm), and the internal surface
44
45 (13.4 × 9.8 mm), with the left M¹ placed in its alveolus. This tooth is fragmented due to longitudinal
46
47 and transversal cracks that affect the crown and roots (Figure 5). Inter-proximal wear facets are
48
49 clear in both sides and the mesial one shows clear grooves on it. This mesial facet shows two
50
51 chippings in its occlusal border. Also, the occlusal surface of the tooth is heavily worn (stage 4-5;
52
53 Molnar, 1971) and the dentine is exposed in all four main cusps, which interferes with the
54
55 observation of several morphological traits.
56
57
58
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60

1
2 The metacone and the hypocone of this molar are well developed (grade 4 ASUDAS), and
3
4 there is no cusp 5 (Table 4). The hypocone is not distolingually projected, but it is aligned with the
5
6 protocone on the lingual side and with the metacone on the distal side. Due to the heavy occlusal
7
8 wear, it is not possible to score the presence of Carabelli's tubercle or the mesial marginal accessory
9
10 tubercle. The EDJ reveals the presence of an intermediate post-paracone tubercle and no sign of
11
12 fifth cusp (Table 4). Moreover, there is a type II *crista obliqua*, continuously connecting the
13
14 metacone to the protocone, which is centrally positioned. The occlusal wear also affects the dentine
15
16 to a large extent, which may influence trait assessments, but a Carabelli's tubercle does not seem to
17
18 be present. The horn tip of the hypocone pulp cavity is small and not projected, in contrast with the
19
20 typical Neandertal morphology (Supplementary Information Figure S14).
21
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26

27 [INSERT TABLE 4 HERE]
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31

32 The three roots are separated, all the radicular canals are divergent and the body is relatively
33
34 short. The canal corresponding to the mesio-buccal root is the widest one, being mesiodistally flat.
35
36 Moreover, the cervical third of this root canal is elongated, presenting a wide morphology, and the
37
38 apical end is bifurcated. This root morphology contrasts with the typical Neandertal taurodont
39
40 configuration.
41
42
43
44

45 Analyses of shape variation show a generally clear separation between Neandertals and
46
47 modern humans, with Neandertals showing a skewed M¹ configuration and modern humans
48
49 showing a squared configuration (Figure 6; Bailey, 2004; Gómez-Robles et al., 2007). Both groups
50
51 show a minor overlapping area where many fossil modern humans, as well as the Axlor M¹, are
52
53 found. Based on shape data, Axlor M¹ is classified as a modern human with a probability of 88.8%
54
55 or 98.6% (before and after correcting the enamel cracks, respectively). Because of the small size of
56
57
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60

1
2 the Axlor M¹, adding size information to the PCA makes this specimen plot comfortably within the
3
4 modern human range of distribution.
5
6
7

8
9 When assessing only the M¹ outline as defined by curve semilandmarks ([Supplementary](#)
10
11 [Information Figure S15](#)), the differentiation between Neandertals and modern humans is less clear.
12
13 There is still an area of the morphospace occupied only for Neandertals and another one occupied
14
15 only by modern humans on the grounds of their skewed or squared outline configurations,
16
17 respectively. However, the overlapping area between both species is larger in this case.
18
19 Irrespectively of whether enamel cracks are corrected or not, the Axlor M¹ plots again in the area of
20
21 overlapping of both species. Outline shape data also classify the Axlor M¹ as a modern human with
22
23 a very high probability of more than 99% (with and without enamel crack corrections). Form
24
25 analyses (including size information) also make Axlor M¹ plot comfortably within the range of
26
27 variation of modern humans.
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36 Ax.13F.265.2 (AX.13E/13F.265-270.2 according to museum records) This tooth is well
37
38 preserved upper left M³. The crown is complete, but the lingual root is broken, and it is possible to
39
40 observe longitudinal cracks on both sides of the preserved root fragment. In addition, it shows
41
42 moderate wear on the buccal cusp tips but there is no exposed dentine on them (stage 2; Molnar,
43
44 1971).
45
46
47
48
49

50 There is a well-developed metacone but the hypocone is absent ([Table 5](#)). Nevertheless,
51
52 there is a small fifth cusp, that is positioned distally to a lingual tubercle. On the EDJ it can be
53
54 observed that there is no crista obliqua, and that the post-paracone tubercle is intermediate ([Table](#)
55
56 [5](#)). Dentine horn tips of the major cusps are not centrally compressed. The preserved part of the root
57
58 corresponds to the two buccal roots, with both apical tips completely closed. These two roots are
59
60

1 fused, but the root canals run independently along most of the root, except in the most apical tip
2
3
4 where they meet again.
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7

8
9 [INSERT TABLE 5 HERE]
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11
12
13 Shape analyses show that the separation between Neandertal and modern human M³s is far
14 from clear (Figure 6; Gómez-Robles et al., 2012). Both species overlap completely along PC1, and
15 they show certain morphological trends only along PC2, with Neandertals tending to show positive
16 values associated with a more expanded hypocone, and modern humans tending to show negative
17 values associated with a strongly reduced hypocone that may be absent altogether. As with the other
18 adult posterior teeth, the M³ from Axlor plots on the area of the morphospace where Neandertals
19 and modern humans overlap. Shape data classify this M³ as a modern human with a probability of
20 78.4%, but it should be noted that the percentage of correct classification for Neandertals is very
21 low. The inclusion of size information makes this molar plot far outside the range of variation of
22 Neandertals on the grounds of its small size.
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38 In summary, based on both morphological and size characteristics, this individual shows
39 stronger affinities with modern humans than with Neandertals.
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48 *3.3-Additional dental remains*

