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Metric and morphological comparison between the Arago (France) and Atapuerca-Sima de los Huesos (Spain) dental samples, and the origin of Neanderthals

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ABSTRACT

The variability observed in the growing Middle Pleistocene hominin fossil record of Europe continues to trigger much debate on taxonomic issues and the biological processes that gave rise to Neanderthals. Here we present a metric and morphological comparative study of the dental samples recovered from the sites of Arago (southeast France) and Sima de los Huesos (SH) in the Sierra de Atapuerca (northern Spain). These sites are key to providing answers to these questions since they have yielded the largest hominin samples so far recovered for this time period. Despite the geographical proximity of the two sites and the contemporaneity of their hominin assemblages, we have observed remarkable metric and morphological differences between the teeth at Arago and SH. Whereas the SH teeth present an almost morphological identity with European Neanderthals, the Arago teeth exhibit a combination of plesiomorphic as well as some Neanderthal-derived features. In addition, the Arago crown dimensions are remarkably larger than those from SH, the differences being statistically significant for most variables. We hypothesize that during the Middle Pleistocene the European continent was settled at different points in time by hominin groups coming from Southwest Asia, probably from a common mother population evolving in this latter region. These first settlers can be identified by their more plesiomorphic morphology, whereas the most recent settlers are closer in appearance to Neanderthals. In addition, genetic processes such as isolation, genetic drift, directional adaptation or hybridization would have given rise to the puzzle we observe in the current fossil record.

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1. Introduction

Over the years, the interpretation of the European Pleistocene fossil record has increasingly captured the attention of many specialists. This interpretation has undergone substantial changes as the number of human fossils has increased, the dating of many sites has improved, and new lines of research have been opened, such as

palaeogenetics. Therefore, presenting an exhaustive history of research on human evolution in Europe during the Pleistocene is beyond the scope of this work. It is nonetheless interesting, and relevant to our present discussion to refer back to the main hypotheses that were proposed during the second half of the twentieth century, and during this century, on the origins of the Neanderthals.

1.1. Theories about the settlement of Europe during the Middle Pleistocene: an overview

The so-called presapiens theory, proposed by Vallois (1954),

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attempted to show a primary bifurcation into two distinct lines: “Neanderthal” and “*sapiens*”. This hypothesis was criticized by [Howell \(1960\)](#), who did not find significant differences between Steinheim and Swanscombe, two key specimens in the presapiens theory. Moreover, [Howell \(1960\)](#) was very clear in his separation of the Pleistocene populations found in the European fossil record and those found in eastern Asia and northern Africa, which today have been attributed by many to *H. erectus*. [Howell \(1960\)](#) divided temporally the European hominin fossil record in two phases: “(1) the pre- Great Interglacial range (early Middle Pleistocene) and (2) the Great Interglacial and subsequent early phase of the Penultimate Glacial range (later Middle Pleistocene)”. After his detailed study of the limited fossil record of that time, [Howell \(1960, p. 223\)](#) conclude that “The evidence would suggest that two distinctive hominid lineages were differentiated within the Middle Pleistocene, one represented by eastern Asian and north-west African populations, and the other by European populations”.

[Aguirre et al. \(1976\)](#) and [Aguirre and de Lumley \(1977\)](#) studied the fossil hominins recovered from the Atapuerca-SH site. These authors included these fossils alongside those of Arago and Mauer in the so-called ‘Anteanderthal population’. This term, which has dominated the scientific literature for decades, alludes to the clear phylogenetic relationship between the human populations of the Middle Pleistocene and the Neanderthals of the Late Pleistocene. [Aguirre and de Lumley \(1977\)](#) were also not comfortable with the idea of including any other Pleistocene remains from Europe in the *H. erectus* taxon which, according to these authors, “should be restricted to the fossils from Java”. Nevertheless, the idea that anteanderthals (or at least some of them) represent a particular lineage of *H. erectus* has persisted for decades (e.g. [Jelinek, 1986](#); [De Lumley, 2015](#), but see [Howell, 1986](#)).

Although [Thoma \(1966\)](#) revived the presapiens hypothesis, the idea that in Europe there was a great biodiversity of human populations, and all of them were related to Neanderthals, appears clearly in the review carried out by [Howells \(1980\)](#). In the same sense, [Bräuer \(1984\)](#) presented evidence against the hypothesis of the origin of *H. sapiens* in Europe. This author proposed the “Afro-European *sapiens* hypothesis” and considered that all European Middle Pleistocene specimens represent a very variable Anteanderthal population. According to this hypothesis, a bottleneck of this population was the origin of the so-called preneanderthals during the late Middle Pleistocene.

In their classic report, [Cook et al. \(1982\)](#) reviewed the ups and downs associated with dating Middle Pleistocene European sites comprising human remains. A lack of dates, or unreliable dates, are two of the main problems when interpreting the fossil record, although geochronological methods have been progressively improving through time and are currently being applied to many of these sites (e.g., [Arsuaga et al., 2014](#); [Daura et al., 2017](#); [Falguères et al., 2004](#); [Wagner et al., 2010](#)). Today, the temporal framework is much more precise, but still requires improvement.

A general consensus on the origin of Neanderthals was reached during the 1980s and at the beginning of the 1990s (e.g. [Arsuaga et al., 1993](#); [Arsuaga et al., 1996](#); [Hublin, 1988a](#); [Hublin, 1990](#); [Stringer, 1993](#)). [Hublin 1988a, 1988b](#) considered that all European Middle Pleistocene fossils were related to Neanderthals, except Mauer, Vértesszöllös, and Bilzingsleben, although, according to his later works ([Hublin, 1996](#)), the possible absence of Neanderthal features in these specimens was not a criterion in itself to exclude them from the Neanderthal lineage. On this matter, it is interesting to mention that other authors have noted some Neanderthal features in the Mauer mandible, the holotype of *H. heidelbergensis* ([Bermúdez de Castro et al., 2016](#); [Mounier et al., 2009](#); [Rosas and Bermúdez de Castro, 1998](#)). The notion that European Middle Pleistocene hominins are distinct from those included in the

H. erectus species led [Stringer \(1983, 1985\)](#) to postulate that specimens like those from Mauer, Vértesszöllös, Bilzingsleben, Arago, and Petralona, together with Broken Hill, Bodo, and Dali would represent the stem species (*H. heidelbergensis*) for Neanderthals and modern humans. This hypothesis was further developed by other colleagues (e.g. [Rightmire, 1996](#); [Rightmire, 1998](#); [Tattersall, 1996](#)). [Arsuaga et al. \(1997a\)](#) also included the SH hominins within this species. However, these last authors believe that *H. heidelbergensis* ought to be considered as an exclusive European chronospecies of the Neanderthal lineage. Later [Arsuaga et al. \(2014\)](#) left the SH hominins out of the *H. heidelbergensis* species, particularly because of the lack of cranial features like those found in other European Middle Pleistocene fossils, such as Ceprano (see below) and Arago, and the clear differences between the Mauer and the SH mandibular samples. The high degree of morphological diversity in the European Middle Pleistocene fossil record had begun to suggest a more complex view, especially after the discovery of the Ceprano calvaria ([Ascenzi et al., 1996](#)), the Mala Balanica mandible ([Roksandic et al., 2011](#)), and the Aroeira 3 cranium ([Daura et al., 2017](#)).

The Ceprano calvaria was first included in *H. erectus*, given its primitive morphology and its presumed early Pleistocene chronology ([Ascenzi et al., 1996](#)). However, new dating points provided an age range between 0.43 and 0.38 million years ago (Ma) ([Manzi et al., 2010](#)). Given this age and the observation that the morphology of the specimen has no equivalent in Europe, its taxonomic status remains controversial. This specimen has been also included in *H. cepranensis* ([Mallegni et al., 2003](#)), whereas new analyses led [Mounier et al. \(2011\)](#) and [Manzi \(2016\)](#) to initially include the Ceprano calvaria in the *H. heidelbergensis* species. The Mala Balanica mandibular fragment lacks Neanderthal features, and has been described as *Homo* sp ([Roksandic et al., 2011](#)). This specimen has been dated to the Middle Pleistocene ([Rink et al., 2013](#)). The Aroeira 3 cranium shows an interesting combination of cranial features present in the Atapuerca-SH, Arago, and Ceprano specimens, thus confirming the complexity that lies behind the interpretation of the European Middle Pleistocene fossil record ([Daura et al., 2017](#)). Finally, the analysis of the impressive cranial sample recovered from the SH hominins ([Arsuaga et al., 2014](#)) confirms the remarkable differences between these hominins and other European Middle Pleistocene specimens. This fact again drives the idea of the coexistence in Europe of more than one hominin lineage during this period ([Tattersall, 2011](#); [Stringer, 2012](#)).

1.2. Aims of this report

As noted above, it is clear that the significant morphological diversity of the European Middle Pleistocene fossil record cannot be avoided when researching human evolution. The complex physical geography, biogeography, and palaeoclimatology of the relatively small European continent may have played an important role in the demographic distribution and interaction of these Pleistocene populations. These factors may have given rise to different genetic processes including drift, founder effect, directional adaptation and hybridization ([Daura et al., 2017](#); [Dennell et al., 2011](#); [MacDonald et al., 2012](#); [Roksandic et al., 2011](#)). Furthermore, the idea that different waves of populations arrived into Europe during the Pleistocene cannot be discarded ([Bermúdez de Castro et al., 2016](#)).

Tooth morphology has been considered to be highly heritable, selectively neutral, and evolutionary conservative, thus providing an excellent proxy for neutral genetic data ([Hillson, 1996](#); [Scott and Turner, 1997](#)). In a recent study, [Rathmann et al. \(2017\)](#) have confirmed that dental phenotypic data (metric and no-metric traits) can be used as proxies for neutral genomic data in studies of population relatedness. Therefore, our aim is to compare the

dental morphology of two important, geographically close, and approximately contemporaneous Middle Pleistocene hominin samples: Arago and Atapuerca-SH. We will evaluate and discuss the meaning of the possible similarities and differences between these two samples. Our null hypothesis is that, given the temporal and geographic proximity of the Arago and Atapuerca-SH sites, the differences noted between these two dental hominin samples are not significant. Thus, the Arago and Atapuerca-SH hominins may belong to the same biological population.

2. The Arago and Atapuerca-SH sites

The Caune de l'Arago (southern France) is a key site for the understanding of human evolution in Europe during the Middle Pleistocene. The sedimentary fill of the cave was assigned to this period on the basis of the mammalian fauna found within it (Chaline, 1981; Crégut, 1980; Guérin, 1981). The Middle Stratigraphical Complex of the Arago site includes, from bottom to top, four geological Units: I, II, III, and IV (De Lumley et al., 2015). Most human fossil remains have been recovered from Unit III, which includes archaeological layers G, F, E, and D, that are separated by sterile levels (Falgouères et al., 2004, De Lumley et al., 2015). Unit IV includes archaeological levels A, B, and C. Only layer C of Unit IV has yielded human remains. Most hominin specimens have been obtained from archaeological layers F and G.

However, we will deal with these fossils as a unique hominin sample, not only for practical reasons, but because the temporal space for the deposition of these fossils is relatively small. The present dating places the D-G archaeological layers in the interval 400 to 450 kiloyears (kyr) (Falgouères et al., 2015; Yokoyama and Nguyen, 1981; Yokoyama et al., 1985). Furthermore, a U-series analysis of the stalagmitic formation located at the bottom of Unit IV confirmed that Unit III is older than 350 kyr (Falgouères et al., 2004).

