



HAL
open science

The human remains found in 1967 in Axlor: Still not convincingly Neandertals: A reply to González-Urquijo et al

Asier Gómez-Olivencia, Diego López-Onaindia, Nohemi Sala, Antoine Balzeau, Ana Pantoja-Pérez, Ignacio Arganda-Carreras, Mikel Arlegi, Joseba Rios-Garaizar, Aida Gómez-Robles

► To cite this version:

Asier Gómez-Olivencia, Diego López-Onaindia, Nohemi Sala, Antoine Balzeau, Ana Pantoja-Pérez, et al.. The human remains found in 1967 in Axlor: Still not convincingly Neandertals: A reply to González-Urquijo et al. *American Journal of Biological Anthropology*, 2023, 180 (2), pp.245-251. 10.1002/ajpa.24633 . hal-03985684

HAL Id: hal-03985684

<https://hal.science/hal-03985684>

Submitted on 19 Oct 2023

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

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



Distributed under a Creative Commons Attribution - NonCommercial - ShareAlike 4.0 International License



The human remains found in 1967 in Axlor: still not convincingly Neandertals. A reply to González-Urquijo et al.

Journal:	<i>American Journal of Biological Anthropology</i>
Manuscript ID	AJPA-2022-00017.R1
Wiley - Manuscript type:	Letter to the Editor
Date Submitted by the Author:	n/a
Complete List of Authors:	Gómez-Olivencia, Asier; Sociedad de Ciencias Aranzadi, Departamento de Prehistoria; Universidad del País Vasco Facultad de Ciencia y Tecnología, López-Onaindia, Diego; Autonomous University of Barcelona (UAB), Biología Animal, Biología Vegetal i d'Ecologia Sala, Nohemi; Centro UCM-ISCI III de Investigación sobre la Evolución y Comportamiento Humanos Balzeau, A; Museum Natl Hist Nat, Dept Prehist, CNRS UMR 7194 du CNRS, Paris, France , Dept. of Prehistory Pantoja-Pérez, Ana; Centro UCM-ISCI III de Investigación sobre la Evolución y Comportamiento Humanos Arganda-Carreras, Ignacio; Dept. Ciencias de la Computacion e Inteligencia Artificial. Facultad de Informatica, Universidad del País Vasco-Euskal Herriko Unibertsitatea (UPV/EHU) Manuel Lardizabal Ibilbidea 1, 20018 Donostia, Gipuzkoa, Spain. Arlegi, Mikel; Universidad del País Vasco, Estadigrafía y Paleontología Rios-Garaizar, Joseba; CENIEH Gómez-Robles, Aida; Konrad Lorenz Institute for Evolution and Cognition Research
Key Words:	<i>Homo sapiens</i>, Neandertal, geometric morphometrics
Subfield: Please select 2 subfields. Select the main subject first.:	Paleontology , Human biology [living humans; behavior, ecology, physiology, anatomy]

SCHOLARONE™
Manuscripts

1
2 Letter to the Editor
3
4
5

6 The human remains found in 1967 in Axlor: still not convincingly Neandertals. A reply to
7
8
9 González-Urquijo et al.
10
11
12

13 Asier Gómez-Olivencia^{a,b,c*}
14

15 Diego López-Onaindia^d
16

17 Nohemi Sala^{e,c}
18

19 Antoine Balzeau^{f,g}
20

21 Ana Pantoja-Pérez^{e,c}
22

23 Ignacio Arganda-Carreras^{h,i,j}
24

25 Mikel Arlegi^{k,l}
26

27 Joseba Rios-Garaizar^m
28

29 Aida Gómez-Robles^{n,o,p}
30
31
32
33
34
35

36 ^aDept. Geología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko
37 Unibertsitatea (UPV/EHU). Barrio Sarriena s/n, 48940 Bilbao, Spain.
38

39 ^bSociedad de Ciencias Aranzadi, Zorroagaina 11, 20014 Donostia-San Sebastian, Spain.
40

41 ^cCentro UCM-ISCIH de Investigación sobre Evolución y Comportamiento Humanos, Avda.
42 Monforte de Lemos 5 (Pabellón 14), 28029 Madrid, Spain.
43

44 ^dUMR 5199, PACEA, Université de Bordeaux, Allée Geoffroy Saint-Hilaire, Bâtiment B8,
45 CS50023 33615 Pessac Cedex, France.
46

47 ^eCentro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo de la Sierra de
48 Atapuerca 3, 09002 Burgos, Spain.
49
50
51
52
53
54
55
56
57
58
59
60

1
2 ^fÉquipe de Paléontologie Humaine, UMR 7194, CNRS, Département Homme et Environnement,
3
4 Muséum national d'Histoire naturelle. Musée de l'Homme, 17, Place du Trocadéro, 75016 Paris,
5
6 France.

7
8
9 ^gDepartment of African Zoology, Royal Museum for Central Africa, Tervuren, Belgium.

10
11 ^hDept. Ciencias de la Computación e Inteligencia Artificial. Facultad de Informatica, Universidad
12
13 del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU) Manuel Lardizabal Ibilbidea 1, 20018
14
15 Donostia, Gipuzkoa, Spain.

16
17
18 ⁱIkerbasque, Basque Foundation for Science, Bilbao, Spain.

19
20
21 ^jDonostia International Physics Center (DIPC). Manuel Lardizabal Ibilbidea 4, 20018 Donostia,
22
23 Gipuzkoa, Spain.

24
25 ^kInstitut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4,
26
27 Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain.

28
29
30 ^lUniversitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de
31
32 Catalunya 35, 43002 Tarragona, Spain.