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52 AX.5B.299.16 This is a well-preserved lower right first incisor, although it shows heavy wear on
53 the incisal edge, having lost between the 20-50% of the crown (roughly equivalent to Grade 4;
54 Molnar, 1971; Figure 7). The degree of shoveling, labial convexity and the interproximal facets
55 cannot be assessed due to the heavy incisal wear. The bucco-lingual diameter (7.7 mm) is larger
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1
2 than the one observed in modern humans and it fits well within the Neandertal range of variation. In
3
4 contrast, the mesio-distal diameter is slightly smaller than the Neandertal minimum and falls within
5
6 the modern human distribution (Table 2). Nonetheless, this mesio-distal measure is most probably
7
8 affected by the wear of the crown. The cingular region is bulky, although there is no tuberculum
9
10 dentale. The heavy wear also affects the observation of the degree of shoveling at the EDJ level,
11
12 where no tuberculum dentale is observed. The root length of this incisor is 20.86 mm, equal to the
13
14 maximum value reported in Neandertals (13.8-20.86 mm), and longer than the currently known
15
16 values for Upper Palaeolithic (11.84-14.20 mm) and recent modern humans (13.18-19.22 mm)
17
18 (comparative samples from Le Cabec et al., 2013). In addition, the root volume is higher than any
19
20 reported value for Neandertals or anatomically modern humans (458.33 mm³). On the other hand,
21
22 the volume of the crown pulp (CrPV) and the radicular canal (RpV) are in the low end of the
23
24 variability of Neandertals, 6.61 mm³ and 2.65 mm³, respectively. The ratio between the volume of
25
26 these two values is 0.4, which is situated in the highest half of the Neandertal variability, indicating
27
28 a proportionally bigger crown pulp segment compared to the root (comparative samples from Le
29
30 Cabec et al., 2013). In sum, the features observed on this tooth (in particular, its crown and root
31
32 length size) align it with Neandertals.
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41 [INSERT FIGURE 7 HERE]
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45 AX.5B.299.31.64.17 This is an upper left first deciduous incisor with a well-preserved crown, but
46
47 the root is not complete (Figure 7). The smooth and twisted aspect of the fracture line of the root
48
49 has been interpreted in other individuals as the result of root resorption, corresponding to a 6-8-
50
51 years-old individual based on modern standards (AlQahtani, Hector, & Liversidge, 2010). Despite
52
53 the heavy wear (Grade 5, Molnar, 1971), a marked shovel shape is observable on the enamel
54
55 surface (>3 ASUDAS). The mesio-distal diameter of this incisor falls within the metric variation of
56
57 both Neandertals and modern humans, but the bucco-lingual diameter is larger than the maximum
58
59
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1
2 value for the latter group (Table 2). There is no tuberculum dentale, and it is not possible to evaluate
3
4 the labial convexity on the enamel. The EDJ shows a strong and asymmetric labial convexity, more
5
6 marked on the mesial side than on the distal. Moreover, there is no tuberculum dentale observed at
7
8 the EDJ level, and it shows a well-developed shovel shape (>3 ASUDAS). In sum, the features
9
10 observed on this tooth (in particular, its strong and asymmetric labial convexity, its well-developed
11
12 shovel shape) and its size align it with Neandertals.
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20 AX.9E.283.103 This tooth is an upper left second deciduous molar that preserves a nearly complete
21
22 crown. The tooth is heavily worn exhibiting dentine in all four cusps, and the mesial inter-proximal
23
24 side of the enamel is missing. This tooth does not preserve the root, likely resorpted and/or
25
26 subsequently broken, and would have belonged to a 10-11-years-old individual based on modern
27
28 standards (AlQahtani et al., 2010). The size of the crown of this specimen does not provide
29
30 taxonomic information due to the large overlap between Neandertals and modern humans (Table 2).
31
32 Both the metacone and the hypocone are well developed (grade 4 ASUDAS). Despite the heavy
33
34 wear, it is possible to observe a big Carabelli's trait (Grade > 2 ASUDAS), but it is not possible to
35
36 assess the presence of any other accessory tubercles. The EDJ presents a big Carabelli's trait that is
37
38 affected by the fracture of the mesial interproximal side of the tooth, which does not allow locating
39
40 the dentine horn. Moreover, the crista obliqua is continuous, and of type II, with a centered placed
41
42 protocone, which is a typical Neandertal trait (Becam et al., 2015; Becam & Chevalier, 2019). A
43
44 quantitative analysis of this molar has not been carried out, but qualitative observation shows that
45
46 the skewed morphology typical of Neandertal dm²s is not present (Bailey et al., 2014). A generally
47
48 squared outline morphology is present in this specimen instead. This squared morphology may
49
50 result from the presence of a well-developed Carabelli's trait, which is reported to give Neandertal
51
52 dm²s a less skewed appearance (Bailey et al., 2014). In sum, most features observed on this tooth
53
54 align it with Neandertals.
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Discussion

Taxonomic assessment of the Axlor fossil remains

The human remains from Axlor can be divided into two different groups. The first group includes a series of published dental remains, traditionally regarded as belonging to a single Neandertal individual (Basabe, 1973), which our results better classify as belonging to a modern human. Indeed, a detailed evaluation of the field notes of J.M. Barandiarán and our own assessment of the stratigraphy at the place where these remains were found cast doubts regarding their belonging to the Middle Paleolithic layers ([Supplementary Information Text S1](#)). The second group of human remains includes three dental remains and a cranial fragment, described here for the first time, which show clear Neandertal affinities and whose attribution to Mousterian layers seems secure based on our assessment of the J.M. Barandiarán field notes.

The first group includes three teeth, P⁴, M¹ and M³ (plus two additional lost specimens), likely belonging to the same individual as already stated by Basabe (1973). The (moderate) wear stage and the fact that the apical tip of the M³ root is closed indicates that they belonged to a young adult. Several features, mainly related to the M¹ morphology, question the previous taxonomic assignment of these teeth. First, the hypocone of the M¹ is not bulky and projected disto-lingually ([Figures 5-6; Supplementary Information Figures S14-S15](#)), the tips of the dentine horns, as far as it can be inferred given the heavy wear of the molar, are not centrally placed, and the molar is not taurodont. In summary, this molar lacks all the traits that are typically associated with Neandertal M¹s. Second, the P⁴ shows a single root channel (an infrequent trait in Neandertals; Pan & Zanolli, 2019), a reduced lingual cusp and a shortened interfoveal distance (typically observed in modern humans). However, other traits in this individual seem to be more frequent in Neandertals. First, the

1
2 bifurcated buccal and lingual essential crests on the P⁴ EDJ and the continuous transverse crest are
3
4 typically Neandertal features (Becam et al., 2019), as it is a generally asymmetric P⁴ crown
5
6 (Gómez-Robles et al., 2011). Second, the presence of crista obliqua is a Neandertal M³ common
7
8 feature (Martin et al., 2017), but the Axlör specimen does not present it in any typology. Moreover,
9
10 in this M³ only the metacone dentine horn tip is slightly centrally placed, while the rest of the cusps
11
12 show the typical morphology of *Homo sapiens*. However, it should be noted that variation of
13
14 UPMH in many of these traits is not completely understood (e.g., for the P⁴, there is only
15
16 information from one UPMH; Becam et al., 2019). Moreover, the discovery of UPMH with
17
18 evidence of recent Neandertal admixture (Fu et al., 2015) and the mounting evidence that
19
20 Neandertal-modern human hybridization may have been common could partially explain the
21
22 differences found between the dental morphology of the UPMH and Holocene populations.
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30 In addition, a qualitative assessment of the teeth that are now lost from the collection (C*
31
32 and M²), based on the information and figures provided by Basabe (1973), indicates that they likely
33
34 belonged to the same individual due to the overall morphology and wear degree compatibility.
35
36 Moreover, the M³ presents a small interproximal facet, compatible with the M² with reduced
37
38 hypocone presented by Basabe (1973). Regarding the morphology of these two lost teeth, it is
39
40 possible to observe on the original publication that the upper canine has some archaic features: a
41
42 bulky tuberculum linguale (ASUDAS grade >3) and well developed mesial ridge (grade 2), more
43
44 common in Neandertals (100% and 42.1%, respectively) and UPMHs (40% and 11.1%,
45
46 respectively) than in recent *Homo sapiens* (8% and 5.3%, respectively) (Martinón-Torres et al.,
47
48 2012). On the other hand, the M² presents a large metacone (ASUDAS grade 3-4), a reduced
49
50 hypocone (ASUDAS grade 0-2), and absence of Carabelli's tubercle (ASUDAS grades 0-1).
51
52 Reduced hypocones are more common in UPMHs (50%) than in Neandertals (24.9%) (Martinón-
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54 Torres et al., 2012).
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1
2 Based on this morphological information, the absence of Holocene recent prehistory remains
3
4 from the Axlor sequence, the presence of an early Upper Paleolithic occupation in the site
5
6 (González-Urquijo et al., 2014), and the unclear previous ascription to the Mousterian level III due
7
8 to their finding in loose sediment close to the rock-shelter wall (see [Supplementary information](#)),
9
10 we hypothesize that these human remains could belong to an UPMH, which should be tested in the
11
12 near future using direct C14 datings. Currently, except for a few skeletons (Lagar Velho, Mirón;
13
14 Duarte et al., 1999; Carretero et al., 2015) most of the Upper Paleolithic remains from the Iberian
15
16 Peninsula consist of isolated teeth or cranial remains (Pérez Iglesias, 2007, and references therein).
17
18
19