A detailed description of the Sima de los Huesos cave site, the history of the discoveries, the possible origin of the deposit, and the geology of the site can be found in Arsuaga et al. (1997b), Arsuaga et al. (2014), and Bischoff et al. (1997). Concerning the dating of the Sima de los Huesos site, more recent information has been published by Arnold et al. (2014). These authors have applied post-infrared-infrared stimulated luminescence (pIR-IR) dating of K-feldspars and thermally transferred optically stimulated luminescence (TT-OSL) dating of individual quartz grains, which have provided weighted mean ages of 433 ± 15 kyr, and 416 ± 19 kyr, respectively for the allochthonous sedimentary horizons overlying the hominin-bearing clay breccia. This study provides a combined minimum age estimate of 427 ± 12 ka for the Sima de los Huesos hominins. Moreover, U-series dating of a cave raft speleothem deposited directly on a hominin cranium (cranium 4) from LU-6 yielded a mean age of $434 + 36/-24$ kyr (Arsuaga et al., 2014). These dates are consistent with the early-to-mid Middle Pleistocene age of the faunal assemblage recovered from the hominin level (Arsuaga et al., 2014; Cuenca-Bescós et al., 1997; García et al., 1997). Therefore, the Sima de los Huesos hominins could be considered roughly contemporaneous with those of Arago and may be attributed to MIS 12 (Lisiecki and Raymo, 2005).

The sedimentary record preserved at SH has been subdivided into 12 lithostratigraphic units (LU1 through to LU12) (Arsuaga et al., 2014). All fossil human remains have been recovered from LU6 (Arsuaga et al., 2014). The variability observed within different skeletal parts suggests that all the individuals represented in the SH hominin assemblage belong to the same biological population (Bermúdez de Castro and Nicolás, 1997, and references therein).

3. Material and methods

The SH dental sample includes 530 permanent teeth (Table 1), whereas the Arago dental sample comprises 61 permanent teeth (Table 1). Details about the composition of the SH sample can be found in Martín-Torres et al. (2012). The Arago sample analyzed in this report comprises 21 upper and 39 lower permanent specimens and 39 lower specimens. The Arago 2 mandible preserves *in situ* the right M₁ and the left M₁, M₂ and M₃. The Arago 13 left hemimandible preserves *in situ* the P₃-M₃ sequence. The Arago 89 mandible preserves *in situ* the right P₃-M₃ sequence and the left molar series (M₁ through to M₃). The maxilla of cranium 21 preserves *in situ* its right molar series, M¹-M³ and the left M² and M³. In addition, the isolated Arago 16 (right P³) and Arago 36 (left P³) specimens belong to this cranium. The following are also associated teeth (belonging to the same individual):

Arago 7 (right P³), Arago 14 (left M²), and Arago 26 (right P⁴).

Arago 40 and Arago 68 (right M¹ and M²).

Arago 10 (right M₂), Arago 25 (left I²), Arago 32 (left M₂), and Arago 24 (left C₁).

Arago 59 (right upper C¹), Arago 60 (right I²), and Arago 61 (right I¹).

All these associations were made by M.A. de Lumley.

The mesiodistal (MD) and buccolingual (BL) dimensions of the Arago and SH teeth were measured on three separate occasions by JMBC to the nearest 0.1 mm following the methodology proposed by Flechier, Lefèvre, and Verdéne (Lefèvre, 1973). In order to carry out the measurements we used a specially-designed caliper with wide, flat and thin tips, and moving arms to allow for measurement to be taken in projection when the reference points and planes are placed at different levels. This method is particularly useful when teeth are found in isolation. This method can be applied identically to both isolated and *in situ* teeth. However, this method works best when the teeth are isolated and when measuring the buccolingual diameter. When the teeth are *in situ* it is more complex to determine the mesiodistal diameter. The measurement obtained may be somewhat smaller, particularly when the tooth has experienced extreme proximal wear. The MD diameter clearly decreases when occlusal wear is ≥ 5 on the Molnar scale (Molnar, 1971). This is the reason why some authors argue that the BL diameter is more reliable (e.g., Wolpoff, 1979). Additionally, this method has been shown to have a low intraobserver error because it employs a reference plane that can be easily identified by different observers. Unfortunately, not all of the Arago specimens were available for

Table 1
Summary of the SH dental sample by tooth class and side.

		SH		Arago	
		Maxillary	Mandibular	Maxillary	Mandibular
I1	Right	14	15	1	2
	Left	17	15	2	0
I2	Right	14	16	1	0
	Left	13	16	2	2
C	Right	16	15	1	4
	Left	15	17	1	4
P3	Right	13	18	2	4
	Left	17	19	1	0
P4	Right	14	19	1	2
	Left	13	18	0	3
M1	Right	16	20	3	4
	Left	13	22	1	1
M2	Right	16	21	1	7
	Left	14	21	3	2
M3	Right	17	23	1	2
	Left	13	20	1	2

measurement-taking. The number of available Arago specimens, however, was significant enough to offer clear insights about the similarities and differences between both samples (Table 2). We have measured the right antimeres, but the left ones were included in the sample when the right was absent (unilateral count, see Scott, 1980). The computed crown area (CCA = MD x BL) was used in some comparisons.

Statistical analyses of the MD and BL diameters were performed using the SPSS software (v. 18.0, SPSS Science, Inc.). When groups were represented by sample sizes greater than three specimens, the non-parametric Mann-Whitney *U* test was employed to examine differences in the crown size among the SH and Arago samples. Means were determined to be significantly different at the $p = 0.05$ level (*) and very significantly different at the $p = 0.01$ level (**).

Because our aim is not to provide a detailed external morphological description, we have focused our observations on those crown features with a contrasted taxonomic signal (e.g., Bermúdez de Castro, 1988; Bailey, 2002a, Bailey, 2002b; Gómez-Robles et al., 2008; Martín-Torres et al., 2007, 2012). When necessary, some morphological radicular features have been used. The descriptive terminology used in this report derives from the following sources: Carlsen (1987), Martín-Torres et al. (2007), Martín-Torres et al. (2008), Scott and Turner (1997), Tobias (1991), Turner et al. (1991), and see Table 4 in Martín-Torres et al. (2012), which includes a modified version of the scoring from the Arizona State University Dental Anthropological System (ASUDAS).

4. Results

4.1. Upper central incisors (I^1)

All the I^1 s from SH show some degree of a shovel shape, although it is generally moderate (ASUDAS grades 1 to 4). The large, round basal eminence occupies one to two-thirds of the lingual surface, thus reducing the lingual fossa associated with the shovel shape. The basal eminence takes the form of a moderate tuberculum dentale (grade 3) in the shape of enamel folds and depressions in only 25% of the specimens (Martín-Torres et al., 2012). From the occlusal view the lingual convexity is remarkable, presenting the highest degrees in all of the I^1 s (grades 4 and 5).

Unfortunately, two of the three I^1 s from Arago (Arago 51 and Arago 61) exhibit an extensive dentine patch (grade 5), thus preventing us from discerning the main features of these teeth. Notwithstanding, the three specimens are characterized by extreme robusticity (Table 3), as is usually the case in the anterior teeth of Eurasian Pleistocene populations (Martín-Torres et al., 2006). Arago 51 and Arago 61 show a large, round basal eminence, whereas Arago 110 exhibits a large tuberculum dentale with a free apex (ASUDAS grade 6). The marginal ridges of this tooth are extremely thickened and invade the lingual fossa, delimiting a lingual groove, whereas in Arago 51 and Arago 61 the marginal ridges seem to be less developed. The lingual convexity is also marked, but less pronounced than in the SH I^1 s (ASUDAS grade 3).

The single root of the SH I^1 s is long, robust and subtriangular in

Table 2
Descriptive statistics of the mesiodistal (MD) and buccolingual (BL) diameters for the upper and lower permanent teeth from Atapuerca-SH and Arago. Mann-Whitney *U* test for differences in dental diameters between Sima de los Huesos (SH) and Arago teeth. Means were determined to be significantly different at $p = 0.05$ level (*) and very significantly different at $p = 0.01$ level (**).

		Atapuerca-SH				Arago				Mann-Whitney U
		N	X	S.D.	Range	N	X	S.D.	Range	P-value
I^1	MD	20	9.54	0.49	8.7–10.6	3	(9.93)	–	9.9–10.0	0.108
	BL	22	7.71	0.35	7.1–8.8	3	8.96	–	8.9–9.0	0.006**
I^2	MD	19	7.75	0.31	7.2–8.2	3	8.13	–	7.9–8.4	0.084
	BL	20	7.74	0.28	7.3–8.2	3	8.56	–	8.2–8.8	0.009**
C^1	MD	22	8.62	0.35	8.1–9.6	2	8.65	–	8.6–8.7	–
	BL	24	9.77	0.52	8.8–10.7	2	10.3	–	10.0–10.6	–
P^3	MD	19	7.82	0.56	7.2–8.9	2	8.70	–	8.3–9.1	–
	BL	19	10.42	0.69	9.2–11.8	2	11.45	–	10.9–12.0	–
P^4	MD	18	7.55	0.54	7.0–8.8	1	8.6	–	–	–
	BL	19	10.25	0.68	9.1–11.5	1	11.4	–	–	–
M^1	MD	17	11.08	0.69	9.9–12.3	3	11.80	–	10.6–12.8	0.289
	BL	17	11.58	0.65	10.3–13.0	3	13.30	–	12.4–14	0.013*
M^2	MD	19	9.95	0.91	8.1–11.6	3	12.03	–	11.3–12.5	0.008**
	BL	19	12.20	0.73	11.0–13.8	3	14.55	–	13.6–16.2	0.010*
M^3	MD	21	8.60	0.57	7.4–9.3	2	9.6	–	9.6	–
	BL	22	11.47	0.90	10.1–13.0	2	12.3	–	12.3	–

		Atapuerca-SH				Arago				
		N	X	S.D.	Range	N	X	S.D.	Range	
I_1	MD	19	5.52	0.26	4.8–6.0	2	6.40	–	6.1–6.7	–
	BL	19	6.54	0.29	5.9–7.1	2	7.50	–	7.3–7.7	–
I_2	MD	18	6.56	0.33	6.1–7.3	2	6.95	–	6.9–7.0	–
	BL	18	7.31	0.39	6.6–8.1	2	7.77	–	7.7–7.8	–
C_1	MD	21	7.62	0.39	6.9–8.5	8	8.15	0.53	7.2–9.0	0.014*
	BL	20	8.56	0.66	7.3–10.1	8	9.38	0.40	9.0–10.0	0.006**
P_3	MD	20	7.90	0.39	7.2–9.0	4	8.30	0.61	7.5–9.0	0.197
	BL	20	8.91	0.57	8.2–10.0	4	9.90	1.09	9.1–11.5	0.032*
P_4	MD	21	7.21	0.43	6.5–7.7	4	8.42	0.82	7.5–9.3	0.006**
	BL	22	8.57	0.60	7.2–10.1	4	10.17	1.02	9.0–11.5	0.005**
M_1	MD	23	11.18	0.52	10.3–12.1	4	12.20	1.11	11.0–13.5	0.064
	BL	23	10.45	0.50	9.6–11.3	4	11.55	0.97	11.1–13.0	0.013*
M_2	MD	25	10.98	0.56	9.9–12.2	7	12.83	1.56	11.1–14.9	0.002**
	BL	25	10.22	0.58	9.2–11.5	6	11.71	1.25	10.5–13.9	0.003**
M_3	MD	26	11.35	0.69	10.0–12.7	4	12.35	1.35	10.5–13.5	0.134
	BL	26	9.80	0.70	8.6–11.3	4	10.95	1.35	9.7–12.6	0.067

Table 3

Main morphological differences and similarities between the Arago and SH dental samples. In this table no assessment of the status (primitive or derived) of the features is made (see main text for further details).