33
34 ^mIndependent researcher.

35
36
37 ⁿDepartment of Anthropology, University College London, WC1E 0BW London, UK.

38
39
40 ^oDepartment of Genetics, Evolution and Environment, University College London, WC1E 6BT
41
42 London, UK.

43
44
45 ^pDepartment of Life Sciences, Natural History Museum, SW7 5BD London, UK.

46 47 48 Correspondence

49
50 Asier Gómez-Olivencia, Dept. Geología, Facultad de Ciencia y Tecnología, Universidad del País
51
52 Vasco/Euskal Herriko Unibertsitatea (UPV/EHU). Barrio Sarriena s/n, 48940 Bilbao, Spain.

53
54 Email: asier.gomez@ehu.eus (A.G.-O.)

ORCID

Asier Gómez-Olivencia <https://orcid.org/0000-0001-7831-3902>

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

Nohemi Sala <https://orcid.org/0000-0002-0896-1493>

Antoine Balzeau <https://orcid.org/0000-0002-4226-611X>

Ana Pantoja-Pérez <https://orcid.org/0000-0001-9302-1756>

Ignacio Arganda-Carreras <https://orcid.org/0000-0003-0229-5722>

Mikel Arlegi <http://orcid.org/0000-0001-5665-9275>

Joseba Rios-Garaizar <https://orcid.org/0000-0001-8474-2156>

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

1
2 In 2020, we published a study that described all the human remains found during J. M. de
3 Barandiarán's excavations in Axlor (Dima, Biscay). Our study first presented two deciduous teeth
4 and a parietal fragment found in an undisturbed Mousterian context, all of which show
5 morphological features consistent with a Neandertal classification (Gómez-Olivencia et al., 2020;
6 Supplementary Text S1). Our study also reassessed the human remains previously described by
7 Basabe (1973), likely belonging to a single individual and traditionally classified as a Neandertal
8 (see e.g., Rostro Carmona, 2013). However, our metric and morphological assessment suggested
9 stronger affinities with modern humans. Recently, a reply to our article has been published,
10 focusing on the remains previously published by Basabe (1973). In their reply, González-Urquijo,
11 Bailey, & Lazuen (2021: 553) state that "Axlor's level IV human remains are convincingly
12 Neanderthals", thus concluding that our taxonomic classification "is not supported by the
13 anatomical evidence" and that the "balance of the evidence-morphological and stratigraphic-is most
14 consistent with a Neandertal classification for these teeth" (González-Urquijo et al., 2021: 557).
15 These authors take issue with two aspects: the taxonomic classification of the human remains found
16 in 1967 and the discussion and reinterpretation of the stratigraphic context of these remains.

17 Here we address the points raised by González-Urquijo et al. (2021).

18 **1 The taxonomic attribution of the human remains found in 1967**

19 The human remains found in 1967 comprise four teeth (left P⁴-M³) found on September 7th
20 1967 in the square 13F at a depth of 265 cm. Two of these teeth (M¹ and M²) were found in a
21 maxillary fragment. Additionally, a left canine was found on September 8th in the square 13E at a
22 depth of 285 cm (Gómez-Olivencia et al., 2020: Figure S6). Two of these teeth (the C' and the M²)
23 are currently lost, and therefore, our taxonomic assessment was based on the P⁴, M¹ and M³. All
24 these remains were originally attributed to the Mousterian level III by Barandiarán (Barandiarán,
25 1980; see also Gómez-Olivencia et al., 2020: Figure S6). However, based on the depth of the
26 findings and the depth attributed by Barandiarán to the level IV in 1968 (Barandiarán, 1980), they

1
2 have been later and repeatedly attributed to level IV (Basabe, 1982; González Urquijo, Ibáñez
3
4 Estévez, Ríos Garaizar, & Bourguignon, 2006; Lazuen Fernández & González-Urquijo, 2019-
5
6 2020).
7

8
9 González-Urquijo et al. (2021: 553) oversimplified our taxonomic assessment, stating that
10
11 we concluded that “those remains should instead be assigned to a single Upper Paleolithic *Homo*
12
13 *sapiens* individual”. However, our study states that “based on both morphological and size
14
15 characteristics, this individual shows stronger affinities with modern humans than with
16
17 Neandertals” (Gómez-Olivencia et al., 2020: 486), while we also clearly recognized that some of
18
19 the teeth (e.g., the canine and the P⁴) showed some features that are present in high percentages in
20
21 Neandertals, but are not exclusive of this group. In our discussion, we hypothesized that “these
22
23 human remains could belong to an UPMH [Upper Paleolithic modern human], which should be
24
25 tested in the near future using direct C14 datings”. This claim was based on the results of our
26
27 morphometric analyses, the absence of Holocene recent prehistory remains from the Axló
28
29 sequence and the presence of an early Upper Paleolithic occupation in the site (Gómez-Olivencia et
30
31 al., 2020: 488). This was summarized in our abstract, which states that the teeth from Axló
32
33 “may represent one of the scarce examples of Upper Paleolithic modern human remains in the northern
34
35 Iberian Peninsula, which should be confirmed by direct dating” (Gómez-Olivencia et al., 2020:
36
37 475). Thus, we suggested that these remains may have belonged to an UPMH, the confirmation of
38
39 which would require further analyses, but we did not discard other possibilities, such as these teeth
40
41 having a more recent chronology.
42
43
44
45
46
47
48
49

50 **2 Dental morphological analysis**

51
52 González-Urquijo et al. (2021) disagree with some of our morphological assessments and
53
54 take issue with the employed methodology. The taxonomic assessment of the Axló 1967 remains
55
56 by González-Urquijo et al. (2021) pivots mainly around the morphology of the lost canine, the
57
58 crown morphology of the P⁴ and the morphology of the M¹.
59
60

