Letter to the Editor

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

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

Here we address the points raised by González-Urquijo et al. (2021) and provide additional anatomical evidence supporting our previous assessment.

1 The taxonomic attribution of the human remains found in 1967

The human remains found in 1967 comprise four teeth (left P^4-M^3) found on September 7th 1967 in the square 13F at a depth of 265 cm. Two of these teeth (M^1 and M^2) were found in a maxillary fragment. Additionally, a left canine was found on September 8th in the square 13E at a depth of 285 cm (Gómez-Olivencia et al., 2020: Figure S6). Two of these teeth (the C' and the M^2) are currently lost, and therefore, our taxonomic assessment was based on the P^4, M^1 and M^3. All these remains were originally attributed to the Mousterian level III by Barandiarán (Barandiarán, 1980; see also Gómez-Olivencia et al., 2020: Figure S6). However, based on the depth of the

findings and the depth attributed by Barandiarán to the level IV in 1968 (Barandiarán, 1980), they have been later and repeatedly attributed to level IV (Basabe, 1982; González Urquijo, Ibáñez Estévez, Ríos Garaizar, & Bourguignon, 2006; Lazuen Fernández & González-Urquijo, 2019-2020).

González-Urquijo et al. (2021: 553) oversimplified our taxonomic assessment, stating that we concluded that "those remains should instead be assigned to a single Upper Paleolithic *Homo sapiens* individual". However, our study states that "based on both morphological and size characteristics, this individual shows stronger affinities with modern humans than with Neandertals" (Gómez-Olivencia et al., 2020: 486), while we also clearly recognized that some of the teeth (e.g., the canine and the P^4) showed some features that are present in high percentages in Neandertals, but are not exclusive of this group. In our discussion, we hypothesized that "these human remains could belong to an UPMH [Upper Paleolithic modern human], which should be tested in the near future using direct C14 datings". This claim was based on the results of our morphometric analyses, the absence of Holocene recent prehistory remains from the Axlor sequence and the presence of an early Upper Paleolithic occupation in the site (Gómez-Olivencia et al., 2020: 488). This was summarized in our abstract, which states that the teeth from Axlor "may represent one of the scarce examples of Upper Paleolithic modern human remains in the northern Iberian Peninsula, which should be confirmed by direct dating" (Gómez-Olivencia et al., 2020: 475). Thus, we suggested that these remains may have belonged to an UPMH, the confirmation of which would require further analyses, but we did not discard other possibilities, such as these teeth having a more recent chronology.

2 Dental morphological analysis

González-Urquijo et al. (2021) disagree with some of our morphological assessments and take issue with the employed methodology. The taxonomic assessment of the Axlor 1967 remains

by González-Urquijo et al. (2021) pivots mainly around the morphology of the lost canine, the crown morphology of the P^4 and the morphology of the M^1.

Firstly, González-Urquijo et al. conclude that "the morphological features of the Axlor teeth seem to be either Neanderthal-like or ambiguous, but there is no reason to suggest these teeth belong to *H. sapiens*". Their comments on our taxonomic assessment are limited to the crown morphology; they do not comment on other features that can be of taxonomic interest (e.g., the root morphology or the P^4), nor do they attempt to carry out additional analyses despite the original micro-CT scans being publicly available.

González-Urquijo et al. (2021: 553) agree with us that the teeth from Axlor are small but they disregard this information as they consider that crown size is a poor discriminator between Neandertals and *Homo sapiens*. The dimensions of the Axlor samples are closer to the Upper Paleolithic *Homo sapiens* (HS) means (C', P^4) or to the recent HS means (M^1, M^2, M^3) than to Neandertals. The published BL measurements of the lost M^2 are below (and outside) our Neandertal and UP range of variation. In addition, our size assessment was complemented with shape information (i.e., form analysis). Geometric morphometric analysis of form variation (including size and shape) is a widely used way to assess taxonomic affinity (Compton et al., 2021; Garralda et al., 2020), and it yielded informative results in some teeth from Axlor (M^1 and M^3) but not in others (P^4), as we clearly stated in our study (Gómez-Olivencia et al., 2020).