	Arago	Atapuerca-SH
I ¹	-Moderate shovel shape -Marked labial convexity -Massive and robust ++	-Moderate shovel shape -Strong labial convexity -Massive and robust +
I ²	-Conspicuous shovel shape -Triangular shovel shape -Marked labial convexity -Massive and robust ++	-Conspicuous shovel shape -Triangular shovel shape -Strong labial convexity -Massive and robust +
C ¹	-Moderate to marked shovel shape -Massive and robust ++	-Moderate to marked shovel shape -Massive and robust +
P ³ & P ⁴	-Lingual cusp ≥ buccal cusp -Asymmetry of the crown -Broad occlusal polygon -Inclination of the sagittal groove -Upper half of the buccal face moderate to strongly bulging -No buccal cingulum	-Lingual cusp < buccal cusp -Trend to symmetry of the crown -Small and centrally positioned occlusal polygone -Short and rectilinear sagittal groove -Upper half of the buccal face moderate to strongly bulging -No buccal cingulum
M ¹	-Large hypocone and metacone -Approximately squared occlusal polygone, and regular contour. -No cusp protrudes on the external outline.	-Large hypocone and metacone -Rhomboidal contour, relative displacement of the lingual cusps. -Protrusion in the external outline of a large bulging hypocone.
M ²	-Large hypocone and metacone -Complicated pattern of enamel crenulations and secondary fissurations.	-Reduced hypocone and metacone -General smooth occlusal relief.
M ³	-Strongly reduced hypocone and metacone.	-Strongly reduced (or absent) hypocone and metacone
I ₁	-Traces of a shovel shape -Moderate labial convexity -Massive and robust ++	-Traces of a shovel shape -Moderate labial convexity -Massive and robust +
I ₂	-Traces of a shovel shape -Pronounced labial convexity -Massive and robust ++	-Traces of a shovel shape -Moderate labial convexity -Massive and robust +
C ₁	-Moderate-to-remarkable shovel shape. -No buccal cingulum -Massive and robust ++	-Moderate-to-remarkable shovel shape. -No buccal cingulum -Massive and robust +
P ₃	-Symmetrical contour, with medium -sized talonid. -Generally small and bulbous lingual cusp -Large occlusal polygone. -Transverse crest joining protoconid and metaconid. -Incipient buccal cingulum in Arago 13 -Tomes root in Arago 13	-Symmetrical contour, without talonid protrusion. -Canine-like aspect. -Small and bulbous lingual cusp. -Narrow and lingually located occlusal polygon. -Transverse crest joining protoconid and metaconid. -No buccal cingulum -Single and mesiodistally compressed root.
P ₄	-Asymmetry of the occlusal contour due to development of the talonid and its distolingual projection. -Reduced occlusal polygon. -Transverse crest joining protoconid and metaconid. -Metaconid mesially displaced. -No buccal cingulum. -2R: MB + DL in Arago 13.	-Asymmetry of the occlusal contour due to development of the talonid and its distolingual projection. -Reduced occlusal polygon. -Transverse crest joining protoconid and metaconid. -Metaconid mesially displaced -No buccal cingulum -One single root.
M ₁	-The five main cusps are well-developed. -“+” groove pattern, frequent. -Hypoconulid buccodistally placed -Concomitant presence of deep anterior fovea and middle trigonid crest.	-Absence of hypoconulid in some specimens. -Near 50%, “+” and X groove pattern. -Hypoconulid buccodistally placed -Concomitant presence of deep anterior fovea and middle trigonid crest.
M ₂	-The five main cusps are well-developed. -Hypoconulid buccodistally or distally placed. -“+” groove pattern, frequent. -Frequent presence of C6 and/or C7 -Concomitant presence of deep anterior fovea and middle trigonid crest.	-About 30% of M ₂ s lack hypoconulid, and in near 40% the cusp is reduced. -When present, the hypoconulid is distally placed. -“+” groove pattern, frequent. -Frequent presence of C6 and/- -Concomitant presence of deep anterior fovea and middle trigonid crest.
M ₃	-The five main cusps are well-developed. Hypoconulid reduced Frequent presence of C6 and/or C7. -“+” or X groove pattern. -Concomitant presence of deep anterior fovea and middle trigonid crest.	-Reduction or absence of the hypoconulid. -Atypical shape of the M ₃ s, but C6 and or C7. -23.5% of specimens with Y groove pattern. -Concomitant presence of deep anterior fovea and middle trigonid crest.

transverse section. The root of the Arago I¹s is also long, sub-triangular, but particularly massive. In summary, although the SH I¹s are robust and follow the characteristic Eurasian pattern (Martinón-Torres et al., 2006; Martinón-Torres et al., 2007), they clearly resemble those of Neanderthals (Bermúdez de Castro, 1988; Martinón-Torres et al., 2012). The Arago I¹s show the same morphology, but are especially massive and robust.

It is a constant in all the dental classes that the Arago teeth are generally larger than those from SH. The difference between the

mean value of the MD diameter of the Arago I¹s sample and that of the SH is not statistically significant ($p > 0.05$) (Table 2). However, the difference between the average of the BL diameter is statistically significant ($p > 0.01$). It is important to note that not only may the small size of the Arago sample be influencing the results, but also the interproximal wear, particularly pronounced in two of the three Arago I¹s. It is also worth noting that the BL dimensions of the three Arago I¹s are out of the variation range of the SH sample.

4.2. Upper lateral incisors (I^2)

The marginal ridges of the SH I^2 s are extremely thickened. They invade the lingual face, delimiting a lingual groove. This groove is either centred or somewhat deviated mesially. Thus, all the SH I^2 s exhibit a conspicuous shovel shape, and in some cases they present the so-called triangular shovel shape, with a strong development of the marginal ridges and a deep lingual groove, associated with the strong expression of the lingual convexity (Table 3). The presence of the tuberculum dentale is very frequent in the sample (89.5%), and about 58% of the specimens express a moderate (ASUDAS grade 3) to strong (grade 6) expression of this feature (Martín-Torres et al., 2012). This feature may be continuous with the marginal ridges or is separated by accessory mesial and distal grooves. All the I^2 s present the maximum expression of the labial convexity (ASUDAS grade 5).

Arago 60 is very worn (grade 5) and the crown is missing some fragments, but Arago 25 and Arago 111 clearly show the morphology of this dental class. The shovel shape is pronounced in Arago 25 (ASUDAS grade 5), with the marginal ridges delimiting a clear lingual groove, and is marked in Arago 111 (ASUDAS grade 6). This tooth is also worn (grade 5), but an enamel fold delimited by mesial and distal grooves is still visible. In Arago 25 there is strong ridging in the lingual face (ASUDAS grade 3), (Fig. 1), whereas Arago 111 shows the maximum expression of tuberculum dentale (ASUDAS grade 6) in the form of a strong cusp with a free apex. The three Arago I^2 s show a pronounced labial convexity (ASUDAS grade 5).

The root of the SH and Arago specimens is long, subtriangular in section, and robust (particularly in the Arago I^2 s). As with the I^1 s, the lateral incisors from these sites are massive, following the characteristic Eurasian pattern (Martín-Torres et al., 2006; Martín-Torres et al., 2007).

Also as in the case of the I^1 s, the difference between the MD diameter of the Arago and SH I^2 s samples is not statistically significant ($p > 0.05$) (Table 2). However, the difference between the BL diameters of the two samples is statistically significant ($p < 0.01$) (see Fig. 2). Again, the small size and the interproximal wear of the Arago sample need to be taken into account.

4.3. Upper canines (C^1)

All the SH C^1 s exhibit moderate-to-well-marked shovel shapes (ASUDAS grades ≥ 3), with thickened mesial and distal marginal ridges (Martín-Torres et al., 2012), the mesial ridge generally being thicker than the distal one. Between these ridges and the canine essential ridge there are clear marginal grooves. It is worth mentioning that only 10% of SH canines present a simple basal eminence, whereas the other specimens exhibit a more or less developed tuberculum dentale (ASUDAS grades 2 to 6). One third of the C^1 s show a well-differentiated tuberculum dentale with a free apex, and half of the specimens express the distal accessory ridge (Martín-Torres et al., 2012). The buccal face presents a moderate basal swelling, but the cingulum is not expressed. This face is strongly inclined from the basal eminence to the incisal edge. The root is single, long and robust, showing a longitudinal groove running along the medial and distal thirds of both the mesial and distal faces. The section of the root is oval, the widest part corresponding to the buccal face. In lateral view the buccal border is arched, with the apical third clearly lingually inclined.

The Arago sample comprises two specimens, Arago 59 and Arago 112. These teeth exhibit extensive dentine patches (grade 5), so most of the morphological features are lost. They preserve traces of the marginal ridges, suggesting that these teeth had a marked shovel shape (ASUDAS grades 3 or 4). It was not possible to estimate the presence/absence of the distal accessory ridge. The basal

eminence adopts the form of a prominent basal swelling, but there is no tuberculum dentale. In lateral view, the two canines show a moderate basal swelling, but the cingulum is absent. The labial surface shows a strong inclination from the basal swelling to the incisal plane. The root is also single, long and robust. It is mesio-distally compressed, with the buccal face being broader than the lingual. In lateral view, the lingual side is strongly arched. A wide longitudinal groove differentiates the buccal and lingual parts of the root on both the mesial and distal faces.

The mesiodistal dimensions of the Arago C^1 s are similar to the average for the SH C^1 s, whereas the buccolingual diameter of the Arago specimens is greater than the average for the SH sample, but, in any case, within the range of variation of this sample. In particular, the BL dimension of Arago 59 is similar to the broadest SH upper canine.

4.4. Upper third premolars (P^3)

In all the SH P^3 specimens the buccal half of the crown is broader than the lingual one (Table 3). The buccal cusp is invariably larger and taller than the lingual one. In 80% of the specimens the apex of this cusp is mesially displaced with regard to the apex of the buccal one (Martín-Torres et al., 2012). The sagittal fissure is usually short and rectilinear, delimiting small accessory tubercles. In lateral view, the upper half of the buccal face shows a moderate-to-strong bulging, but without signs of cingulum. The essential ridge of the buccal cusp is bifurcated in 23.5% of cases, whereas the essential ridge of the lingual cusp is bifurcated in 10.5% of cases (Martín-Torres et al., 2012). No enamel wrinkles and secondary fissures are present in the unworn or almost unworn SH P^3 s.

The Arago sample includes three specimens, two of them (Arago 16 and Arago 36) belonging to cranium 21. Arago 7 (Fig. 1) is unworn and the enamel is moderately crenulated, whereas Arago 16 is worn, exhibiting wide dentine patches (grade 4). In contrast to that observed in the SH P^3 s, the buccal cusp is only a little greater or similar (Arago 7) than to the lingual one. The sagittal groove is oblique with respect to the mesiodistal axis of the premolar, and the mesial fovea is located buccally with respect to this axis. In Arago 7 the essential ridge is bifurcated in both the buccal and lingual cusps. The upper half of the buccal face is moderately bulging in Arago 16 and strongly bulging in Arago 7. The mesially buccal bulging of this tooth contributes to the asymmetrical aspect of the crown.