1
2 Firstly, González-Urquijo et al. conclude that “the morphological features of the Axlor teeth
3
4 seem to be either Neanderthal-like or ambiguous, but there is no reason to suggest these teeth
5
6 belong to *H. sapiens*”. Their comments on our taxonomic assessment are limited to the crown
7
8 morphology; they do not comment on other features that can be of taxonomic interest (e.g., the root
9
10 morphology or the P⁴), nor do they attempt to carry out additional analyses despite the original
11
12 micro-CT scans being publicly available.
13
14

15
16 González-Urquijo et al. (2021: 553) agree with us that the teeth from Axlor are small but
17
18 they disregard this information as they consider that crown size is a poor discriminator between
19
20 Neandertals and *Homo sapiens*. The dimensions of the Axlor samples are closer to the Upper
21
22 Paleolithic *Homo sapiens* (HS) means (C¹, P⁴) or to the recent HS means (M¹, M², M³) than to
23
24 Neandertals. The published BL measurements of the lost M² are below (and outside) our Neandertal
25
26 and UP range of variation. In addition, our size assessment was complemented with shape
27
28 information (i.e., form analysis). Geometric morphometric analysis of form variation (including size
29
30 and shape) is a widely used way to assess taxonomic affinity (Compton et al., 2021; Garralda et al.,
31
32 2020), and it yielded informative results in some teeth from Axlor (M¹ and M³) but not in others
33
34 (P⁴), as we clearly stated in our study (Gómez-Olivencia et al., 2020).
35
36
37

38
39 González-Urquijo et al. (2021: 553) also consider that the grades of expression of the non-
40
41 metric traits for the P⁴, M¹ and M³, “rather than being *H. sapiens*-like [...] have trait express that are
42
43 ambiguous”. We struggle to understand where we disagree here, as our study explicitly stated that
44
45 some of the Axlor teeth have features that are observed in Neandertals in high frequencies (e.g., the
46
47 bifurcated essential crest of both the lingual and buccal cusps in the P⁴ at the EDJ level). González-
48
49 Urquijo et al. (2021: 553) also consider that “most of the traits do not clearly distinguish
50
51 Neandertals and Upper Paleolithic *H. sapiens*”. For that exact reason, we combined qualitative and
52
53 quantitative methods for the taxonomic assessment of the Axlor teeth, as opposed to the qualitative-
54
55 only evaluation performed by González-Urquijo and colleagues.
56
57
58
59
60

1
2 González-Urquijo et al. (2021: 553) disagree with one of our assessments of the M¹
3
4 characters as they consider that the hypocone is slightly larger than the metacone at the occlusal
5
6 enamel surface (OES) and the enamel-dentine junction (EDJ). However, they do not provide an
7
8 image showing how they measured these areas. Indeed, our original study did not include a formal
9
10 metric comparison of the hypocone and the metacone of the M¹ because the high degree of wear of
11
12 this molar makes these measurements tentative. Therefore, we simply stated that both the hypocone
13
14 and the metacone of Axlor show a grade 4 of expression based on the ASUDAS scoring system
15
16 (Turner, Nichol, & Scott, 1991; Gómez-Olivencia et al., 2020: Table 4).
17
18
19

20
21 González-Urquijo et al. (2021: 553) enumerate a series of methodological issues related to
22
23 the analysis of the Axlor's M¹ that were explicitly addressed or that indicate their lack of
24
25 understanding of the methods we used in our study. Firstly, they consider "curious that a
26
27 quantitative assessment of this tooth was even undertaken since Gómez-Robles et al. explicitly
28
29 excluded severely worn teeth". Our study explicitly discussed the limitations of identifying cusp
30
31 tips in worn molars, which is why we performed the geometric morphometric analysis of the M¹
32
33 from Axlor twice: once using both the cusp tips and the outline, and once using only the outline.
34
35 Discriminant analyses indicated a probability of around 99% for this molar to belong to *Homo*
36
37 *sapiens* in both cases.
38
39

40
41 González-Urquijo et al. (2021) state that we did not indicate whether the outline was
42
43 corrected. The outline of the M¹ was indeed corrected as it is the standard procedure in geometric
44
45 morphometric analyses of molar shape (Gómez-Robles et al., 2007). We clearly stated that we used
46
47 "the Neandertal and modern human samples used in Gómez-Robles et al. (2007), Gómez-Robles,
48
49 Bermúdez de Castro, Martínón-Torres, Prado-Simón, and Arsuaga (2012), and Gómez-Robles,
50
51 Martínón-Torres, Bermúdez de Castro, Prado-Simón, and Arsuaga (2011)." (Gómez-Olivencia et
52
53 al., 2020: 479). While not explicitly stated, this was meant to imply that the same methodology was
54
55 used: "When mesial and/or distal borders of the teeth were affected by light interproximal wear,
56
57 original borders were estimated by reference to overall crown shape and the buccolingual extent of
58
59
60

1
2 the wear facets, following Wood and Engleman (1988) and Bailey (2004)” (Gómez-Robles et al.,
3
4 2007: 275-276).