González-Urquijo et al. (2021: 553) also consider that the grades of expression of the non-metric traits for the P^4, M^1 and M^3, "rather than being *H. sapiens*-like […] have trait express that are ambiguous". We struggle to understand where we disagree here, as our study explicitly stated that some of the Axlor teeth have features that are observed in Neandertals in high frequencies (e.g., the bifurcated essential crest of both the lingual and buccal cusps in the P4 at the EDJ level). González-Urquijo et al. (2021: 553) also consider that "most of the traits do not clearly distinguish Neanderthals and Upper Paleolithic *H. sapiens*", which is exactly the reason why we combined qualitative and quantitative methods for the taxonomic assessment of the Axlor teeth. On the

contrary, González-Urquijo and colleagues seem to believe that their vague qualitative description suffices to demonstrate a Neandertal classification for these teeth beyond any reasonable doubt.

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

González-Urquijo et al. (2021: 553) enumerate a series of methodological issues related to the analysis of the Axlor's M^1 that were explicitly addressed or that indicate their lack of understanding of the methods we used in our study. Firstly, they consider "curious that a quantitative assessment of this tooth was even undertaken since Gómez-Robles et al. explicitly excluded severely worn teeth". Our study explicitly discussed the limitations of identifying cusp tips in worn molars, which is why we performed the geometric morphometric analysis of the M^1 from Axlor twice: once using both the cusp tips and the outline, and once using only the outline. Discriminant analyses indicated a probability of around 99% for this molar to belong to *Homo sapiens* in both cases.

González-Urquijo et al. (2021) state that we did not indicate whether the outline was corrected. The outline of the M^1 was indeed corrected as it is the standard procedure in geometric morphometric analyses of molar shape (Gómez-Robles et al., 2007). We clearly stated that we used "the Neandertal and modern human samples used in Gómez-Robles et al. (2007), Gómez-Robles, Bermúdez de Castro, Martinón-Torres, Prado-Simón, and Arsuaga (2012), and Gómez-Robles, Martinón-Torres, Bermúdez de Castro, Prado-Simón, and Arsuaga (2011)." (Gómez-Olivencia et al., 2020: 479). While not explicitly stated, this was meant to imply that the same methodology was

used: "When mesial and/or distal borders of the teeth were affected by light interproximal wear, original borders were estimated by reference to overall crown shape and the buccolingual extent of the wear facets, following Wood and Engleman (1988) and Bailey (2004)" (Gómez-Robles et al., 2007: 275-276).

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

González-Urquijo et al. (2021: 554) state that "the absence of clear divisions between cusps complicates accurately positioning the centroid that is used to place the semilandmarks." Firstly, the location of the centroid depends on the location of the cusp tips, not on the presence of "clear divisions between cusps". As stated above, the degree of wear of this molar does interfere with the accurate location of the four landmarks that the centroid position is based on. However, the specific location of each semilandmark on the outline, which does depend on the calculated centroid, is modified through a sliding algorithm that, again, is a standard step of geometric morphometric analyses (Bookstein, 1996, 1997; Bookstein, Sampson, Connor, & Streissguth, 2002; Gunz, Mitteroecker, & Bookstein, 2005). Hence, any ambiguity in the original positioning of the semilandmarks is ameliorated by the sliding procedure.

[INSERT FIGURE 1 HERE]

Our geometric morphometric analysis revealed that: a) Axlor's M^1 falls closer to the modern human consensus shape than to the Neandertal consensus shape; and b) the M^1 discriminant analysis provided a very high probability to belong to a modern human, while P^4 and M^3 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), and our analysis yielded a 99% probability for the Axlor M^1 to belong to a modern human (Gómez-Olivencia et al., 2020). When considering PC1 and PC2, the Axlor 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 Axlor 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 Axlor M^1 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 Axlor 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 ridge (although smaller than the distal one), which is attached to the tuberculum dentale as in the canine from Axlor (see Frayer et al., 2006: Figure 19 *vs* Basabe, 1973: Figure 7).

González-Urquijo et al. (2021: 553) disagree with our assessment of two additional traits and state that the "lingual essential crest of the P^4 that Gómez-Olivencia et al. scored as absent is clearly present at both the OES and the EDJ". However, we clearly stated that the lingual essential crest is present at the EDJ with a score of 2. This crest was scored as "NO" at the OES level, which means "non observable" (although we failed to spell this out in the legend of our table). Unlike González-Urquijo and colleagues, we considered that the assessment of this trait at the OES level is too tentative given the substantial degree of wear present in this tooth. In our table, those traits that are absent are clearly indicated by "0 (absent)" (Gómez-Olivencia et al., 2020: Table 3). While we admit our error for not spelling out the abbreviation, this does not make these teeth any more Neandertal.