The geometric morphometric study of the occlusal outline of the P^3 s carried out by Gómez-Robles et al. (2011) found an extensive overlap in the area of distribution of the morphospace of the relative warp analysis (principal components, PC1 and PC2) of different hominin species, with some morphological trends. For instance, the reduction of the lingual cusp and the symmetry (or a slight asymmetry) of the crown is particularly present in modern humans, the SH hominins and Neanderthals. Moreover, the place of most SH P^3 s in the positive area of the PC1 and in the negative area of the PC2 is determined by some asymmetry of the crown and a small and centrally positioned occlusal polygon, which includes the tips of the protocone and the paracone and the place of the two foveae. The two Arago specimens are placed in the negative score of the PC1 and PC2, far from the SH P^3 s, due to the large lingual cusp and inclination of the sagittal groove. These features may be considered as a part of the primitive morphology for the hominin clade, as it is shared with most of the Plio-Pleistocene P^3 s analysed by Gómez-Robles et al. (2011).

The MD and BL dimensions of the two Arago specimens are greater than the SH mean values, although within the range of variation of the SH sample (Table 2, and Fig. 2).

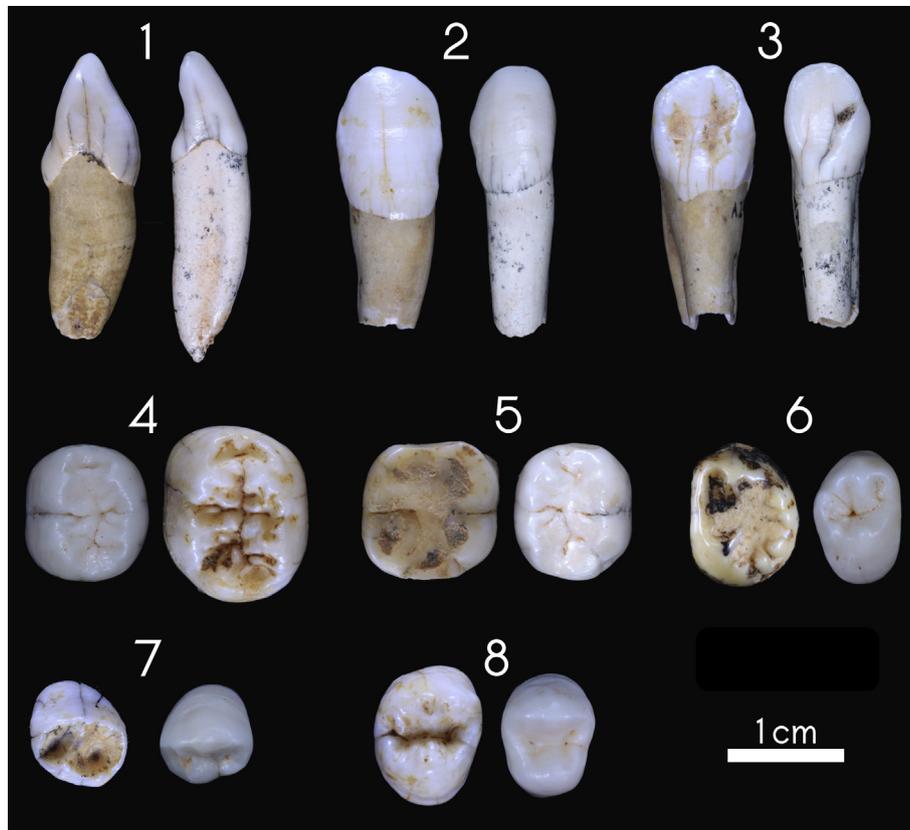


Fig. 1. Comparison of different anatomical views of the Arago and Sima de los Huesos teeth (left side in every pair). 1) Distal view of the I_2 s (Arago 25 and AT-957); 2) buccal view of the C,s (Arago 24 and AT-2165); 3) lingual view of these same lower canines; 4) occlusal view of the M_2 s (Arago 32 and AT-941); 5) occlusal view of the M_1 s (Arago 40 and AT-829); 6) occlusal view of the M_3 s (Arago 103 - AT-601); 7) occlusal view of the lower P_3 (Arago 71 - AT-2027); 8) occlusal view of the upper P^3 (Arago 7 - AT-2399). Scale bar = 1 cm.

4.5. Upper fourth premolars (P^4)

The occlusal outline of the SH P^4 s is more symmetrical than that of the P^3 s. The buccal cusp is generally larger and somewhat higher than the lingual one (Table 3). But the size difference between the two cusps is clearly less pronounced than in the P^3 s. In 73.7% of cases, the tip of the lingual cusp is mesially placed with regard to the buccal cusp (Martín-Torres et al., 2012). In the remaining P^4 s both tips are centred. Mesial and distal accessory tubercles are frequent. The buccal essential ridge is bifurcated in one third of the sample, whereas 50% of the specimens show bifurcation of the lingual essential ridge. The upper half of the buccal face is moderately swollen, but no traces of cingulum are present.

The only P^4 from Arago (Arago 26) belongs to the same individual as Arago 7. This tooth is unworn and all occlusal morphological features are evident. The lingual cusp is clearly greater than the buccal one, a feature which is absent in the SH P^4 s. The sagittal ridge is oblique in terms of the buccolingual axis of the tooth, and the distal half of the crown is somewhat expanded, presenting a distobuccal cusp. Like Arago 7, the crown is moderately crenulated. The upper half of the buccal face is moderately swollen. Note that the MD and BL dimensions of this tooth (Table 2) are similar to the highest values in the SH range.

The geometric morphometric study of the occlusal outline of the P^4 s carried out by Gómez-Robles et al. (2011) shows no clear pattern for most hominins, except for *H. sapiens*. There is an overlap between different hominin species in the negative region of the morphospace for the PC2 of the relative warp analysis, and a large distribution along the PC1, without a clear pattern. In general, the P^4 s of most hominins exhibit a more-or-less expanded distolingual

region, a buccolingually reduced and mesiodistally broad occlusal polygon. This may be a primitive pattern for hominins, whereas *H. sapiens* exhibits a derived condition, with symmetrical P^4 s supplied with a reduced lingual cusp and a short sagittal groove (mesial and distal foveae very close together). Arago 26 is, in terms of morphospace, placed far away from these hominins, and shares its morphology with some early *Homo*, *Australopithecus* and *Paranthropus* in the positive regions of both PC1 and PC2. This position is mainly due to the large lingual cusp and an expanded distolingual region.

4.6. Upper first molars (M^1)

The SH M^1 s are characterized by a large or very large hypocone and a large or very large metacone (ASUDAS grades 4 and 5). The reduction (ASUDAS grade 3) is exceptional in only one specimen in this sample. 56.3% of the specimens exhibit a C5 or metaconule, and the continuous crista obliqua is expressed in 100% of the M^1 s (Martín-Torres et al., 2012). The mesial marginal accessory tubercles are also frequent (50%), and the Carabelli complex is present in its negative expression (ASUDAS grade 1) in 56% of the specimens (Martín-Torres et al., 2012).

The three Arago specimens also show a large or very large hypocone and metacone. The metaconule and the mesial marginal accessory tubercle is only expressed in Arago 31, although dental wear may be obscuring their presence in the case of Arago 21 and Arago 54. Arago 31 lacks a continuous crista obliqua, which is present in Arago 21 and Arago 54. The Carabelli complex is expressed in the three specimens: in Arago 21 there is a negative expression of this feature (ASUDAS grade 1), whereas a medium-

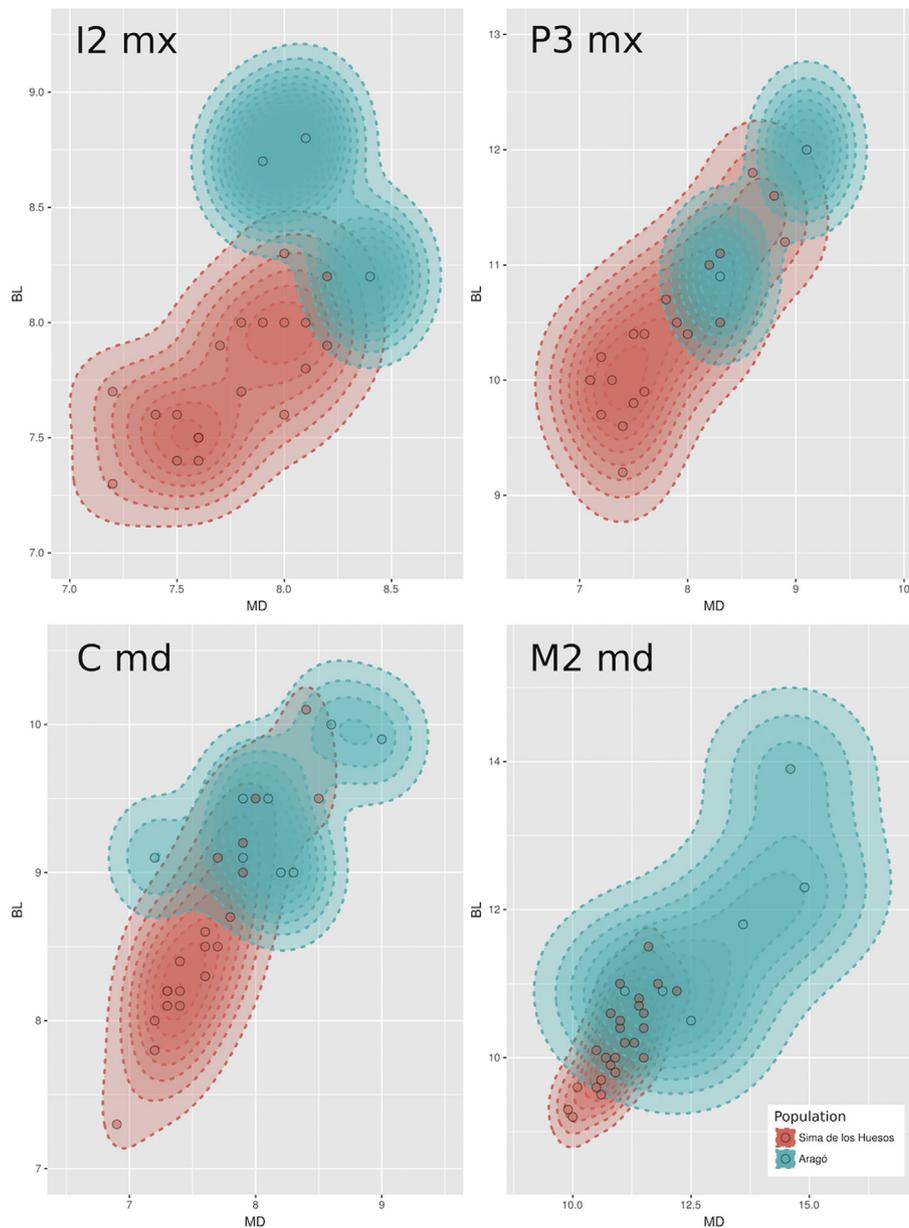


Fig. 2. Scatterplots and density areas of the mesiodistal (MD) and buccolingual (BL) diameters of the upper lateral incisors (top left), upper third premolars (top right), lower canines (bottom left) and lower second molars (bottom right) from SH (red) and Arago (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sized cusp with a free apex (ASUDAS grade 5) is present in Arago 31 and Arago 54. In Arago 31 there is very crenulated enamel, with well-developed crests and fissures.