20 We consider that the stratigraphic ascription of these teeth, rather than their morphology *per*
21
22 *se*, have contributed to incorrectly classify the published teeth from Axlor as belonging to
23
24 Neandertals. While Basabe (1973) considers that their general morphology resembles that of other
25
26 individuals found in Mousterian contexts, he still underlines their “evolved” status with the
27
28 presence of “intermediary characters” (Basabe, 1973:200), especially referring to the low degree of
29
30 taurodontism in the M¹ and the M². The same author did classify the M¹ from Lezetxiki, which
31
32 shows the typical Neandertal occlusal morphology and a clear taurodontism (Basabe, 1970), as
33
34 belonging to a Neandertal individual.
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37

38 The second study that classified the Axlor teeth as Neandertals compared them with Sima de
39
40 los Huesos, Neandertals and modern humans both morphologically (using the data by Martín-
41
42 Torres et al., 2012) and metrically (using the data by Rodríguez-Cuenca (2003) and García-Bour,
43
44 Pérez-Pérez, & Chimenos (1997). However, most traits included in that study (Rostro-Carmona,
45
46 2013) are not taxonomically distinctive and, for those which are, the Axlor teeth show modern
47
48 human affinities. In terms of size, and using the data provided by Rostro-Carmona (2013), only the
49
50 canine would show a size closer to the Neandertal mean, the P⁴ and M¹ would show intermediate
51
52 affinities while the size of the M² and M³ would be more similar to modern humans. Our study
53
54 shows that, after including UPMHs in the comparative samples, and despite the overlap between
55
56 modern humans and Neandertals, the general size of the Axlor teeth is either non-determinant or
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1
2 more similar to modern humans. Finally, Rostro-Carmona (2013) used the presence of taurodontism
3
4 in the Axlor teeth to classify them as belonging to Neandertals, but our assessment indicates that the
5
6 Axlor teeth show a very limited degree of taurodontism, particularly when compared with classic
7
8 Neandertal molars.
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10
11 The second group would encompass the cranial fragment and three additional tooth remains
12
13 that have clear Neandertal affinities and their stratigraphic position is secure within the Mousterian
14
15 levels. The bone thickness distribution pattern and endocranial anatomy of the cranial fragment are
16
17 consistent with Neandertal anatomy. Additionally, both incisors and the dm^2 present characteristics
18
19 that allow us to ascribe them to Neandertals. Although heavily worn, the I_1 shows Neandertal
20
21 affinities in its root configuration and proportions. Nevertheless, the CrPV and RpV values are
22
23 lower than the Neandertal values reported to date (Le Cabec et al., 2013; Becam & Chevalier,
24
25 2019). This might be related to an advanced age for the individual, as aging related deposition of
26
27 secondary dentine causes the reduction of the pulp channel (Aboshi, Takahashi, & Komuro, 2010;
28
29 Solheim, 1992). This would be consistent with the heavy wear present in this tooth. Second, both
30
31 the OES and EDJ of the deciduous upper incisor from Axlor present a set of characteristics
32
33 observed in other Neandertal specimens such as Portel-Ouest, La Ferrassie 8 (strong mesial and
34
35 distal marginal ridges, pronounced and asymmetric labial convexity) (Becam & Chevalier, 2019).
36
37 Third, although the dm^2 does not show the typical Neanderthal skewed configuration, it does show
38
39 a notable development of the hypocone in relation to the metacone, the presence of the crista
40
41 obliqua, and a large Carabelli's tubercle at the OES and EDJ. These are common features to other
42
43 Neandertal dm^2 s, such as Arrillor, La Ferrassie 8 or Portel-Ouest (Becam & Chevalier, 2019;
44
45 Bermúdez de Castro & Saenz de Buruaga, 1999). These new remains confirm the presence of
46
47 Neandertal fossil remains in Axlor, thus increasing the Neandertal hypodigm recovered in the
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49 Eastern Cantabrian Region.
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1
2 *Origin of the accumulation of the human fossil remains*
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6 Taphonomic and forensic analyses on hominin fossils are important to determine the origin of
7 bone deposition and reconstruct the processes occurred during the fossil-diagenetic processes even
8 for isolated fossils (Sanz et al., 2018). In some cases, it is even possible to determine causes of
9 death (Sala et al., 2015) or drawing inferences about the mortuary practices of hominin groups, such
10 as cannibalism (Rougier et al., 2016; Sala & Conard, 2016; Saladié et al., 2012; Saladié &
11 Rodríguez-Hidalgo, 2017) or funerary activities (Gómez-Olivencia et al., 2018b).
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22 In the case of the two deciduous teeth, they were lost by two different Neandertal individuals
23 during the formation of levels V (left di¹) and IV (right dm²). The presence of isolated deciduous
24 teeth is not rare in Middle Paleolithic layers, and the closest example is found less than 25 km south
25 from Axlør, in Arrillor (Figure 1; Bermúdez de Castro & Saénz de Buruaga, 1999; Iriarte-
26 Chiapusso, Wood, & Sáenz de Buruaga, 2019), with other example from Le Portel Ouest (Becam &
27 Chevalier, 2019). The cranial fragment from Axlør displays evidence of postmortem and
28 perimortem fractures, but the absence of traces that could indicate the causes of such fractures
29 makes it difficult to interpret its origin. Although we cannot rule out intentional causes for the
30 perimortem fractures, the lack of clear anthropic cut marks or signs of anthropic manipulation does
31 not allow us to go further in our interpretation. The absence of weathering could be interpreted as a
32 non-aerial (or short-term) exposure of the fossils in the biostratigraphic phase. On the other hand,
33 trampling has been documented on the cranial fragment suggesting certain displacement of the
34 fossils which could be one of the explanations of the scarcity of human remains at the site.
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Additionally, the Barandiarán collection shows some significant bias in comparison with the
richness in fossil remains that we have observed at the site during recent excavations (Gómez-
Olivencia et al., 2018a), in which smaller shaft fragments are absent. This bias could be a secondary

1
2 reason of this scarcity. In this context, the recovery of additional human fossils in the Axlor site
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4 would help elucidate the nature of these isolated remains found in a human occupation context.
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8 9 **Conclusions**

10
11 Axlor (Dima, Biscay) is one of the most important Middle Paleolithic sites in the Cantabrian
12 region (northern Iberian Peninsula). The excavations performed by J.M. Barandiarán at the Axlor
13 site 50 years ago yielded a cranial vault fragment and eight teeth, five of which likely belonged to
14 the same individual, although two are currently lost. Three teeth (a left dm^2 , a left di^1 , and a right I_1)
15 and the cranial fragment show morphological features consistent with their classification as
16 Neandertals, and were found in undisturbed Mousterian context. However, the remaining three teeth
17 (plus two that have been lost since the initial finding), traditionally classified as Neandertals
18 (Basabe, 1973; Rostro Carmona, 2013), show morphological features and a general size more
19 compatible with their classification as modern humans. Moreover, the review of the original notes
20 by J.M. Barandiarán and our own observations during the recent excavations at the site suggest that
21 the archaeological context of these remains should be carefully reconsidered. We hypothesize that
22 these teeth may constitute one of the scarce examples of Upper Paleolithic remains in the Iberian
23 Peninsula, a hypothesis that would require a direct C14 dating to be tested, which currently is not
24 possible due to access limitations.
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15 **Data Availability Statement**