In the case of the hypocone in the M^3, we considered that this as an additional cusplet/tubercle, since it is not clearly visible in the original OES (and thus our scoring as 0). As the scoring of other qualitative traits, our assessment (as González-Urquijo and colleagues') bears certain degree of subjectivity, which is why a quantitative assessment is always preferred. In any case, even if the presence of a hypocone in the M^3 were accepted, this trait would still be unable to distinguish between Neandertals and modern humans (see Martinón-Torres et al., 2012).

4 Stratigraphic study

In his field notes and in the published report of Axlor excavations, J. M. de Barandiarán describes quite clearly the context of the human remains: i) The site of Axlor was severely affected during the end of the XIX century and or the beginning of the XX century, resulting in the destruction of a large part of the site, mostly the upper levels, situated in the right part of the site

(Barandiarán, 1980); ii) The human remains under discussion, according to his field notes, were found in the limit of the preserved area, immediately below the mixed sediment that covered the destructed area, and they were the first archaeological remains noted in square 13F; iii) The remains were found in a loose sediment that contrasts with the encrusted sediments excavated beside squares 13E and 13F by J. González Urquijo between 2000 and 2008 (González Urquijo, 2009; González Urquijo et al., 2003).

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

i) The radiocarbon date table published by González-Urquijo et al. (2021) does not include the spatial information of the samples, nor the information about methods, pretreatment and quality of the samples. Additionally, they omit two published dates from level F made by themselves (Rios-Garaizar, 2017). One of these dates yielded a result of 33,310±360 (sample Beta-225485) which is extremely important for addressing possible disturbances at the site (Rios-Garaizar, 2012). González-Urquijo et al. (2021) reassign one sample (sample Beta-144262) traditionally published as belonging to level D (González Urquijo et al., 2006) to level B without further explanation. Finally, they omit the radiocarbon dates from Axlor published by Marin-Arroyo et al. (2018) (see Table 1).

[INSERT TABLE 1 HERE]

ii) González-Urquijo et al. (2021) base their argument on the poor preservation of the Upper Paleolithic (UP) faunal remains found in F8 and F9, but they neglect to mention that a human tooth was found in this level in 2008 (González Urquijo, 2009). Furthermore, González-Urquijo et al. (2021) propose a geometry for the UP level omitting that original extension of this level is unknown

for two reasons. First, due to the aforementioned partial destruction of the site; and second, due to the excavation of J. M. de Barandiarán who barely recovered, accordingly with the available records, 13 lithic artifacts from level I and 8 lithic artifacts from level II.

iii) The currently available information about the stratigraphic context adjacent to the place where the human remains under discussion were found indicates that the stratigraphic sequence is very difficult to read, that the sediment is encrusted (González Urquijo et al., 2006), and that no new human remains have been recovered there (González Urquijo et al., 2003).

5 Discussion and conclusions

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

As stated in our original publication, the body of evidence points to a modern human classification for these teeth, with very high probabilities (99%) in one of the most informative teeth, the M^1. Though species-specific morphologies exist, dental size and shape are variable in both species and unable to unquestionably discriminate between them, particularly for specimens that do not show the most extreme species-specific traits. In addition, the Middle to Upper Paleolithic transition entailed a complex scenario that included both cultural changes and population replacement. Recent developments in ancient DNA analyses have complicated the picture, with evidence of admixture between Neandertals and modern humans (Fu et al., 2015). Fossil remains with ambiguous Neandertal and modern human traits may represent the anatomical evidence of

those admixture events (see Compton et al., 2021), although molecular analyses are required to confirm this point.

In sum, the teeth found in Axlor in 1967 show a few features which appear in Neandertals in high frequencies, but which are also present in *H. sapiens*. However, the morphology of the root of the P^4, the quantitative morphometric analysis of the M^1 show clear *H. sapiens* affinities. Therefore, we favor this taxonomic classification. Genetic analyses and direct dating, however, are the only way forward to unequivocally clarify their chronology and ancestry.

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Data Availability Statement

The original micro-ct scans, the derived segmentation files, and 3D volumes are available in figshare at https://doi.org/10.6084/m9.figshare.10308272.