The expression of these and other features, like the parastyle and the transverse crest, are very variable in the hominin fossil record. The C5 is generally more frequent in early *Homo* and *Australopithecus* (Martín-Torres et al., 2012), and the presence of positive expressions of the Carabelli complex tends to also be frequent in these hominins. However, both the C5 and the Carabelli cusp are also present and frequent in all hominins, including modern humans (e.g. Bermúdez de Castro and Martínez, 1986; Bermúdez de Castro, 1989; Hanihara, 1967; Harris and Bailit, 1980; Scott et al., 1983). Therefore, all these features are of limited diagnostic utility. However, the studies carried out by Bailey (2004) and by Gómez-Robles et al. (2007) on the geometric morphometrics of the M¹s has shed light on the diagnostic value of this tooth when

distinguishing between certain hominins. The general shape of the M¹s and the spatial configuration of the main cusps are captured by this method, which shows that *H. neanderthalensis* exhibits a particular morphology characterized by a rhomboidal contour, a relative displacement of the lingual cusps, and protrusion in the external outline of a large bulging hypocone (Table 3). It is important to note that this configuration has also been observed in the SH M¹s, and in *H. antecessor*, and the Steinheim and Pontnewydd specimens (Compton and Stringer, 2012, 2015). The canonical variates analysis carried out by Gómez-Robles et al. (2007) emphasizes the morphological similarity between the Middle Pleistocene specimens, like SH, Steinheim and Pontnewydd, and the Neanderthals. It is not possible to distinguish among them using the particular derived morphology of the M¹s. In contrast, all the analyses carried out by Gómez-Robles et al. (2007) showed that three Arago M¹s (Arago 9, Arago 21 and Arago 54) display the

hypothetical primitive configuration. These specimens exhibit an approximately square occlusal polygon and a regular contour in which no cusp protrudes on the external outline. This shape is shared by *Australopithecus*, early *Homo* and modern humans (Gómez-Robles et al., 2007).

The crown measurements of the three Arago M¹s are considerably larger than those of the majority of the SH specimens (Table 2). Particularly, the BL diameter of two of the Arago M¹s is greater than that of the maximum value of the SH sample, and the differences between the average of the two samples are statistically significant ($p < 0.05$).

4.7. Upper second molars (M²)

The reduction of the hypocone in the SH M²s is remarkable (Table 3). In 33.4% of M²s the hypocone is absent or residual, only detectable by a short deep distal groove. In 44.5% of cases, the hypocone is small (ASUDAS grade 2). The maximum classification (grade 5) is not present in this particular sample (Martinón-Torres et al., 2012). The metacone is also reduced, with more than 60% of the specimens exhibiting grades 2 and 3 (Martinón-Torres et al., 2012). A continuous crista obliqua is very frequent (83.3%), whereas 33.4% express a moderate C5. The Carabelli cusp is absent, and only slight depressions and fissures could correspond to a negative expression of the Carabelli complex (Martinón-Torres et al., 2012).

The Arago sample includes four specimens, two of which belong to the Arago 21 cranium. The right M² shows a square outline, with a large hypocone and metacone. The left antimeres exhibits a particularly large hypocone and a more reduced metacone. The crista obliqua is present, but interrupted by the transversal groove in both the right and left antimeres. They display a smooth surface, without particular reliefs except a medium-sized C5 and a small distal cusp at the region of the metacone. In contrast, Arago 14 shows a clear rectangular crown outline, a large C5, a large Carabelli cusp (ASUDAS grade 7), a more reduced hypocone (ASUDAS grade 4), as well as a complicated pattern of crenulations and secondary fissures. The size and morphological aspect of this tooth is clearly primitive. The occlusal outline of Arago 45 is also rectangular, but wear has erased most reliefs and the dentine occupies a large portion of the lingual part of the crown. The crown dimensions are considerably larger than those of the SH sample (Table 2).

The geometric morphometric study of the occlusal outline of the M²s carried out by Gómez-Robles et al. (2012) reveals a general overlap in the relative warp analysis of most hominins species included in this study. However, the presence of a well-developed hypocone and metacone place the Arago 14 and Arago 21 specimens in the negative half for both the PC1 and PC2 together with some *H. erectus*, *H. habilis*, *Australopithecus*, *Paranthropus* and *Dmanisi*, whereas the SH specimens are placed in the positive half for both the PC1 and PC2, and are generally found mixed with *H. neanderthalensis* and *H. sapiens*. That is, it seems that the Arago M²s exhibit a primitive shape, in contrast with the derived condition presented by the SH specimens. Nevertheless, the absence of the hypocone in the M²s from SH is particularly frequent compared to Neanderthals and modern humans (Bailey, 2002b; Martinón-Torres, 2006; Martinón-Torres et al., 2012). This morphology may reflect an exclusive characteristic of the SH population (Gómez-Robles et al., 2012) in the same way that the small dimensions of these teeth represent an anomaly for the populations of the Middle Pleistocene (Bermúdez de Castro, 1993).

In line with the cusp reduction, the SH M²s are considerably smaller than those from Arago (Table 2). Again, the BL diameters of the three Arago M²s are equal to or larger than the maximum value obtained in the SH sample, but the differences between the

averages of the two samples are not statistically significant ($p > 0.05$). Obviously, the small size of the Arago sample may lie behind this particular result. In contrast, the difference between the mean values of the MD diameter is statistically significant ($p < 0.05$).

4.8. Upper third molars (M³)

The hypocone of the SH M³s is practically absent in all of the M³s. This cusp is minimally represented (ASUDAS grades 1 and 2 in about 43% of the specimens) (Martinón-Torres et al., 2012). The metacone is also remarkably reduced (grades 1 and 2) in 80% of the specimens. That is, most SH M³s exhibit a morphology similar to that of the upper premolars. The Carabelli complex (grades 1 to 3) is present in 20% of the cases (Martinón-Torres et al., 2012). Although the roots of many SH M³s were still growing, the total fusion or joining of the three roots by a thick lamina is a common occurrence (Martinón-Torres et al., 2012).

The Arago sample includes only two M³s. The right M³ of cranium 21 and Arago 103 (Fig. 1) show a rectangular crown outline, with a reduced distolingual corner. The metacone and hypocone are remarkably reduced, and formed by a succession of five small cusps, well defined and separated by grooves. In Arago 103 the three roots are joined forming a strong column-like anchorage of the tooth.

The geometric morphometric study of the occlusal outline of the M³s carried out by Gómez-Robles et al. (2012) again highlights the strong morphological reduction of the distal cusps in the SH hominins (Table 3), which is greater than that of Neanderthals and modern humans. However, in this case the two Arago M³s are not particularly different from those from SH. According to this geometric morphometric analysis, the primitive condition exhibited for *Australopithecus*, *Paranthropus*, and early *Homo* includes the presence of the four main cusps, with a broader mesiodistal diameter of the lingual half, or a square shape. Arago and SH present this derived condition, with a clear reduction of the distal half of the crown.

The crown dimensions of the Arago M³s are greater than those of the majority of the SH M³s (Table 2).

4.9. Lower first incisors (I₁)

The SH I₁s show a generally smooth lingual surface, without signs of remarkable reliefs. The basal swelling is slight in only 26.3% of cases, whereas in the rest of the specimens this surface is smooth (Martinón-Torres et al., 2012). None of the I₁s exhibit tuberculum dentale, lingual fossae or pronounced marginal ridges. Traces of a shovel shape (grade 2) are present in only two specimens. In the rest of the I₁s the labial convexity (grades 2 to 4) gives the false impression of a shovel shape. The labial convexity is slight to moderate (grades 2 and 3) in most cases, and pronounced in only one specimen (Table 3).

The Arago sample includes three specimens, although one of them (Arago 30) is represented only by a crown fragment. The two complete Arago specimens are large and their measurements are out of the range of the SH sample (Table 2). However, the morphology of the Arago teeth does not differ from that observed at SH. The buccal convexity of Arago 76 and Arago 100 is moderate. In Arago 30 it is possible to appreciate a grade 1 convexity. In Arago 76 there is a remarkable central ridge, representing the only relevant feature of the lingual face.

The two Arago specimens are larger (MD and BL) and out of the range of the SH sample (Table 2).

4.10. Lower second incisors (I_2)

The lingual face of the SH I_2 s is also generally smooth. The basal eminence is greater than in the I_1 s, with 73.7% of cases exhibiting a grade 1 tuberculum dentale (Martínón-Torres et al., 2012). According to these authors, 42.2% of cases show traces of a shovel shape (grade 2), whereas 21.1% of the cases show grade 3 of this feature. The buccal convexity is moderate (47% of cases) or weak (52.6%) (Martínón-Torres et al., 2012).

The two Arago specimens exhibit a similar morphology, although one I_2 has a pronounced buccal convexity of grade 4. Both Arago 81 and Arago 97 show a strong basal eminence. The crown dimensions of these teeth are larger than those of most SH I_2 s (Table 2).

The measurements for the two Arago I_2 s are greater than the averages of the SH sample, although within the range of variation of this sample (Table 2 and Fig. 2).

4.11. Lower canines (C_1)

The SH C_1 s show an incisor-like morphology, with more-or-less developed mesial and distal marginal ridges. The degree of a shovel shape ranges from moderate (ASUDAS grades 1 and 2) to marked (ASUDAS \geq grade 3). The marked expression is present in close to 80% of the specimens (Martínón-Torres et al., 2012). The distal marginal ridge is generally thicker than the mesial one, and its length is restricted to the lower third of the crown. In some cases, this ridge adopts the aspect of a tubercle. The mesial canine ridge is absent. The lingual aspect of the lingual face is smooth, without an expression of the essential ridge, and weak signs of the distal accessory ridge in 25% of the specimens (Martínón-Torres et al., 2012). No tuberculum dentale is present in any of the SH specimens, and about one third of them exhibit a moderate and round basal eminence. There is no buccal cingulum. The single root is long and robust, presenting a deep longitudinal groove running along the mesial and distal faces. One exception is AT-2438. This tooth shows a deep mesial groove, which differentiates two clear radicals, one lingual and one buccal.

The Arago C_1 sample includes eight specimens. Some of them (Arago 84, 87, and 108) are severely worn (grade 5) meaning it has not been possible to evaluate certain of their features. All C_1 s exhibit a moderate-to-remarkable shovel shape, and at least 70% show grades ≥ 3 in the ASUDAS classification. This feature is shared with the SH sample, and Neanderthals, whereas it is less frequent in recent *H. sapiens* (Martínón-Torres et al., 2012). In Arago 77 the distal marginal ridge adopts the shape of a small cusp. In other specimens both the mesial and distal marginal ridges show an approximately similar development. As in the SH sample, the mesial canine ridge is absent, a feature only developed in some Neanderthal specimens (Martínón-Torres et al., 2012). None of the specimens present a developed tuberculum dentale with free apex, although a mild lingual basal eminence is common in all of them. The relief of the lingual face is more complicated than that of the SH sample by the presence of a moderately developed essential ridge, which can be noted in the less worn specimens (Arago 24, 77, 94, and 101). A barely perceptible distal accessory ridge is present in Arago 24 (Fig. 1). There is no buccal cingulum in any of the Arago C_1 s. The single root is long and robust, with the buccal and lingual radical well differentiated by a deep longitudinal groove, running along the mesial and distal faces (Table 3).

The difference between the mean values of the Arago and SH C_1 s samples for both the MD and BL diameters are statistically significant ($p < 0.05$) (Table 2 and Fig. 2).