5
6 Additionally, González-Urquijo et al. (2021) estimate that between 30% and 37% (between
7
8 9 and 11) of the semilandmarks are missing in Axlor’s M¹ (see their Figure 1, where they provide a
9
10 new outline for Axlor’s M¹). This outline assumes that landmarks 22-28 are affected by wear, and
11
12 thus the suggested outline enlarges both the metacone and, especially, the hypocone. While we fully
13
14 agree with González-Urquijo and colleagues on the correction performed on the mesial outline,
15
16 which is similar to the one we performed to carry out our analysis, their distal correction is clearly
17
18 incorrect. An inspection of the Axlor’s M¹ 3D model (which is freely available in Figshare; see the
19
20 Data Availability Statement below and in Gómez-Olivencia et al., 2020) clearly reveals that the
21
22 surface of the inter-proximal facet is very limited and does not extent to the hypocone
23
24 semilandmarks (Figure 1). Therefore, the outline correction illustrated by González-Urquijo et al.
25
26 on the distal aspect of the molar substantially exceeds the actual interproximal wear of this molar,
27
28 making it look more Neandertal.
29
30
31
32
33

34 González-Urquijo et al. (2021: 554) state that “the absence of clear divisions between cusps
35
36 complicates accurately positioning the centroid that is used to place the semilandmarks.” Firstly, the
37
38 location of the centroid depends on the location of the cusp tips, not on the presence of “clear
39
40 divisions between cusps”. As stated above, the degree of wear of this molar does interfere with the
41
42 accurate location of the four landmarks that the centroid position is based on. However, the specific
43
44 location of each semilandmark on the outline, which does depend on the calculated centroid, is
45
46 modified through a sliding algorithm that, again, is a standard step of geometric morphometric
47
48 analyses (Bookstein, 1996, 1997; Bookstein, Sampson, Connor, & Streissguth, 2002; Gunz,
49
50 Mitteroecker, & Bookstein, 2005). Hence, any ambiguity in the original positioning of the
51
52 semilandmarks is ameliorated by the sliding procedure.
53
54
55
56
57
58
59
60

[INSERT FIGURE 1 HERE]

Our geometric morphometric analysis revealed that: a) Axlор's M¹ falls closer to the modern human consensus shape than to the Neandertal consensus shape; and b) the M¹ discriminant analysis provided a very high probability to belong to a modern human, while P⁴ and M³ were not conclusive (Gómez-Olivencia et al., 2020). However, it is widely accepted that upper first molars are one of the most diagnostic teeth when distinguishing between Neandertals and modern humans (e.g., Gómez-Robles et al., 2007). When considering PC1 and PC2, the Axlор M1 falls closer to both recent and fossil *Homo sapiens* centroids than to the Neandertal distribution centroid. Overlap is minimal in this plot and only one Neandertal individual from our Neandertal sample (the one from Pech de l'Azé) falls close to Axlор and the recent human centroid (Gómez-Olivencia et al., 2020: Figure 6).

It is also important to note that the discriminant analyses in Gómez-Olivencia et al. (2020) were based on the first 10 PCs not just on the two first PCs shown in the figures. Although not reported in our original study, we include here the cross-validated percentages of correct classification: 93.3% overall, with 73.3% of Neandertals and 100% of modern humans correctly classified. Additionally, when the form space is analyzed, the Axlор M¹ falls outside the range of variation of the Neandertal sample (Gómez-Olivencia et al., 2020).

With respect to the other teeth, we agree with González-Urquijo et al. (2021) that the well-developed mesial ridge and lingual tubercle present in the Axlор canine are traits present in Neandertals in high percentages. Interestingly, they mention the presence of one UP canine (out of 10) with a well-developed mesial ridge, but then question its taxonomic attribution. Our revision of published UP specimens reveals that a tuberculum dentale is also present in other UP specimens (Sunghir 2, Sunghir 3, Mladeč 9; Frayer, Jelínek, Oliva, & Wolpoff, 2006; Trinkaus, Buzhilova, Mednikova, & Dobrovolskaya, 2014). Moreover, Mladeč 9 also presents a well-developed mesial

1
2 ridge (although smaller than the distal one), which is attached to the tuberculum dentale as in the
3
4 canine from Axlor (see Frayer et al., 2006: Figure 19 vs Basabe, 1973: Figure 7).
5

6 González-Urquijo et al. (2021: 553) disagree with our assessment of two additional traits
7
8 and state that the “lingual essential crest of the P⁴ that Gómez-Olivencia et al. scored as absent is
9
10 clearly present at both the OES and the EDJ”. However, we clearly stated that the lingual essential
11
12 crest is present at the EDJ with a score of 2. This crest was scored as “NO” at the OES level, which
13
14 means “non observable” (although we failed to spell this out in the legend of our table). Unlike
15
16 González-Urquijo and colleagues, we considered that the assessment of this trait at the OES level is
17
18 too tentative given the substantial degree of wear present in this tooth. In our table, those traits that
19
20 are absent are clearly indicated by “0 (absent)” (Gómez-Olivencia et al., 2020: Table 3). While we
21
22 admit our error for not spelling out the abbreviation, this does not make these teeth any more
23
24 Neandertal.
25
26
27
28

29 In the case of the hypocone in the M³, we considered that this as an additional
30
31 cusplet/tubercle, since it is not clearly visible in the original OES (and thus our scoring as 0). As the
32
33 scoring of other qualitative traits, our assessment (as González-Urquijo and colleagues’) bears
34
35 certain degree of subjectivity, which is why a quantitative assessment is always preferred. In any
36
37 case, even if the presence of a hypocone in the M³ were accepted, this trait would still be unable to
38
39 distinguish between Neandertals and modern humans (see Martín-Torres et al., 2012).
40
41
42
43
44

45 **4 Stratigraphic study**

46
47 In his field notes and in the published report of Axlor excavations, J. M. de Barandiarán
48
49 describes quite clearly the context of the human remains: i) The site of Axlor was severely affected
50
51 during the end of the XIX century and or the beginning of the XX century, resulting in the
52
53 destruction of a large part of the site, mostly the upper levels, situated in the right part of the site
54
55 (Barandiarán, 1980); ii) The human remains under discussion, according to his field notes, were
56
57 found in the limit of the preserved area, immediately below the mixed sediment that covered the
58
59
60

1
2 destroyed area, and they were the first archaeological remains noted in square 13F; iii) The remains
3
4 were found in a loose sediment that contrasts with the encrusted sediments excavated beside squares
5
6 13E and 13F by J. González Urquijo between 2000 and 2008 (González Urquijo, 2009; González
7
8 Urquijo et al., 2003).