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18 The original micro-ct scans, the derived segmentation files, and 3D volumes are available in
19
20 figshare at <https://doi.org/10.6084/m9.figshare.10308272>.
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2 **Figure legends**
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9 **FIGURE 1** Location of Axlor (red star) and other Paleolithic sites with human remains in the
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11 Center and East of the Cantabrian Region (northern Iberian Peninsula and southwestern France). 1:
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13 La Pasiega (González Echegaray & Ripoll Perelló, 1954); 2: Castillo (N; HS; Garralda, 2005;
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15 Garralda, Maíllo-Fernández, Higham, Neira, & Bernaldo de Quirós, in press; Obermaier, 1925;
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17 Tejero et al., 2010; Vallois & Delmas, 1976; 3 Covalejos (N, HS; Sanguino González & Montes
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19 Barquín, 2005); 4: Pendo (Basabe, 1982); 5: Morín (HS; González Echegaray & Freeman, 1973;
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21 Obermaier, 1925); 6: Rascaño (Guerrero Sala & Lorenzo Lizalde, 1981); 7: La Chora (González
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23 Echegaray, García Guinea, Begines Ramírez & Madariaga de la Campa, 1963); 8: Mirón (HS;
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25 Carretero et al., 2015); 9: Arrillor (N, Bermúdez de Castro & Sáenz de Buruaga, 1999); 10: Axlor
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27 (N; HS; this work); 11: Lezetxiki (N; Basabe, 1970); 12: Santa Catalina (HS; Albisu Andrade,
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29 Etxeberria Gabilondo, & Herrasti Erlogorri, 2014); 13: Aitzbitarte III (HS; de la Rúa & Hervella,
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31 2011); 14: Alkerdi (Barandiarán & Cava, 2008); 15: Isturitz (HS; Henry-Gambier, Normand, &
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33 Pétilion, 2013); 16: Duruthy (HS; Henry-Gambier, 2006). N=Neandertal; HS=*Homo sapiens*. Base
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35 map made with QGIS 2.18.17 (QGIS Development Team, 2009) with data by Jarvis, Reuter,
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37 Nelson, & Guevara (2008).
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45 **FIGURE 2** Excavation plan (a) and stratigraphic column (b) of Axlor cave (modified from
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47 Gómez-Olivencia et al., 2018a). (a) In the excavation plan the grid system used by J.M. Barandiarán
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49 (black square and white numbers) and the excavation area is shadowed in gray. The grid system
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51 used by the recent excavations is marked using black letters and numbers and the excavation area is
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53 outlined using a thick black line. The dotted line represents the rock-shelter wall when the site was
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55 first excavated, during the excavation this wall went back, revealing a possible cave infilling. The
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57 colors correspond to the levels to which these remains were attributed based on the notes by
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2 Barandiarán. (b) Synthetic section of the 1967–1974 excavation stratigraphy, drawn from the
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4 description of the layers by J. M. Barandiarán (1980). Different levels are marked with different
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6 colors, and the human remains are marked by silhouettes.
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11 **FIGURE 3** Ax.11B.415.400 left parietal fragment. The original fossil and the 3D model are
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13 shown on different views. On the lower row, the approximate location of this fragment is shown on
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15 the La Ferrassie 1 Neandertal cranium (left), a thickness map (from 2 to 12 mm) is shown (middle)
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17 with PC that correspond to thicker bone where is located the postcentral sulcus and V to a relative
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19 thinning produced by the anterior ramus of the meningeal system; and the anatomical features on
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21 the endocranial surface (right): including meningeal veins, A = anterior branch, O = obelic branch,
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23 and sulcal imprints C = central sulcus, PC = postcentral sulcus.
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30 **FIGURE 4** Ectocranial view of the specimen Ax.11B.415.400 with the location of zones a-d,
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32 and detailed images of these zones, where striations are located. In some cases, the grooves show a
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34 close “V” shape but do not show microstriations. The general morphology of these grooves (see
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36 text) make them compatible with trampling marks.
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42 **FIGURE 5** Dental remains previously studied by Basabe (1973) and Rostro-Carmona (2013),
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44 and likely belonging to the same individual. The teeth are shown in mesial, buccal, distal, lingual
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46 (top) and occlusal (bottom) views, together with the results of the enamel segmentation and the EDJ
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48 surface morphology. Pulp chamber volumes (in blue) are shown in mesial (P^4 , M^1) and lingual (M^2)
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50 views. A virtual reconstruction of the teeth in buccal and occlusal views is also provided. Scale bars
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52 = 1 cm.
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58 **FIGURE 6** Principal components analysis of shape (left column) and form variation (right
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60 column), corresponding to the teeth previously studied by Basabe (1973) and Rostro-Carmona

1
2 (2013), and likely belonging to the same individual. The Axlor remains have been compared to
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4 Neandertals (NEA), fossil *Homo sapiens* (FSAP) and recent *Homo sapiens* (RSAP). In both form
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6 and shape space, the Axlor remains align more closely with modern humans. TPS-grids show
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8 anatomical variation corresponding to the positive and negative extreme of each PC when all the
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10 other PCs are held equal to 0. For M¹ variation, the two data points correspond to Axlor's variation
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12 before (darker red) and after (lighter red) correcting the enamel cracks ([Supplementary information](#)
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14 [Figure S13](#)).
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20 **FIGURE 7** New dental remains from the Barandiarán collection of Axlor. AX.5B.299.16 (right
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22 permanent first lower incisor, I₁): root canal morphology (blue) in mesial view; mesial, buccal,
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24 distal, lingual and occlusal views. AX.5B.299.31.64.17 (upper left first deciduous incisor, dI¹): top,
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26 mesial, buccal, distal, lingual and occlusal views. AX.9E.283.103 (left dM²): top, mesial, buccal,
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28 distal, lingual and occlusal views. In the virtual reconstructions, enamel is represented in white and
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30 dentine in brown. Scale bars = 1 cm
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Table 1

Inventory of the Axlor human remains found during the Barandiarán excavations.

Label	Year	Archaeological context ^a	Revised archaeological context	Museum data base (MDB)/Basabe, 1973 (B)	Present study	Figure
Ax.13F.265.1 ^a Ax.13E/13F.265-270.3 ^b	1967	Level IV (Mousterian)	Doubtful	Neandertal (MDB) Left P ⁴ (B)	Modern human Left P ⁴	Figure 5
Ax.13F.265.3 ^a Ax.13E/13F.265-270.3 ^b	1967	Level IV (Mousterian)	Doubtful	Neandertal (MDB) Left maxillary fragment with M ¹ (B)	Modern human Left maxillary fragment with M ¹	Figure 5
Ax.13F.265.3 ^a	1967	Level IV (Mousterian)	Doubtful	Left M ² (B)	Specimen lost	-
Ax.13F.265.2 ^a Ax.13E/13F.265-270.3	1967	Level IV (Mousterian)	Doubtful	Neandertal (MDB) Left M ³ (B)	Modern human Left M ³	Figure 5
Ax.13E.285.3 ^a	1967	Level IV (Mousterian)	Doubtful	Left C' (B)	Specimen lost	-
Ax.11B.415.9 ^a Ax.11B.415.400 (physical label: Ax.11B.415)b	1969	Level VIII (Mousterian)	Mousterian	Human cranial fragment (MDB) Neandertal (MDB)	Neandertal Left parietal bone	Figure 3
Ax.9E.283.103	1973 or 1974	Level IV (Mousterian)	Mousterian	Fauna (indeterminate taxon) (MDB)	Neandertal Right dm ²	Figure 7
Ax.5B.299.31.64.17	1974	Level V (Mousterian)	Mousterian	Human tooth (MDB)	Neandertal Left di ¹	Figure 7
Ax.5B.299.16	1974	Level V (Mousterian)	Mousterian	Human tooth (MDB)	Neandertal Adult right I ₁	Figure 7

^a Based on the information provided by J.M. de Barandiarán field notes. The M¹ and the M² were found together.