4.12. Lower third premolars (P_3)

All the SH P_3 s show a characteristic canine-like aspect. The buccal cusp (protoconid) is large and high, whereas the lingual cusp (metaconid) is small, low and bulbous. The broad mesial and distal marginal ridges descend from the apex of the buccal cusp and curve until reaching the lingual cusp. A fine cleft separates this cusp either from the mesial marginal ridge or from the distal marginal ridge. The combined presence of both mesial and distal clefts is also frequent. A transverse crest joining the protoconid and metaconid is very frequent (95%) (Martínón-Torres et al., 2012). This morphology is also common in *H. neanderthalensis* P_3 s (Bermúdez de Castro, 1988; Martínón-Torres et al., 2012). Single rooted P_3 s are the norm in the SH sample, except in the case of the AT-172 mandible, which preserves a part of the root inside the socket of the P_3 . The visible part of the root of this tooth exhibits a deep mesiolingual indentation. As a consequence, the root shows a large buccal component and a small distolingual component. The roots are connected, but have independent canals, the buccal one having a crescent shape.

The P_3 from the Arago 13 mandible is very large, but its morphology is essentially similar to that of the SH P_3 s. The metaconid, which is connected with the protoconid by a transverse crest, is low and bulbous and the occlusal outline is almost symmetrical. However, the occlusal polygon is large and centred, as in Arago 75 (Gómez-Robles et al., 2008). Although Arago 75 exhibits a medium-sized talonid, its morphology also resembles that of the SH P_3 s. The same applies to the P_3 from the Arago 119 mandible. In contrast, the metaconid of Arago 71 is not bulbous and is clearly mesially displaced (Fig. 1). This cusp is connected via a transverse crest to the protoconid. There are no mesial and distal clefts differentiating the metaconid from the mesial and distal marginal ridges, and the latter forms a medium-sized talonid. The occlusal polygon is broad and the occlusal outline is more asymmetrical than the other Arago specimens. In the P_3 from the Arago 89 mandible the lingual face is bulbous, but the tip of the metaconid is also mesially displaced and connected with the protoconid via a transverse ridge. As in Arago 75, the distal marginal ridge forms a medium-sized talonid and the occlusal outline is asymmetrical. We only have information available about the roots of Arago 71 and Arago 13. In Arago 71 we noted that only 7.6 mm of the root is formed, and at this level no bifurcation is observed. A CT of the Arago 13 mandible shows that the root of the P_3 has two canals (Tomes' root), one buccal and one lingual, which bifurcate about 8.0 mm from the neck of the tooth. A slight mesiolingual indentation is observed near the apex.

Gómez-Robles et al. (2008) defined the shape of the P_3 s in hominins using geometric morphometric analyses. These authors used four landmarks: 1) the tip of the protoconid; 2) the deepest point of the distal fovea, or the intersection of the median longitudinal fissure with the distal fovea-fissures/transverse fissures (when present); 3) the tip of the metaconid; 4) the deepest point of the mesial fovea, or the intersection of the median longitudinal fissure with the mesial fovea fissures/transverse fissures (when present). Using these landmarks, four semi-landmarks and the relative warp analysis (Bookstein, 1991), Gómez-Robles et al. (2008) found that the SH P_3 s share the same morphospace with Neanderthal specimens in the positive region for both the PC1 and PC2. In summary, the results in Gómez-Robles et al. (2008) show that the SH and Neanderthal P_3 s are almost symmetrical, with a smooth outline and lacking a talonid protrusion. The occlusal polygon formed by the four landmarks is comparatively small and linguallongated due to the migration of the protoconid tip toward the lingual face (Table 3).

The primitive morphology includes an asymmetrical outline, with a well-developed talonid occupying the distal and distolingual

regions of the occlusal surface, causing an obliquity of the maximum buccolingual length relative to the mesiodistal axis (e.g. Arambourg, 1963; Bermúdez de Castro et al., 1999; Martínón-Torres et al., 2008). The geometric morphometric analysis carried out by Gómez-Robles et al. (2008) clearly distinguishes this primitive morphology, which also includes a relatively large occlusal polygon and a mesial displacement of the protoconid and metaconid apices.

Whereas some of the Arago specimens clearly resemble the Neanderthal pattern, the broad and centred occlusal polygon is closer to that of early hominins. The occlusal outline is symmetrical in Arago 13, but the tendency towards a certain asymmetry due to the development of a medium-sized talonid is evident in this sample, especially in Arago 71. Thus, the morphology of the crown of the Arago P₃s is half way between that of the SH and Neanderthal samples and that of earlier hominins. Additional information and a larger sample are needed to evaluate the shape of the roots of the Arago P₃s.

In addition, it is worth mentioning the particular rough appearance of the lower part of the buccal of the P₃ of Arago 13, which suggests the presence of an incipient cingulum. This feature is absent in all P₃s of SH. Nevertheless, both the Arago and SH P₃s exhibit a swollen buccal face.

As in all tooth classes, the mean values of the MD and BL P₃s diameters are greater in Arago than in SH (Table 2). In this case, the difference in the MD diameter is not statistically significant ($p > 0.05$). In contrast, the difference between the mean values for the BL diameter is statistically significant ($p < 0.01$).

On the other hand, in 1986 (Bermúdez de Castro, 1986) we carried out a comparative approach to the relative size between the P₃s and the M₁s in the SH individuals. We use the BL dimension for obtaining this index. The samples were then limited and no firm conclusions were obtained. With a remarkably greater sample we have obtained the following data for the relationship BL P₃/BL M₁ in SH: $n = 15$; $X = 85.24$, S.D. = 4.41; Range = 79.04–95.23. The values obtained for Arago 13 (88.46) and Arago 89 (83.03) are comprised in the range of variation of the SH sample. The mean value of the SH sample is greater than that of Neanderthals, but the differences were not statistically different ($t = 2.36$; $p > 0.01$). In contrast, the mean value of a recent modern human sample is remarkably less than that of SH and the Neanderthals (see Bermúdez de Castro, 1986).

4.13. Lower fourth premolars (P₄)

The SH P₄s show a primitive morphology in terms of the *Homo* clade, with the exception that the occlusal polygon is more compressed than in early *Homo* (Martínón-Torres et al., 2006). The primitive morphology is defined by a certain asymmetry of the occlusal outline, caused by the development of the talonid and its distolingual projection. The talonid usually presents one, two or more small cusps. Moreover, an additional cusp may be present in a distobuccal position. In the SH P₄s the asymmetry is less marked than in early Pleistocene hominins (e.g. Sangiran 6 or KNM-WT-15000), but there are also accessory cusps in the lingual part, not always well defined, but formed by thickened ridges delimited by shallow grooves (Martínón-Torres et al., 2012). Furthermore, in the primitive pattern the metaconid is clearly displaced mesially. The majority of the SH P₄s exhibit this morphology, and the protoconid and the metaconid are joined by a continuous transverse crest (75% of the specimens). This crest is also very frequent in Neanderthals (69%) (Martínón-Torres et al., 2012). The concomitant presence of this crest, a well-developed talonid with additional generally small lingual, and a mesial displacement of the metaconid are the most common patterns found in Neanderthals (Bailey, 2002a, 2002b). The root of the SH P₄s is single. It is mesiodistally compressed,

showing a wide and shallow groove running along the distal face. The root is straight or slightly deviated towards the distal part. The apex is arched in a lingual direction.

The P₄ in the Arago 13 mandible shows a well-developed talonid with three accessory lingual cusps, the asymmetry is not pronounced, the metaconid is mesially displaced, and the essential ridges of the main cusps are separated by the sagittal groove. In the isolated Arago 28 P₄ and the P₄ from the Arago 89 mandible the occlusal morphology is very similar to that of Neanderthals and SH hominins, with a relatively asymmetrical contour, additional small cusps in the talonid and a continuous transverse crest. A small distobuccal cusp is present in Arago 28. Occlusal and interproximal wear has erased most of the morphological features and has altered the occlusal outline of Arago 99. However, the general aspect of the crown of this particular tooth resembles that of the other specimens.

The root of Arago 28 was in the process of forming, and therefore no data could be obtained on its morphology. The root of Arago 99 is single, massive, and mesiodistally compressed. Furthermore, we have additional information available (CT-image) on the root morphology of the Arago 13 P₄. Interestingly, this tooth shows the pattern 2R: MB + DL (Table 3), which probably derives from the presumed primitive condition 2R: M + D of the hominin clade (Wood et al., 1988). About 5 mm from the neck, a buccolingual indentation emerges, and which progressively gets deeper. About 8 mm from the neck the main root canal separates into buccolingual and distolingual ramifications. Just a little lower, the buccolingual canal bifurcates into buccal and lingual ramifications. This root was first described in the P₃ of the *H. antecessor* holotype (Bermúdez de Castro et al., 1999), and is also present in the P₃ of the ATD6-96 specimen.

The shape of the occlusal outline of the P₄s has been studied by geometric morphometric analysis (Martínón-Torres et al., 2006). In this study, the four landmarks were defined as was done for the P₃s (see above). Martínón-Torres et al. (2012) found a remarkable overlap between the SH hominins and the Neanderthals, as well with other European Middle Pleistocene hominins, like those of Arago, in the morphospace of the relative warps. All these hominins show a reduced occlusal polygon, possibly related to the diminution of the lingual portion of the crown (Martínón-Torres et al., 2006).

The differences between the mean values of the Arago and SH samples for both the MD and BL dimensions (Table 2) are significantly greater than that of the SH sample ($p < 0.05$).

As in the P₃s, the number of individuals to estimate the size relationship between the BL P₄/BL M₁ in the SH sample is now remarkably greater than in 1986 (Bermúdez de Castro, 1986). We have obtained the following data: $N = 19$; $X = 81.53$; S.D. = 4.57; Range = 77.14–90.47. The values obtained in Arago 13 (88.46) and Arago 89 (80.35) are included in the range of variation of the SH sample. Again, the differences between the SH sample and the Neanderthals are statistically not significant ($t = 0.73$; $p > 0.2$), whereas the mean value of a modern sample is remarkably less than these Pleistocene samples (see Bermúdez de Castro, 1986).

4.14. Lower first molars (M₁)

The majority of the SH M₁s possess the main five cusps (Table 3), well integrated into the external contour of the tooth. However, two M₁s lack the hypoconulid and exhibit only four main cusps (8.6% of the sample). The C6 is always absent, but about 50% of the sample shows some expression of the C7 (ASUDAS grades 1 to 4). The Y groove pattern is present in about 55% of the specimens and, therefore, the + and X patterns are frequent in the M₁s of these hominins (Martínón-Torres et al., 2012). The anterior fovea is

always present and generally (85%) has the aspect of a short and deep fissure or a pit, not open toward the mesial marginal ridge. The middle trigonid crest, the crest joining the metaconid and protoconid, is always present and continuous (Martínez de Pinillos et al., 2014; Martínez de Pinillos, 2017). The continuous distal trigonid crest is absent in these molars (Martínez de Pinillos et al., 2014; Martínez de Pinillos, 2017). The deflecting wrinkle is also frequent (about 32% of the specimens), and traces of a protostylid (ASUDAS grade 1) are seen in one third of the M_1 s.