9
10
11 In their reply, González-Urquijo et al. (2021) do not present any new information that
12
13 contradicts the description made by J. M. de Barandiarán or by González-Urquijo's own team in
14
15 previous reports and publications (Barandiarán, 1980; González Urquijo et al., 2006; Rios Garaizar
16
17 et al., 2003). Moreover, some of the interpretations and data presented by González-Urquijo et al.
18
19 (2021) suffer from important omissions:

20
21
22 i) The radiocarbon date table published by González-Urquijo et al. (2021) does not include the
23
24 spatial information of the samples, nor the information about methods, pretreatment and quality of
25
26 the samples. Additionally, they omit two published dates from level F made by themselves (Rios-
27
28 Garaizar, 2017). One of these dates yielded a result of $33,310 \pm 360$ (sample Beta-225485) which is
29
30 extremely important for addressing possible disturbances at the site (Rios-Garaizar, 2012).
31
32 González-Urquijo et al. (2021) reassign one sample (sample Beta-144262) traditionally published as
33
34 belonging to level D (González Urquijo et al., 2006) to level B without further explanation. Finally,
35
36 they omit the radiocarbon dates from Axlor published by Marín-Arroyo et al. (2018) (see Table 1).
37
38
39
40
41
42

43 [INSERT TABLE 1 HERE]
44
45
46
47

48 ii) González-Urquijo et al. (2021) base their argument on the poor preservation of the Upper
49
50 Paleolithic (UP) faunal remains found in F8 and F9, but they neglect to mention that a human tooth
51
52 was found in this level in 2008 (González Urquijo, 2009). Furthermore, González-Urquijo et al.
53
54 (2021) propose a geometry for the UP level omitting that original extension of this level is unknown
55
56 for two reasons. First, due to the aforementioned partial destruction of the site; and second, due to
57
58
59
60

1
2 the excavation of J. M. de Barandiarán who barely recovered, accordingly with the available
3 records, 13 lithic artifacts from level I and 8 lithic artifacts from level II.

4
5
6 iii) The currently available information about the stratigraphic context adjacent to the place where
7 the human remains under discussion were found indicates that the stratigraphic sequence is very
8 difficult to read, that the sediment is encrusted (González Urquijo et al., 2006), and that no new
9 human remains have been recovered there (González Urquijo et al., 2003).
10
11
12
13
14
15
16
17

18 **5 Discussion and conclusions**

19
20 Here we reiterate that a Neandertal classification for the teeth found in Axlor in 1967 is
21 unlikely. Firstly, the supposedly Neandertal traits discussed by González-Urquijo and colleagues
22 (2021) are ambiguous, unclear or based on an erroneous assessment of the teeth. Second, we show
23 that González-Urquijo et al. (2021) do not present any new information that contradicts the
24 stratigraphic description made by J. M. de Barandiarán or by his team in previous reports and
25 publications, and that they omit important information regarding the archaeological context of the
26 human remains found in 1967.
27
28
29
30
31
32
33
34
35

36 As stated in our original publication, the body of evidence points to a modern human
37 classification for these teeth, with very high probabilities in one of the most informative teeth, the
38 M¹. Though species-specific morphologies exist, dental size and shape are variable in both species
39 and unable to unquestionably discriminate between them, particularly for specimens that do not
40 show the most extreme species-specific traits. In addition, the Middle to Upper Paleolithic transition
41 entailed a complex scenario that included both cultural changes and population replacement. Recent
42 developments in ancient DNA analyses have complicated the picture, with evidence of admixture
43 between Neandertals and modern humans (Fu et al., 2015). Fossil remains with ambiguous
44 Neandertal and modern human traits may represent the anatomical evidence of those admixture
45 events (see Compton et al., 2021), although molecular analyses are required to confirm this point.
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2 In sum, the teeth found in Axlor in 1967 show a few features which typically appear in
3
4 Neandertals in high frequencies, but which are also present in *H. sapiens*. However, most traits,
5
6 including the quantitative morphometric analysis of the M¹ show *H. sapiens* affinities. Therefore,
7
8 we favor this taxonomic classification. Genetic analyses and direct dating, however, are the only
9
10 way forward to unequivocally clarify their chronology and further inform discussions about their
11
12 ancestry.
13
14
15
16
17

18 **ACKNOWLEDGMENTS**

19
20 This research has received support from the Spanish Ministerio de Ciencia e Innovación
21
22 (proyecto PGC2018-093925-B-C33, MCI/AEI/FEDER, UE), Research Group IT1418-19 from the
23
24 Eusko Jaurlaritza-Gobierno Vasco, and N. Ergal Foundation. AGO was supported by Ramón y
25
26 Cajal fellowship (RYC-2017-22558). NS was supported by DEATHREVOL project that has
27
28 received funding from the European Research Council (ERC) under the European Union's Horizon
29
30 2020 research and innovation program (Grant agreement No. 949330) and by Ramón y Cajal
31
32 fellowship (RYC2020-029656-I). DLO was supported by an MSC Actions Individual Fellowship
33
34 (Project N°895713). IA-C acknowledges the support by the University of the Basque Country
35
36 UPV/EHU grant GIU19/027. We would like to thank the Editor, the AE, and the reviewers for very
37
38 useful comments that have helped to improve this paper.
39
40
41
42
43
44
45