^b Based on the information provided by the Arkeologi Museoa (Bilbao, Biscay).

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Table 2

Comparison of external crown metric data between Axlor teeth and Neandertals, Upper Paleolithic modern humans (UPMH), and recent modern humans (RMH).

Tooth	Variable	Axlor			Neandertals ^a					Upper Palaeolithic modern humans ^a					Recent modern humans ^a				
		This study	Rostro-Carmona, 2013	Basabe, 1973	Mean	SD	Min	Max	<i>n</i>	Mean	SD	Min	Max	<i>n</i>	Mean	SD	Min	Max	<i>n</i>
C	M-D	-	-	8.0	8.74	0.67	7.40	10.00	31	8.06	0.58	6.90	9.50	36	7.58	0.43	6.80	8.5	38
	B-L	-	-	9.2	9.92	0.65	8.40	11.40	34	9.02	0.77	7.50	10.74	38	8.26	0.68	7.20	9.4	38
P ⁴	M-D	6.6	6.7	6.6	7.49	0.78	6.10	8.80	30	6.84	0.52	5.90	7.90	38	6.45	0.46	5.50	7.5	38
	B-L	9.7	9.8	9.7	10.39	0.70	9.00	11.70	34	9.69	0.69	7.50	11.29	38	9.04	0.49	8.10	9.9	38
M ¹	M-D	9.8	10.2	10.0	11.61	1.09	9.30	13.60	28	10.71	0.71	8.40	12.30	41	10.03	0.52	8.40	11.4	42
	B-L	11.1	11.2	11.8	12.34	0.70	11.10	14.20	33	12.12	0.63	10.00	13.98	42	11.27	0.56	10.20	12.5	42
M ²	M-D	-	-	9.3	10.84	1.23	9.10	15.90	34	10.10	0.72	8.90	11.80	41	9.22	0.66	7.80	10.5	41
	B-L	-	-	10.0	12.60	0.94	10.54	14.60	38	12.27	0.90	8.30	14.00	42	11.35	0.84	9.90	13.9	41
M ³	M-D	8.7	8.6	8.6	9.74	0.94	6.80	11.35	30	9.01	1.09	7.00	11.60	39	8.55	0.84	7.30	10.5	30
	B-L	10.2	10.1	10.0	11.96	1.16	7.70	14.25	30	11.40	1.10	6.90	13.30	40	10.88	0.98	9.30	13.2	30
I ₁	M-D	4.8	-	-	5.73	0.44	4.92	6.35	24	5.51	0.60	3.70	6.60	22	5.24	0.45	4.60	6.7	31
	B-L	7.7	-	-	7.37	0.51	6.10	8.15	29	6.23	0.45	5.30	7.10	42	6.03	0.44	5.10	6.8	32
di ¹	M-D	7.6	-	-	7.03	0.81	5.60	8.00	11	6.85	0.77	6.20	7.70	4					
	B-L	6.0	-	-	5.67	0.48	4.70	6.20	11	5.30	0.29	4.90	5.70	5					
dm ²	M-D	(9.0)	-	-	9.18	0.70	8.00	10.40	15	9.19	0.30	8.97	9.40	2					
	B-L	10.3	-	-	10.14	0.57	9.00	11.10	16	10.32	0.57	9.90	11.10	4					

B-L= Bucco-lingual; M-D = Mesio-distal. Values between parentheses are estimated.

The C*, P⁴, M¹, M² and M³ were firstly published by Basabe (2013) and are from the same individual.

^aFor sample information see [Supplementary Information Table S5](#).

Table 3

Comparison of non-metric traits at the occlusal enamel surface (OES), at the enamel-dentine junction (EDJ) and root number between the P⁴ and Neandertals, Upper Paleolithic modern humans (UPMH), and recent modern humans (RMH).

Tooth region	Trait	Grade for Axlor	Neandertals		UPMH		RMH	
			<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
OES	Transverse crest	Absent	2/16	12.4	2/11	18.2	0/113	0.0
	Buccal essential crest (BEF)	2	10/15	66.6	4/11*	36.4	10/106	9.4
	Lingual essential crest (LEF)	NO	11/14	78.6	0/11	0.0	9/108	8.3
	BMaxPAR	1 (Dist)	5/12	41.7	5/9	55.6	18/88	20.5
EDJ	Transverse crest	2 (continuous, but not complete)	9/13	69.2	0/1	0.0	2/14	14.3
	Buccal essential crest	2 (bifurcated)	8/13	61.5	0/1	0.0	4/20	20.0
	Lingual essential crest	2 (bifurcated)	12/13	92.3	0/1	0.0	0/20	0.0
	Distal accessory ridge	1 (present)	5/13	38.4	0/1	0.0	12/20	60.0
	Mesial accessory ridge	0 (absent)	8/13	61.5	1/1	100.0	8/20	40.0
	Mesial accessory cusp	0 (absent)	13/13	100.0	1/1	100.0	20/20	100.0
	Distal accessory cusp	0 (absent)	10/13	76.9	1/1	100.0	20/20	100.0
Root	Root canal type	1R ₁	1/10	10.0	-	-	4/13	30.8

OES trait frequencies from Martín-Torres et al. (2012); EDJ data from Becam et al. (2019); Root channel data from Bayle, Le Luyer, & Robson Brown (2017; Las Palomas 53 and 68 left P⁴s), Zapata, Bayle, Lombardi, Pérez-Pérez, & Trinkaus (2017), and Pan & Zanolli (2019).

Table 4

Comparison of non-metric traits at the occlusal enamel surface (OES) and enamel-dentine junction (EDJ) between the Axlor M¹, Neandertals, Upper Paleolithic modern humans (UPMH) and recent modern humans (RMH).

Tooth region	Trait	Grade for Axlor	Neandertals		UPMH		RMH	
			<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
OES	Metacone	4	13/23	56.5	11/19	57.9	73/127	57.5
	Hypocone	4	10/23	43.5	10/19	52.6	58/127	45.7
	Cusp 5	0	1/22	4.5	1/18	5.6	44/125	35.2
	Parastyle	0	14/20	70.0	15/15	100.0	121/123	98.4
EDJ	Crista Obliqua	Type II	2/19	10.0	-	-	1/12	8.3
	Post Paracone	Intermediate	10/19	52.6	-	-	0/12	0.0

OES trait frequencies from Martín-Torres et al. (2012); EDJ data from Martin et al. (2017; combining data from early and late Neandertals together).

Table 5

Comparison of non-metric traits at the occlusal enamel surface (OES) and enamel-dentine junction (EDJ) between the Axlor M³, Neandertals, Upper Paleolithic modern humans (UPMH) and recent modern humans (RMH).