The Arago M_1 sample includes five specimens, two of them belonging to the Arago 89 mandible. The right M_1 of the Arago 2 mandible is heavily worn (grade 6) and therefore it was not possible to observe any of the key features considered in this report. The isolated Arago 40 M_1 exhibits a grade 4 of occlusal wear, but some features are still visible (Fig. 1). The less worn Arago 13 (left) and Arago 89 (right and left) M_1 s show the five main cusps, also well integrated into the external contour of the tooth. In Arago 13 there is a small C6 (ASUDAS, grade 1–2), whereas C7 is present in Arago 13 and it is particularly well-developed in the Arago 89 right and left M_1 s (ASUDAS grade 4). In Arago 40 the presence of a continuous middle trigonid crest and the anterior fovea are still visible (Martínez de Pinillos, 2017). In Arago 89 the middle trigonid crest is discontinuous. In both the right and left antimeres the anterior fovea is complex, branched, and open towards the mesial marginal ridge. In Arago 13 the middle trigonid crest is continuous, and the anterior fovea looks like a deep fissure, although there is a narrow groove connecting the anterior fovea with the external border across the thick mesial marginal ridge. A discontinuous distal trigonid crest is present in Arago 13 and Arago 89. The + groove pattern is present in Arago 40, Arago 13, and the left M_1 of Arago 89. The right M_1 of Arago 89 exhibits minimum contact between the metaconid and entoconid (Y-pattern). No traces of protostylid are present in this small M_1 sample.

The geometric morphometric analysis of M_1 s in hominins (Gómez-Robles et al., 2015) shows that there is relatively low variation between *Homo* species (and even between *Homo* and other genera), except in terms of the presence/absence of the middle trigonid crest and the concomitant presence of a deep anterior fovea. However, the third component of the relative warp analysis clearly separates specimens assigned to *H. neanderthalensis* and *H. heidelbergensis* from those classed as *H. sapiens* and other hominins species (Gómez-Robles et al., 2015). This separation is mainly due to the presence in Neanderthals and European Middle Pleistocene hominins of a mesiodistally elongated crown shape, a well-developed hypoconulid, a trend towards a + groove pattern, and the mesial displacement of the anterior fovea. The latter is associated with the presence of the middle trigonid crest.

The mean values of the MD and BL diameters of the Arago sample are greater than those of the SH sample (Table 2). The difference for the MD diameter is not statistically significant ($p > 0.05$), but it is significant for the BL diameter ($p < 0.05$).

4.15. Lower second molars (M_2)

In the SH M_2 sample the absence of hypoconulid in almost 30% of the specimens is noteworthy, as well as the reduction of this cusp, which never reaches the maximum expression as described in the ASUDAS classification scheme (Martínón-Torres et al., 2012). Moreover, and when present, the position of the hypoconulid is central. As in the case of the M_1 s, the main and accessory cusps are well integrated into the external contour of the tooth. The anterior fovea is generally pit-like, and its presence is concomitant with a continuous middle trigonid crest, which is present in 100% of the specimens. In contrast, a continuous distal trigonid crest is absent in all of the SH M_2 s (Martínez de Pinillos et al., 2014; Martínez de

Pinillos, 2017). A more-or-less developed C7 is present in the majority (94%) of the specimens, whereas C6 is present in almost half of the SH sample (Martínón-Torres et al., 2012). The Y-pattern is present in about 40% of the M_2 s, and almost half of the specimens show a pit-like protostylid placed at the end of the groove separating the protoconid and hypoconid.

The Arago M_2 s sample comprises nine M_2 s. The Arago 2 and Arago 89 mandibles preserve the two antimeres, and two isolated M_2 s (Arago 10 and Arago 32, Fig. 1) belong to the same individual. The Arago 2 M_2 s are heavily worn (grade 5) and it is not possible to evaluate their morphology. In Arago 68 the occlusal wear is also remarkable (grade 4), but it is nonetheless possible to observe some of its main features. The other specimens show the main five cusps well integrated into the external contour of the crown. The hypoconulid is generally well developed, and occupies a distal (Arago 6, Arago 10, Arago 32, Arago 13) or buccodistal position (Arago 69 and Arago 89). In Arago 6 and Arago 13 the hypoconulid cannot be well differentiated from the hypoconid. It is difficult to ascertain the presence of a C6 due either to the crenulations observed in the less worn M_2 s, or to the occlusal wear (Arago 6 and Arago 68), but it seems present at least in Arago 13, Arago 32, Arago 69, and Arago 89 with a variable expression. C7 is present in Arago 10, Arago 32, Arago 69, and Arago 89. In Arago 6 a part of the mesiolingual region of the crown is missing and it is not possible to ascertain this feature. The anterior fovea is present in all of the specimens, and the expression of an uninterrupted middle trigonid crest is present in Arago 6, Arago 10, Arago 32, Arago 68 and Arago 69 (Martínez de Pinillos, 2017). Half of the specimens exhibit the Y-pattern, whereas other show either the + or X pattern (Table 3). The protostylid is absent in any of its expressions.

The geometric morphometric analysis carried out by Gómez-Robles et al. (2015) reveals a clear distinction between five-cusped and four-cusped M_2 s, particularly due to the reduction of the talonid in terms of the total area of the crown. In the relative warp analysis, the large and five-cusped Arago 10, 32, 69, and 89 occupy the extreme part of the distribution of the Middle Pleistocene specimens and Neanderthals along the negative values of the PC1, together with some specimens assigned to *H. habilis*, *H. erectus* and *H. antecessor*.

In this molar, the mean values of the MD and BL diameters of the Arago sample are also greater (Table 2) and statistically significant ($p < 0.01$) compared with the mean values of the SH sample (Fig. 2).

4.16. Lower third molars (M_3)

The SH M_3 s exhibit a remarkable reduction of the size of the main cusps, and particularly those of the talonid. The presence of secondary grooves and enamel crenulations complicates the occlusal morphology. Moreover, in some cases the main cusps alter their usual position, giving atypical shapes to these teeth and hindering the identification of the cusps. The absence or remarkable reduction of the hypoconulid affects at least half of the specimens. However, the presence of C6 and C7 exhibits relatively large percentages. The concomitant presence of C6, C7, and hypoconulid is expressed in more than one third of the SH M_3 s (Martínón-Torres et al., 2012). As in the other molars, a high percentage of the M_3 s (more than 70%) shows a combination of a deep and pit-like anterior fovea and a middle trigonid crest. More than 60% of the specimens exhibit a continuous distal trigonid (Martínez de Pinillos et al., 2014; Martínez de Pinillos, 2017). It is also difficult to discern the groove pattern between the main cusps. The Y-pattern is observed in less than 25% of the specimens, whereas the other M_3 s exhibit either the + or the X patterns. The protostylid is expressed either by a pit at the end of the buccal groove (23.8%) or by a short groove present in the buccal aspect of the protoconid (28.6%)

(Martínón-Torres et al., 2012).

The Arago M₃ sample includes five specimens, two of which belong to the Arago 89 mandible. The left Arago 2 (*in situ*) shows strong occlusal wear (grade 5), and besides the presence of the five main cusps arranged in a + pattern, it is difficult to note additional features. The other M₃s also exhibit the five main cusps, well integrated into the external contour of the crown. The hypoconulid is very large and buccodistally placed in the right M₃ of Arago 89 and in Arago 106. It is smaller (but well defined) in the left M₃ of Arago 89, and integrated with the hypoconid in Arago 13. A C6 is present in Arago 13 and the two antimeres of Arago 89. C7 is absent or minimally expressed (Arago 13). In all M₃s the anterior fovea is always present, and the middle trigonid crest is interrupted by the main transversal groove (Martínez de Pinillos, 2017). The distal trigonid crest is always present, but equally interrupted. The + or X-pattern is constant in the Arago M₃s sample. The protostylid is absent.

The geometric morphometric analysis carried out on the shape of the crown (Gómez-Robles et al., 2015) distinguished between the well-formed and mesiodistally elongated Arago specimens (with a relatively large talonid) and the SH M₃s, characterized by a short talonid and a distortion of the normal shape of the molars.

Concerning size, no significant differences were noted between the mean values for the MD and BL diameters in spite of the M₃s from Arago being generally greater in size than those from SH. Again, it is important to remember the influence of the sample size on the results from these analyses.

5. Discussion

5.1. Comparative assessment

In this report we have carried out a comparative study of the Arago and Atapuerca-SH hominin dental samples. The distance between the two sites is only 630 kilometres as the crow flies, and the stratigraphic levels comprising hominin remains are roughly contemporaneous. Of course, the Pyrenees was one of the multiple geographical barriers of the European continent. The Pyrenees slowed down the passage of species between northern Europe and the Iberian Peninsula. But it is important to note that the Arago site is located right in one of the two free passes between the south of the current state of France and the Iberian Peninsula. In addition, the composition of large mammals (Ungulates and Carnivora) is almost similar in the Caune de l'Arago and Atapuerca, denoting lack of isolation on one side and another of the Pyrenees (Moigne et al., 2006; Rodríguez et al., 2011).

We have observed remarkable crown size differences in all dental classes. We are aware that the Arago sample sizes are small, but a considerable number of the Arago specimens have MD and BL diameters which are above the maximum recorded for the SH range. Despite the Arago small sample sizes, when the application of the Mann Whitney test was possible, most of the differences were shown to be statistically significant. The size of the SH posterior teeth is particularly small, and similar to that observed in some modern humans (Bermúdez de Castro and Nicolás, 1995). The SH anterior teeth are proportionally bigger than the posterior teeth, following the same pattern as that observed in the European Middle Pleistocene and in Neanderthals (Bermúdez de Castro and Nicolás, 1995). Both the anterior and posterior teeth of the Arago hominins are significantly greater than those from SH, thus confirming that the dimensions of the teeth from the Middle Pleistocene French site express a different genetic regulation.

In relation to this, the Arago upper and lower anterior teeth are massive and exhibit long roots. Thus, these hominins exhibit the so-called Eurasian dental pattern (Martínón-Torres et al., 2007), which

is characterized by high percentages of the higher degrees of expression of “mass additive” traits, like the shovel shape and tuberculum dentale. Furthermore, the Arago posterior teeth fulfill this pattern, exhibiting higher percentages of middle trigonid and premolar transverse crests. Below we will return to the assessment of these features. The presence of the accessory cusps and complex occlusal morphology of the Arago posterior teeth is more characteristic of the African pattern (Martínón-Torres et al., 2007), but it is not unusual in Pleistocene Eurasian hominins.

It is also noteworthy that in two of the Arago mandibles (Arago 2 and Arago 13) and the Arago 21 maxilla the molar size sequence is M₁ < M₂ for the CCA. This is a primitive feature for the *Homo* clade lost in most of the SH hominins, but preserved in many Neanderthal specimens, like most of the Krapina specimens, Chateaufort 2, Devil's Tower, La Quina 5, Ehringsdorf (child and adult), or Ochoz. In a large sample of Neanderthals, 70% of the individuals show the M₁ > M₂ size relationship for the mandibular sequence (Bermúdez de Castro, 1993). Concerning the upper dentition, we have counted a total of 9 individuals (out of a total of 17) in which M₁ > M₂ (53%), while in 4 individuals (23.6%) the sequence is M¹ = M² for the CCA.