46 **Data Availability Statement**

47
48 The original micro-ct scans, the derived segmentation files, and 3D volumes are available in
49
50 figshare at <https://doi.org/10.6084/m9.figshare.10308272>.
51
52
53

54 **REFERENCES**

55
56
57 Bailey, S. E. (2004). A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene
58
59 hominins. *Journal of Human Evolution*, 47(3), 183-198. doi:10.1016/j.jhevol.2004.07.001
60

- 1
2 Barandiarán, J. M. (1980). Excavaciones en Axlor. 1967-1974. In J. M. Barandiarán (Ed.), *Obras*
3 *Completas de José Miguel de Barandiarán Tomo XVII* (pp. 127-384). Bilbao: La Gran Enciclopedia
4 Vasca.
- 5 Basabe, J. M. (1973). Dientes humanos del Musteriense de Axlor (Dima, Vizcaya). *Trabajos de*
6 *Antropología*, 16, 187-207.
- 7 Basabe, J. M. (1982). Restos fósiles humanos de la región Vasco-Cantábrica. *Cuadernos de Sección.*
8 *Antropología-Etnografía Prehistoria-Arqueología*, 1, 67-84.
- 9 Bookstein, F. L. (1996). Applying landmark methods to biological outline data. In K. V. Mardia, C. A. Gill
10 & I. L. Dryden (Eds.), *Image Fusion and Shape Variability Techniques*. Leeds: Leeds University
11 Press.
- 12 Bookstein, F. L. (1997). Landmark methods for forms without landmarks: morphometrics of group
13 differences in outline shape. *Medical Image Analysis*, 1(3), 225-243. doi:10.1016/S1361-
14 8415(97)85012-8
- 15 Bookstein, F. L., Sampson, P. D., Connor, P. D., & Streissguth, A. (2002). Midline corpus callosum is a
16 neuroanatomical focus of fetal alcohol damage. *The Anatomical Record*, 269.
- 17 Compton, T., Skinner, M. M., Humphrey, L., Pope, M., Bates, M., Davies, T. W., . . . Stringer, C. (2021).
18 The morphology of the Late Pleistocene hominin remains from the site of La Cotte de St Brelade,
19 Jersey (Channel Islands). *Journal of Human Evolution*, 152, 102939.
20 doi:10.1016/j.jhevol.2020.102939
- 21 Frayer, D. W., Jelínek, J., Oliva, M., & Wolpoff, M. H. (2006). Aurignacian female crania and teeth from
22 the Mladeč Caves, Moravia, Czech Republic. In M. Teschler-Nicola (Ed.), *Early Modern Humans*
23 *at the Moravian Gate. The Mladeč Caves and their remains* (pp. 185-272). Wien: Springer.
- 24 Fu, Q., Hajdinjak, M., Moldovan, O. T., Constantin, S., Mallick, S., Skoglund, P., . . . Pääbo, S. (2015). An
25 early modern human from Romania with a recent Neanderthal ancestor. *Nature*, 524, 216-219.
26 doi:10.1038/nature14558
- 27 Garralda, M. D., Maureille, B., Le Cabec, A., Oxilia, G., Benazzi, S., Skinner, M. M., . . . Vandermeersch,
28 B. (2020). The Neanderthal teeth from Marillac (Charente, Southwestern France): Morphology,
29 comparisons and paleobiology. *Journal of Human Evolution*, 138, 102683.
30 doi:10.1016/j.jhevol.2019.102683
- 31 Gómez-Olivencia, A., López-Onaindia, D., Sala, N., Balzeau, A., Pantoja-Pérez, A., Arganda-Carreras, I., .
32 . . . Gómez-Robles, A. (2020). The human remains from Axlor (Dima, Biscay, northern Iberian
33 Peninsula). *American Journal of Physical Anthropology*, 172(3), 475-491. doi:10.1002/ajpa.23989
- 34 Gómez-Robles, A., Bermúdez de Castro, J. M., Martínón-Torres, M., Prado-Simón, L., & Arsuaga, J. L.
35 (2012). A geometric morphometric analysis of hominin upper second and third molars, with
36 particular emphasis on European Pleistocene populations. *Journal of Human Evolution*, 63(3), 512-
37 526. doi: <http://dx.doi.org/10.1016/j.jhevol.2012.06.002>
- 38 Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J. M., Margvelashvili, A., Bastir, M.,
39 Arsuaga, J. L., . . . Martínez, L. M. (2007). A geometric morphometric analysis of hominin upper
40 first molar shape. *Journal of Human Evolution*, 53, 272-285. doi:10.1016/j.jhevol.2007.02.002
- 41 Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J. M., Prado-Simón, L., & Arsuaga, J. L.
42 (2011). A geometric morphometric analysis of hominin upper premolars. Shape variation and
43 morphological integration. *Journal of Human Evolution*, 61(6), 688-702.
44 doi:10.1016/j.jhevol.2011.09.004
- 45 González Urquijo, J. (2009). Axlor. IX Campaña. *Arkeoikuska*, 08, 245-248.
- 46 González Urquijo, J., & Ibáñez Estévez, J. J. (2002). Abrigo de Axlor (Dima). *Arkeoikuska*, 2001, 90-93.
- 47 González Urquijo, J., Ibáñez Estévez, J. J., & Ríos Garaizar, J. (2003). *Excavación en el yacimiento*
48 *arqueológico de Axlor (Dima, Bizkaia). Un estudio arqueológico y antropológico de la transición*
49 *entre el Paleolítico Medio y el Superior. La extinción de los neandertales y la aparición de los*
50 *humanos modernos en el País Vasco*.
- 51 González Urquijo, J., Ibáñez Estévez, J. J., Ríos Garaizar, J., & Bourguignon, L. (2006). Aportes de las
52 nuevas excavaciones en Axlor sobre el final del Paleolítico Medio. In V. Cabrera Valdés, F.
53 Bernaldo de Quirós Guidotti & J. M. Maíllo Fernández (Eds.), *En el centenario de la cueva de El*
54
55
56
57
58
59
60