Tooth region	Trait	Grade for Axlor	Neandertals		UPMH		RMH	
			<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
OES	Metacone	>3	9/18	50.0	5/10	50.0	58/93	62.4
	Hypocone	0	3/17	17.6	2/10	20.0	15/93	16.1
	Cusp 5	1	1/17	5.9	1/10	10.0	4/93	4.3
	Carabelli	0	12/15	80.0	5/9	55.6	68/89	76.4
	Parastyle	0	14/16	87.5	9/9	100	81/88	92.0
EDJ	Crista Obliqua	absent	0/12	0.0	-	-	3/7	42.9
	Post Paracone	intermediate	1/12	8.3	-	-	2/7	28.6

OES trait frequencies from Martín-Torres et al. (2012); EDJ data from Martín et al. (2017; combining data from early and late Neandertals together).



FIGURE 1 Location of Axlor (red star) and other Paleolithic sites with human remains in the Center and East of the Cantabrian Region (northern Iberian Peninsula and southwestern France). 1: La Pasiega (González Echegaray & Ripoll Perelló, 1954); 2: Castillo (N; HS; Garralda, 2005; Garralda, Maíllo-Fernández, Higham, Neira, & Bernaldo de Quirós, in press; Obermaier, 1925; Tejero et al., 2010; Vallois & Delmas, 1976); 3: Covalejos (N, HS; Sanguino González & Montes Barquín, 2005); 4: Pendo (Basabe, 1982); 5: Morín (HS; González Echegaray & Freeman, 1973; Obermaier, 1925); 6: Rascaño (Guerrero Sala & Lorenzo Lizalde, 1981); 7: La Chora (González Echegaray, García Guinea, Begines Ramírez & Madariaga de la Campa, 1963); 8: Mirón (HS; Carretero et al., 2015); 9: Arrillor (N, Bermúdez de Castro & Sáenz de Buruaga, 1999); 10: Axlor (N; HS; this work); 11: Lezetxiki (N; Basabe, 1970); 12: Santa Catalina (HS; Albisu Andrade, Etxeberria Gabilondo, & Herrasti Erlogorri, 2014); 13: Aitzbitarte III (HS; de la Rúa & Hervella, 2011); 14: Alkerdi (Barandiarán & Cava, 2008); 15: Isturitz (HS; Henry-Gambier, Normand, & Pétilion, 2013); 16: Duruthy (HS; Henry-Gambier, 2006). N=Neandertal; HS=Homo sapiens. Base map made with QGIS 2.18.17 (QGIS Development Team, 2009) with data by Jarvis, Reuter, Nelson, & Guevara (2008).

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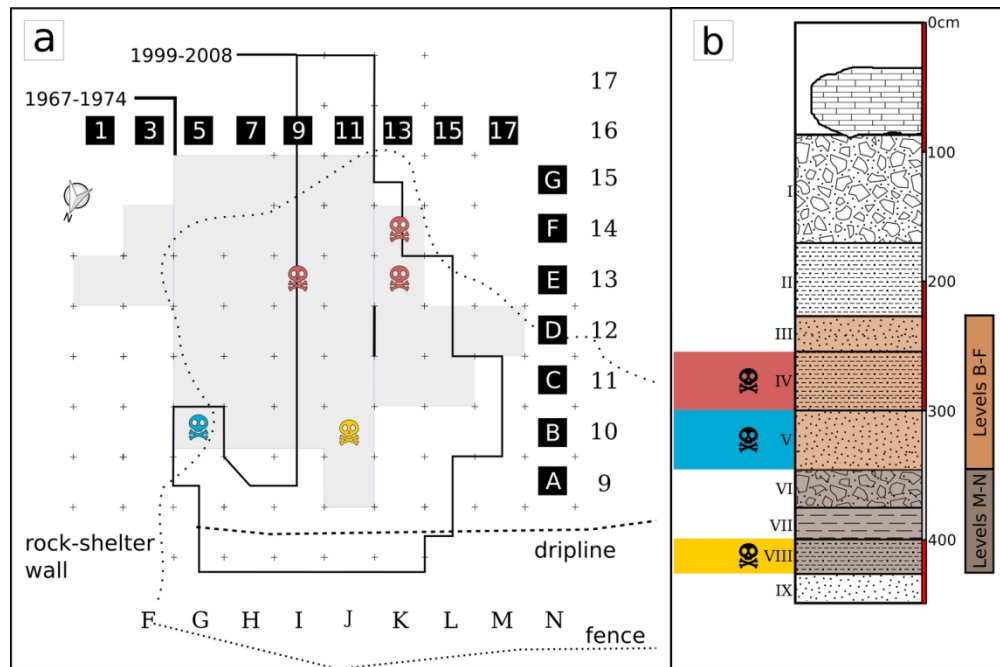
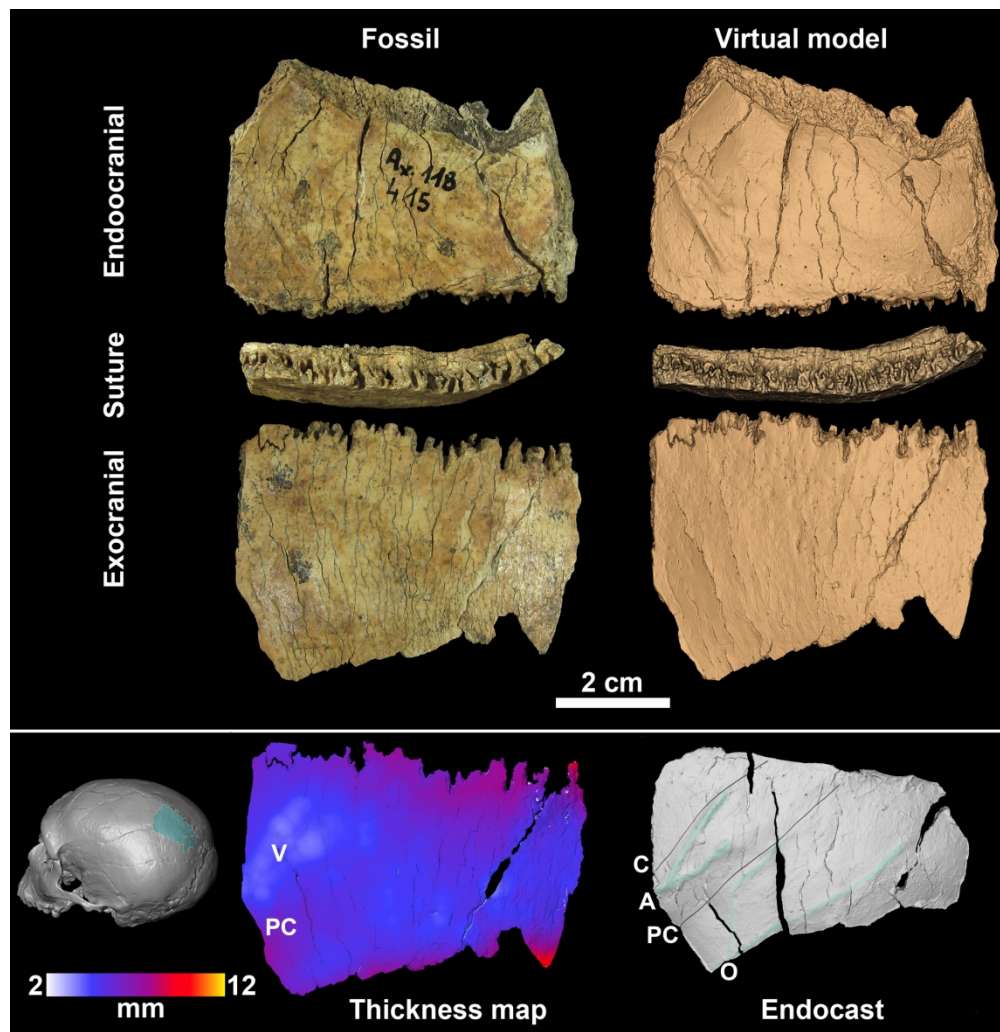