In terms of the upper premolars it is interesting to note that the Arago P³s show a broad lingual cusp and an inclined sagittal groove, two primitive features which are not present in the SH P³s. Another interesting aspect is the broad lingual cusp of Arago P⁴, which shows a primitive occlusal aspect shared with *Australopithecus* and *Paranthropus* as confirmed by the geometric morphometric study carried out by Gómez-Robles et al. (2011). Similarly, the three Arago M¹s present the hypothetical primitive occlusal outline, with an approximately square occlusal polygon and a regular contour, in which no cusp protrudes on the external outline. By contrast, the SH M¹s show the derived condition exhibited by Neanderthals, characterized by a rhomboidal contour, a relative displacement of the lingual cusps, and a protrusion on the external outline of a large bulging hypocone. Interestingly, this derived condition is also observed in the Early Pleistocene Gran Dolina-TD6 specimens (Gómez-Robles et al., 2007) suggesting that this feature is not a Neanderthal apomorphy, but a trait that appeared in the Early Pleistocene. The small size of the hypocone and metacone in the majority of the SH M²s and M³s is also remarkable. This observation is concomitant with the size reduction of these teeth. By contrast, the Arago M²s preserve the primitive condition, with well-developed distal cusps. The Arago M³s show a reduction of the hypocone and metacone, as is usually the case in Eurasian Pleistocene hominins.

The occlusal morphology of the P₃s has a strong taxonomic signal. The simple observation of the morphology has been corroborated with the geometric morphometric analysis carried by Gómez-Robles et al. (2008). The SH P₃s are indistinguishable from those of Neanderthals, showing a clear symmetry, the absence of a developed talonid, and a comparatively small and lingually displaced occlusal polygon. The Arago P₃s (except Arago 71) show the small and bulbous lingual cusp (derived), but the presence of a medium-sized talonid and a more centred and large occlusal polygon suggest an intermediate morphology between that of the SH and Neanderthal samples, and that of earlier hominins.

By contrast, we have not detected relevant morphological discrepancies between the Arago, SH and Neanderthals P₄s. The morphology of this tooth is primitive for the *Homo* clade and does not contribute anything to elucidate further taxonomic information. It is interesting that the P₄ of Arago 13 shares its primitive root morphology with two of the *H. antecessor* P₃s.

The almost constant and concomitant presence of a deep pit-like anterior fovea and a middle trigonid crest in the three SH lower molars is of great importance to this study because, once

again, it confirms the similarities between these hominins and Neanderthals. This pattern is characteristic of Neanderthals (Bailey, 2002a, 2002b; Bailey et al., 2011), whereas it is less frequent in Asian *H. erectus* and is quite uncommon in African Pleistocene hominins (Martinón-Torres et al., 2007, 2012). The Arago molars show the Eurasian pattern, and share with Neanderthals and the SH hominins a high frequency of a deep pit-like anterior fovea together with a continuous middle trigonid crest in the M₁s and M₂s. The Arago M₃s also show this pattern, but the middle trigonid crest is always discontinuous.

The small size of the SH teeth is also linked to a reduction of the hypoconulid. The fact that two SH M₁s, a 30% of the M₂s, and more than 25% of the M₃s lack the fifth cusp is noteworthy. By contrast, the presence of C6 and C7 is common in the Arago and SH molars.

In summary, the null hypothesis put forward in section 1.2 (i.e., given the temporal and geographic proximity of the Arago and Atapuerca-SH sites, the differences between the dental hominin samples obtained from these sites are not significant) should be rejected. However, we observe common morphological aspects between the two samples which must be explained.

5.2. What does the comparison of Arago and SH tell us about the origin of Neanderthals?

It is worth highlighting previous studies that have looked at the close relationship between the SH hominins and Neanderthals (e.g., Arsuaga et al., 2014, and references therein; Meyer et al., 2016). According to Arsuaga et al. (2014) and Bermúdez de Castro et al. (2016), the suite of features observed in different anatomical parts of the SH hominins fits with a cladogenetic model, a hypothesis also proposed by Tattersall (2009). All these authors recognize the existence of a Neanderthal clade, one of their branches represented by the SH hominins. Furthermore, Arsuaga et al. (2014) underline the fact that the features observed in different anatomical parts of the SH hominins are very constant, lacking polymorphisms or different trait combinations. These observations have allowed these scholars to conclude that there is more variation between paleodemes in the European Middle Pleistocene than there is within the SH paleodeme.

In this study we have in fact checked that the dental variation in the Arago hominins is clearly beyond the variation observed in the SH hominins. The dental evidence also suggests that these hominins possess the Eurasian pattern proposed by Martinón-Torres et al. (2007). That is to say, although the Arago teeth show a large amount of plesiomorphic dental features, the hominins at this site can be considered as genuine Europeans of the Middle Pleistocene. The large anterior teeth or the almost constant presence of a pit-like anterior fovea together with the middle trigonid crest are unquestionable signs of their European identity. In addition, some of the Arago dental features clearly relate the hominins of this site to Neanderthals. The Arago 21 cranium does not exhibit Neanderthal-derived traits (Daura et al., 2017), but the presence of some Neanderthal features in the Arago mandibles has been highlighted on several occasions (e.g., Aguirre and de Lumley, 1977; Bermúdez de Castro et al., 2016; Mounier et al., 2009; Rosas, 2001).

Given the limited geographic distance and the contemporaneity of the two hominin assemblages it does not seem reasonable to put forward the idea that genetic drift processes may have been behind the differences noted between the hominins at the two sites. The more primitive aspect of the Arago and other Middle Pleistocene specimens, like the Mauer mandible, has led some authors (Arsuaga et al., 2014; Tattersall, 2007, 2011; Stringer, 2012) to hypothesize that two (or even more than two: Hanegraef et al., 2018) different hominin lineages may have coexisted in Europe during the Middle Pleistocene. One of these lineages could include the

Atapuerca-SH, Swanscombe, Steinheim, or the Pontnewydd hominins (Compton and Stringer, 2012, 2015), all of them younger than MIS 12 or MIS 11, and all showing a clear suite of derived Neanderthal features. The other lineage could include Mauer, Arago, Petralona, Aroeira, and perhaps Bilzingsleben or Verteszsölös, which exhibit a less derived Neanderthal morphology. We cannot forget that the Ceprano calvarium and the Mala Balanica mandible do not exhibit any Neanderthal features.

In this very complicated context, two competing hypotheses try to explain the origin of Neanderthals. According to Hublin (2009, p. 16022) “climatic adaptations and an increase in encephalization, genetic drift seems to have played a major role in their evolution. To date, a clear speciation event is not documented, and the most likely scenario for the fixation of Neanderthal characteristics seems to be an accretion of features along the second half of the MP (Middle Pleistocene)”. Rosas et al. (2006) point to a more “quantic” model comprising a two-phase hypothesis. The first phase could have been characterized by an increase in body size, postcranial robusticity, and midfacial prognathism. The second phase would have taken place in the late Middle Pleistocene and would have produced a major reorganization of cranial architecture, including a relative increase in the size of the occipital and temporal neural areas. The lack of reliable geochronological data complicates the testing of these competing hypotheses. In addition, it would be necessary to explain the considerable variability observed in the assumed various contemporaneous European paleodemes, all of which were subject to similar selective pressures.

Would it be enough to refer to the existence of refugia in the Mediterranean peninsulae, and processes such as genetic drift, founder effect, directional adaptation or hybridization to explain this variability? We have proposed that the origin of the Neanderthal clade could be in Southwest Asia (Bermúdez de Castro et al., 2016; Dennell et al., 2011). First, it is important to remember that some features, previously considered as autapomorphic Neanderthal features, are present in *H. antecessor* (Bermúdez de Castro et al., 2017). That is, these features appeared in a hominin population at present only represented in the westernmost part of Europe. Moreover, we have proposed that there may have been discontinuity between the European population of the Early Pleistocene and the European population of the Middle Pleistocene (Bermúdez de Castro et al., 2016). If this hypothesis is correct the only way to explain that *H. antecessor* and the new European Middle Pleistocene settlers present ‘Neanderthal’ features would be if these hominins had shared a common ancestor. If Europe received at least two population waves, it is to be expected that throughout the Middle Pleistocene populations living in Southwest Asia would have moved towards Europe in a pulsating fashion, taking advantage of favourable climatic and geographical circumstances. The most ancient paleodemes would have been characterized by a higher percentage of plesiomorphic features, whereas the most recent paleodemes would have been closer to the typical Neanderthal appearance. Of course, isolation, genetic drift, hybridization, etc., may have played a major role in the diversity of the European Pleistocene population. The taxonomic debate among specialists is therefore justified (e.g. Hublin, 2009; De Lumley, 2015; Mallegni et al., 2003; Manzi, 2016; Stringer, 2012) since there are important differences between the various paleodemes. The possible relationship between *H. antecessor* and the Neanderthals is a matter of great interest. This question is an unresolved issue that are under investigation for future publications.

One key site to discuss this hypothesis is Qesem (Israel). This cave site has two main lithostratigraphic sequences, Upper and Lower, dated by ²³⁰Th/²³⁴U series between 420 kyr and 200 kyr (Barkai et al., 2003). All archaeological finds at Qesem have been assigned to the Acheulo-Yabrudian Cultural Complex, which

postdates the Acheulean Complex and predates the Mousterian Complex (Barkai et al., 2009). A small sample of hominin teeth was recovered from this site, and some of these specimens were published by Hershkovitz et al. (2010). These authors conclude that a few features of this dental sample suggest some affinities with Neanderthals, although in general the conclusions of this study lean towards a relationship of the Qesem teeth with the Skhul and Qafzeh dental assemblages. Three lower teeth, C₁ P₃, and P₄, were recovered from the Lower Unit, which has dated between 300 and 400 kyr. Pictures of these teeth and our own observations (JMBC and MM-T) clearly suggest that these specimens are within the variability from the SH teeth and those of Neanderthals. The Qesem C₁ shows a moderate shovel shape (incisor-like morphology), with a thicker distal marginal ridge, and a smooth lingual face. The single and mesiodistally compressed root exhibit broad mesial and distal longitudinal grooves. The Qesem P₃ shows a large buccal cusp, and a small and bulbous lingual cusp, joined by a transverse crest. This tooth is almost symmetrical and, although we have not carried out a geometric morphometric analysis, it is evident at the first sight that the occlusal polygon is linguallongated due to the presence of the protoconid tip near the lingual face. Regarding the Qesem P₄, the talonid is moderately developed, but causing some asymmetry of the crown. The metaconid is mesially displaced and are joined by a transverse crest to the protoconid. The root is single. It is mesiodistally compressed, showing a wide and shallow groove running along the distal face. The root is straight. Furthermore, the size of these specimens is smaller than the mean values obtained in the SH sample, but within its range of variation.

6. Concluding remarks

The comparison between the Arago and SH dental samples is consistent with the hypothesis that more than one hominin lineage lived in Europe during the Middle Pleistocene. Given the geographic and temporal proximity between these two sites, we cannot suggest isolation, genetic drift, founder effect, or directional adaptation to explain the differences observed between Arago and SH. However, the two dental assemblages share the Eurasian pattern of anterior and posterior dentition previously described by Martínón-Torres et al. (2007). Whereas the SH teeth are practically indistinguishable from European Neanderthal teeth, the Arago specimens exhibit a suite of plesiomorphic features alongside some characteristic Neanderthal traits. This fact prevents these and other European hominins from being classed as belonging to the *H. erectus* species.

In order to explain the variability observed in European Middle Pleistocene hominins we suggest that different human groups from Southwest Asia arrived in Europe during the Middle Pleistocene, perhaps taking advantage of favourable geographic and climatic circumstances, or perhaps driven by demographic pressures. In any case, these groups would have a common origin, as evidenced by the presence of shared derived features, which are characteristic of the Neanderthals of the Late Pleistocene. The Qesem site, in Israel, seems like a key site to further test this hypothesis given that the small dental sample recovered from the Lower Unit is almost contemporaneous and shows evident similarities with the SH teeth. The biological process that originated the *H. neanderthalensis* species remains an open debate.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quascirev.2018.04.003>.

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