- 1
2 *Castillo: el ocaso de los neandertales* (pp. 269-291). Santander: Universidad Nacional de
3 Educación a Distancia – UNED.
- 4 González-Urquijo, J., Bailey, S. E., & Lazuen, T. (2021). Axlors level IV human remains are convincingly
5 Neanderthals: A reply to Gómez-Olivencia et al. *American Journal of Physical Anthropology*,
6 176(4), 553-558. doi:10.1002/ajpa.24252
- 7
8 Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). Semilandmarks in three dimensions. In D. Slice
9 (Ed.), *Modern morphometrics in Physical Anthropology* (pp. 73-98). New York: Kluwer
10 Academic/Plenum Publishers.
- 11 Lazuen Fernández, T., & González-Urquijo, J. (2019-2020). El estudio de las formas de vida de las
12 sociedades neandertales en el yacimiento de Axlors (Dima, Bizkaia): las excavaciones de J.M.
13 Barandiaran y el proyecto del siglo XXI. *Anuario de Eusko Folklore Urtekaria*, 54, 47-69.
- 14 Marín-Arroyo, A. B., Rios-Garaizar, J., Straus, L. G., Jones, J. R., de la Rasilla, M., González Morales, M.
15 R., . . . Ocio, D. (2018). Chronological reassessment of the Middle to Upper Paleolithic transition
16 and Early Upper Paleolithic cultures in Cantabrian Spain. *Plos one*, 13(4), e0194708.
17 doi:10.1371/journal.pone.0194708
- 18
19 Martínón-Torres, M., Bermúdez de Castro, J. M., Gómez-Robles, A., Prado-Simón, L., & Arsuaga, J. L.
20 (2012). Morphological description and comparison of the dental remains from Atapuerca-Sima de
21 los Huesos site (Spain). *Journal of Human Evolution*, 62(1), 7-58.
- 22 Rios Garaizar, J., González Urquijo, J. E., & Ibáñez Estévez, J. J. (2003). La excavación en Axlors. Las
23 formas de vida de los últimos neandertales. *Boletín de la SEDECK*, 5, 62-83.
- 24 Rios-Garaizar, J. (2012). *Industria lítica y sociedad en la transición del Paleolítico Medio al Superior en*
25 *torno al Golfo de Bizkaia*. Santander: PubliCan-Ediciones de la Universidad de Cantabria.
- 26 Rios-Garaizar, J., 2017. A new chronological and technological synthesis for Late Middle Paleolithic of the
27 Eastern Cantabrian Region. *Quaternary International*, 433, 50-63.
- 28 Rostro Carmona, J. (2013). Estudio comparado de las piezas dentales de *Homo neanderthalensis* del
29 yacimiento Musteriense de Axlors (Dima, Vizcaya). *CKQ Estudios de Cuaternario/Kuaternario*
30 *Ikasketak/Quaternary Studies*, 3, 91-100.
- 31
32 Trinkaus, E., Buzhilova, A. P., Mednikova, M. B., & Dobrovolskaya, M. V. (2014). *The People of Sunghir.*
33 *Burials, Bodies, and Behavior in the Earlier Upper Paleolithic*. Oxford: Oxford University Press.
- 34 Turner II, C. G., Nichol, C. R., & Scott, G. R. (1991). Scoring procedures for key morphological traits of
35 the permanent dentition: the Arizona State University dental anthropology system. In M. Kelley &
36 C. Larsen (Eds.), *Advances in Dental Anthropology* (pp. 13-31). New York: Wiley-Liss.
- 37
38 Wood, B. A., & Engleman, C. A. (1988). Analysis of the dental morphology of Plio-Pleistocene hominids.
39 V. Maxillary postcanine tooth morphology. *Journal of Anatomy*, 161, 1-35.
- 40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
FIGURE LEGENDS

Figure 1. A) Semilandmarks proposed by González-Urquijo et al. (2021) as an accurate correction of Axlor's M¹ outline; B) Corrected outline used by Gómez-Olivencia et al. (2020) in their original assessment. C and D) Occlusal-distal showing that the extension of the distal facet (marked in red in D) does not affect the occlusal outline. E) Outline of a M¹ from Krapina (Krapina 100) showing the bulging hypocone, typical of Neandertal populations (and also of European Middle Pleistocene populations) (Bailey, 2004; Gómez-Robles et al., 2007; Martínón-Torres, Bermúdez de Castro, Gómez-Robles, Prado-Simón, & Arsuaga, 2012).

Table 1
Available radiocarbon dates for Axlor late Middle Paleolithic levels B, D and F.