FIGURE 2 Excavation plan (a) and stratigraphic column (b) of Axlora cave (modified from Gómez-Olivencia et al., 2018a). (a) In the excavation plan the grid system used by J.M. Barandiarán (black square and white numbers) and the excavation area is shadowed in gray. The grid system used by the recent excavations is marked using black letters and numbers and the excavation area is outlined using a thick black line. The dotted line represents the rock-shelter wall when the site was first excavated, during the excavation this wall went back, revealing a possible cave infilling. The colors correspond to the levels to which these remains were attributed based on the notes by Barandiarán. (b) Synthetic section of the 1967–1974 excavation stratigraphy, drawn from the description of the layers by J. M. Barandiarán (1980). Different levels are marked with different colors, and the human remains are marked by silhouettes.

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FIGURE 3 Ax.11B.415.400 left parietal fragment. The original fossil and the 3D model are shown on different views. On the lower row, the approximate location of this fragment is shown on the La Ferrassie 1 Neanderthal cranium (left), a thickness map (from 2 to 12 mm) is shown (middle) with PC that correspond to thicker bone where is located the postcentral sulcus and V to a relative thinning produced by the anterior ramus of the meningeal system; and the anatomical features on the endocranial surface (right): including meningeal veins, A = anterior branch, O = obelic branch, and sulcal imprints C = central sulcus, PC = postcentral sulcus.

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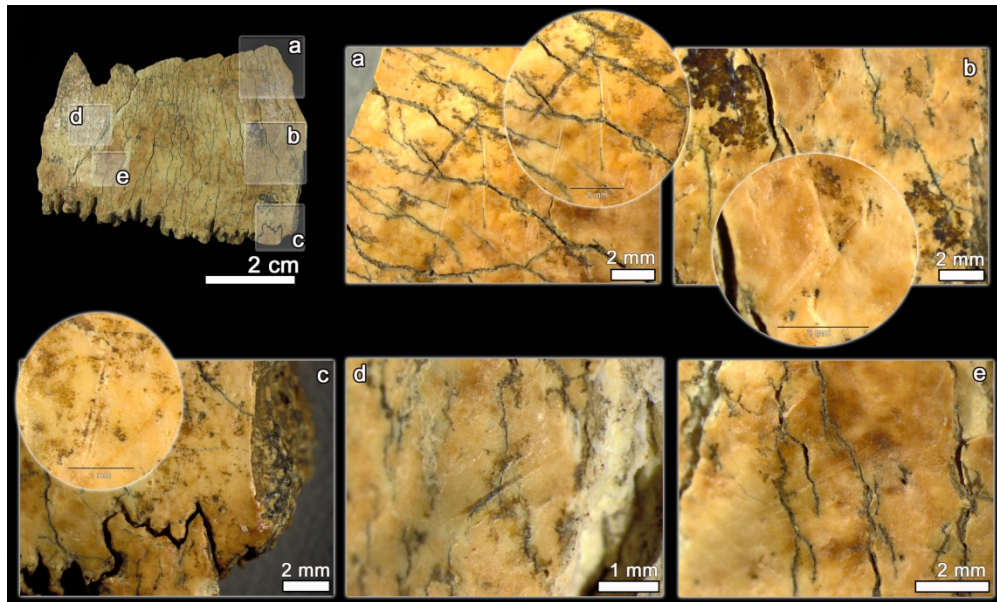


FIGURE 4 Ectocranial view of the specimen Ax.11B.415.400 with the location of zones a-d, and detailed images of these zones, where striations are located. In some cases, the grooves show a close "V" shape but do not show microstriations. The general morphology of these grooves (see text) make them compatible with trampling marks.