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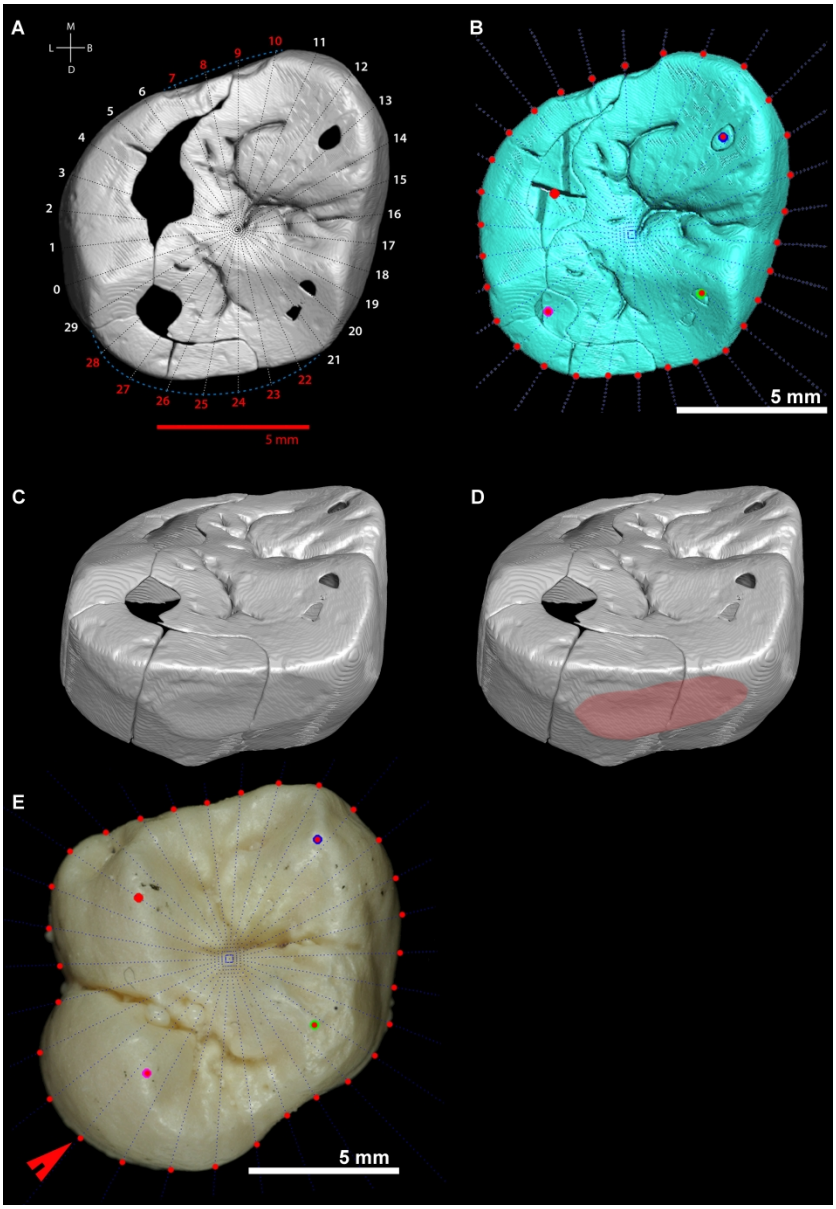
FIGURE LEGENDS

Figure 1. A) Semilandmarks proposed by González-Urquijo et al. (2021) as an accurate correction of Axlor's M^1 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 M^1 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; Martinón-Torres, Bermúdez de Castro, Gómez-Robles, Prado-Simón, & Arsuaga, 2012).

Table 1
Available radiocarbon dates for Axlor upper middle Paleolithic levels B, D and F.

Level*	Sample reference	Lab Code	Date (BP)	Method	Material	Taxon, anatomical part	%C	%N	C:N	$\delta^{13}C$	$\delta^{13}C$ (‰ VPDB)	$\delta^{15}N$ (‰ 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	*Bos/Bison*; tibia							González Urquijo et al., 2021
D	na	Beta-203107	44,920±1950	AMS	Bone	*Bos/Bison*; axis							González Urquijo et al., 2021
D	na	Beta-225486	>43,000	AMS	Bone	*Cervus*; metapodial							Rios-Garaizar, 2012; González Urquijo et al., 2021
F	na	Beta-225478	>47,500	AMS	Bone	*Cervus*; metapodial							Rios-Garaizar, 2012
F	na	Beta-225485	33,310±360	AMS	Bone	*Cervus*; metapodial							Rios-Garaizar, 2012
IV	AX.11C.290.149	OxA-32428	>49,300	UF-AMS	Bone	*Cervus elaphus*; 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	*Cervus elaphus*; 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.



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