Level*	Sample reference	Lab Code	Date (BP)	Method	Material	Taxon, anatomical part	%C	%N	C:N	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ (‰ VPDB)	$\delta^{15}\text{N}$ (‰ AIR)	References
B**	na	Beta-144262	42,010±1280	AMS	Bone	Non determ.							González Urquijo & Ibañez Estévez, 2002; González Urquijo et al., 2021
B	na	Beta-203108	42,720±900	AMS	Bone	<i>Bos/Bison</i> ; tibia							González Urquijo et al., 2021
D	na	Beta-203107	44,920±1950	AMS	Bone	<i>Bos/Bison</i> ; axis							González Urquijo et al., 2021
D	na	Beta-225486	>43,000	AMS	Bone	<i>Cervus</i> ; metapodial							Ríos-Garaizar, 2012; González Urquijo et al., 2021
F	na	Beta-225478	>47,500	AMS	Bone	<i>Cervus</i> ; metapodial							Ríos-Garaizar, 2012
F	na	Beta-225485	33,310±360	AMS	Bone	<i>Cervus</i> ; metapodial							Ríos-Garaizar, 2012
IV	AX.11C.290.149	OxA-32428	>49,300	UF-AMS	Bone	<i>Cervus elaphus</i> ; phalanx 2	42.3	3.5	3.3	-19.8	3.5	3.1	Marín-Arroyo et al., 2018
IV	AX.11C.300.178	OxA-32429	>49,900	UF-AMS	Bone	<i>Cervus elaphus</i> ; carpal	43.0	6.3	3.3	-19.2	6.3	6.0	Marín-Arroyo et al., 2018

* Level attribution with letters (B, D and F) correspond with 2000-2008 excavations; Roman ordinals with 1967-1974 excavations.

** In the original publication this sample is attributed to level D, in the recent publication to level B.

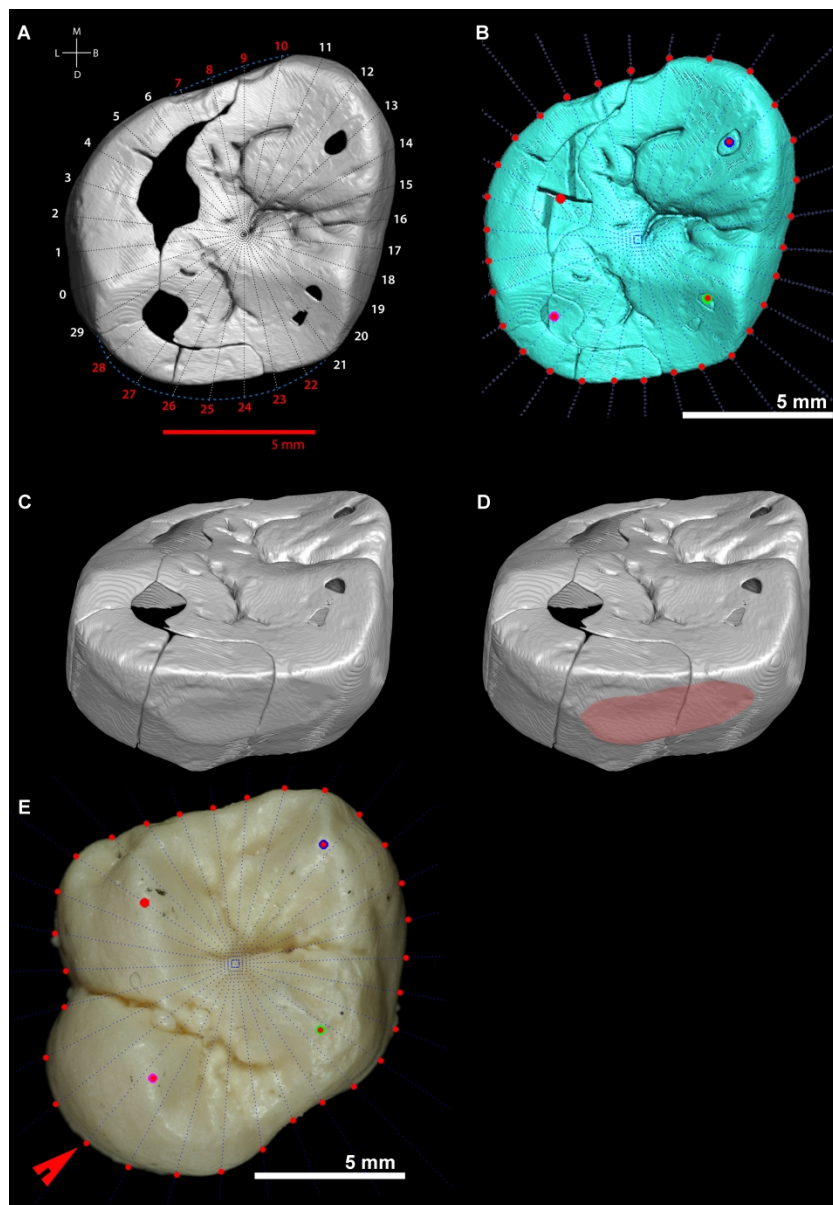


Figure 1. A) Semilandmarks proposed by González-Urquijo et al. (2021) as an accurate correction of Axlor's M1 outline; B) Corrected outline used by Gómez-Olivencia et al. (2020) in their original assessment. C and D) Occlusal-distal showing that the extension of the distal facet (marked in red in D) does not affect the occlusal outline. E) Outline of a M1 from Krapina (Krapina 100) showing the bulging hypocone, typical of Neandertal populations (and also of European Middle Pleistocene populations) (Bailey, 2004; Gómez-Robles et al., 2007; Martínón-Torres, Bermúdez de Castro, Gómez-Robles, Prado-Simón, & Arsuaga, 2012).