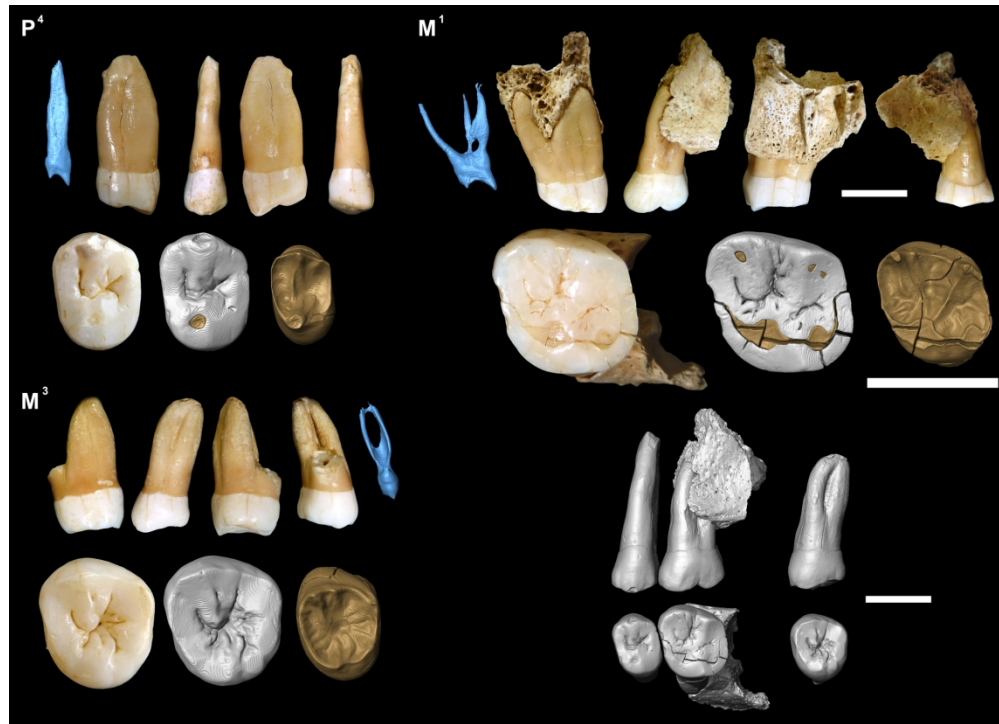
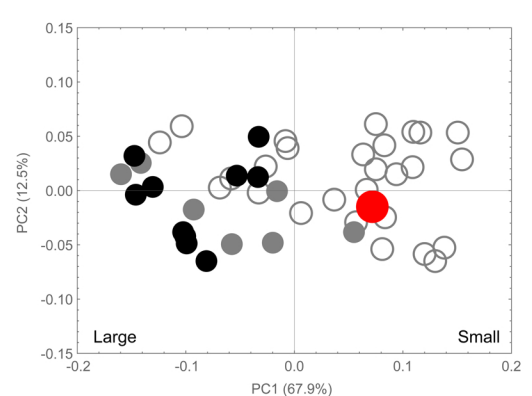
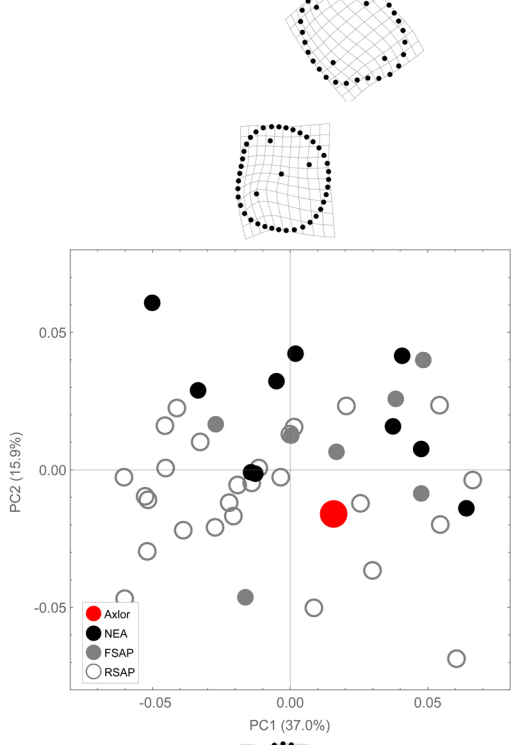
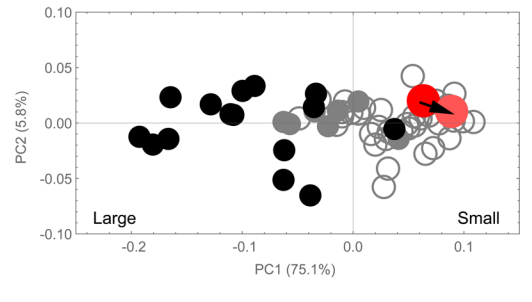
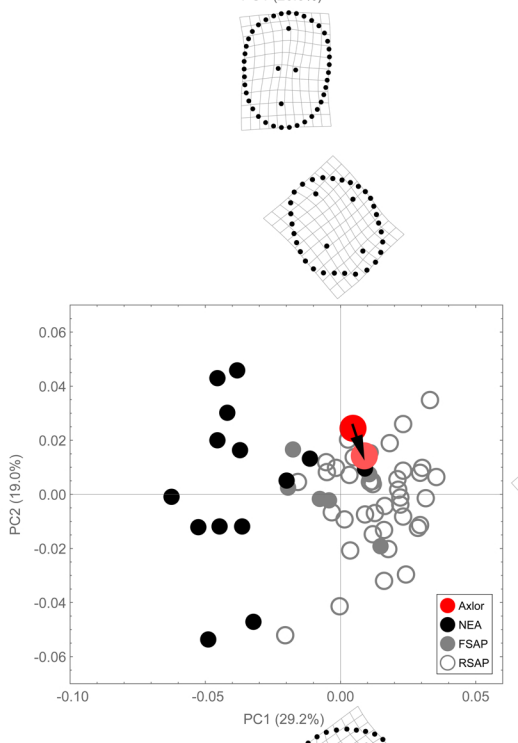
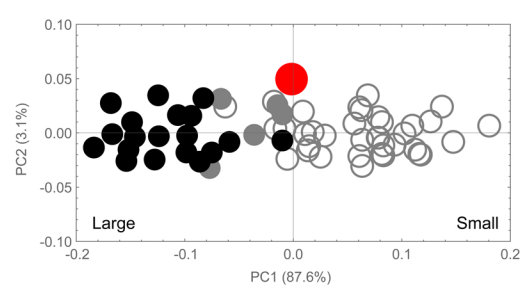
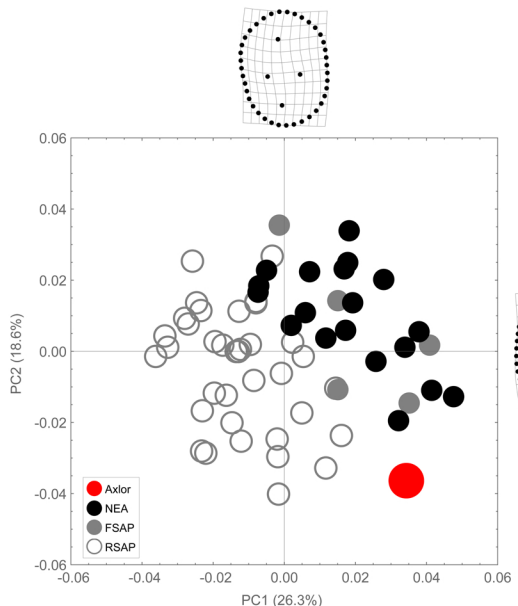


FIGURE 5 Dental remains previously studied by Basabe (1973) and Rostro-Carmona (2013), and likely belonging to the same individual. The teeth are shown in mesial, buccal, distal, lingual (top) and occlusal (bottom) views, together with the results of the enamel segmentation and the EDJ surface morphology. Pulp chamber volumes (in blue) are shown in mesial (P4, M1) and lingual (M2) views. A virtual reconstruction of the teeth in buccal and occlusal views is also provided. Scale bars = 1 cm.

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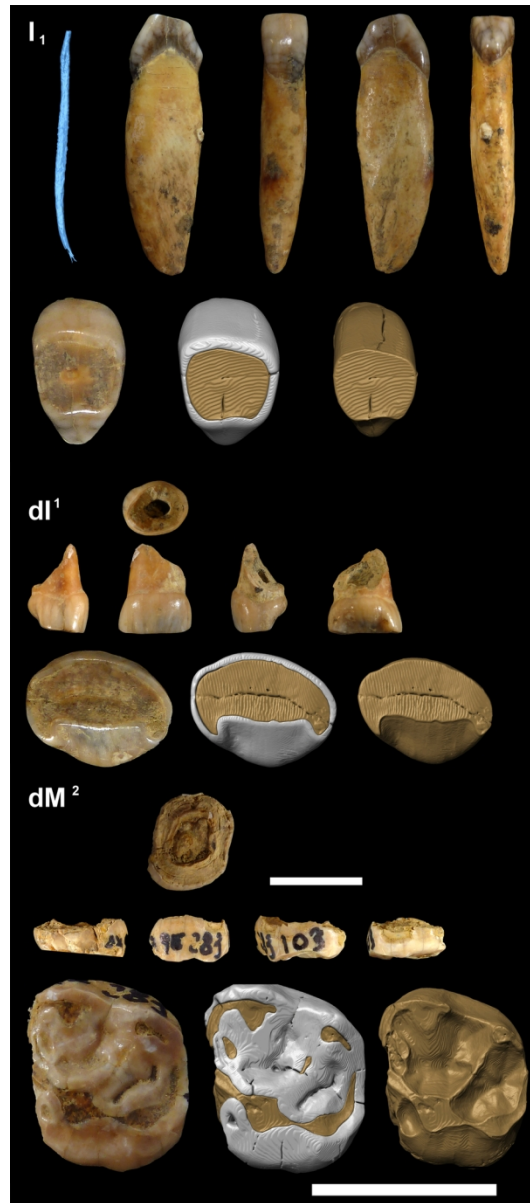


FIGURE 7 New dental remains from the Barandiarán collection of Axlór. AX.5B.299.16 (right permanent first lower incisor, I₁): root canal morphology (blue) in mesial view; mesial, buccal, distal, lingual and occlusal views. AX.5B.299.31.64.17 (upper left first deciduous incisor, dI₁): top, mesial, buccal, distal, lingual and occlusal views. AX.9E.283.103 (left dM₂): top, mesial, buccal, distal, lingual and occlusal views. In the virtual reconstructions, enamel is represented in white and dentine in brown. Scale bars = 1 cm

80x180mm (300 x 300 DPI)