JASs *Journal of Anthropological Sciences* Open Access

Reports Vol. 99 (2021), pp. 1 - 18 e-pub ahead of print doi. 10.4436/jass.99001

Indicators of sexual dimorphism in *Homo antecessor* permanent canines

Cecilia García-Campos[1,2], María Martinón-Torres[1,2] , Mario Modesto-Mata[1,2], Laura Martín-Francés[1,2,3], Marina Martínez de Pinillos[1,2] & José María Bermúdez de Castro[1,2]

1) *Centro Nacional de Investigación sobre la Evolución Humana, Paseo de la Sierra de Atapuerca 3, 09002, Burgos, Spain*
e-mail: ceciliagc.bio@gmail.com

2) *Anthropology Department, University College of London, 14 Taviton Street, London WC1H 0BW, UK*

3) *Université de Bordeaux, CNRS, MCC, PACEA, UMR 5199 F-33615, Pessac Cedex, France*

Summary - *One of the main concerns of paleoanthropologists is to make a correct interpretation of the variability observed in the fossil record. However, the current knowledge about sexual dimorphism in the human lineage comes mainly from the study of modern human, Neanderthal and pre-Neanderthal populations, whereas information available about the intrapopulation variability of the groups that preceded these taxa is still ambiguous. In this preliminary study,* Homo antecessor *dental sample was assessed with the aim of trying to evaluate the degree of variability of their permanent canines' dental tissue proportions. Microtomographic techniques were here employed in order to measure and compare the crown volumes and surface areas of their enamel caps and dentine-pulp complexes. Then, the Pearson´s Coefficient of Variation and the Euclidean Distance were assessed to evaluate of intrapopulation variability of dental sample. The values obtained were also compared with those of the dental samples from Sima de los Huesos site (Spain), the Neanderthal site of Krapina (Croatia), as well as from a broad forensic collection of known sex. Our results showed a marked intrapopulation variability in the dental tissues measurements of the canines of the individuals H1 and H3 from this site. This variability may be interpreted as an indicator of sexual dimorphism. If this is the case, H1 may be considered as a male individual, whereas H3 would be a female. Future discoveries of new fossils in the level TD6.2 of Gran Dolina site might help to confirm or refute this hypothesis.*

Keywords - *H. antecessor, Canines, Dimorphism, Enamel, Dentine.*

Introduction

Sexual dimorphism is an important part of the total variability observed in the fossil record (e.g., Stringer 1986; Johanson et al. 1987; Wood 1992; Antón 2003; Skinner et al. 2006). However, in most cases the scarcity of fossils hinders an accurate assessment of the intrapopulation variability in extinct groups and, as a consequence, the sex estimation of isolated specimens. Likewise, when only small fragments of the skeleton are available, it is difficult to evaluate certain features such as the size of the supraorbital torus, the morphology of the pelvis or the robustness of the muscle attachments that may be potentially useful for sex estimation. In addition, many of these secondary sexual traits are indistinguishable in the skeleton of subadult individuals, who have not already reached adolescence (Dirkmaat 2012). In this cases, it is not easy to discern whether we are dealing with a female individual or a male individual who has not yet completed his development. Fortunately, thanks to their chemical composition, teeth are usually found in a good state of conservation in geological deposits. Additionally, these skeletal structures also offer the advantage of completing their formation early in an individual life. Therefore, sexual estimation techniques based on dental features can be especially useful in paleoanthropology for estimating the sex of immature individuals. In particular, methodologies based on permanent canines, the tooth that presents the greatest degree of sexual dimorphism in the human dentition (e.g., Harris and Bailit 1988; Hillson 1996; Işcan and Kedici 2003; Peckmann et al. 2015), allow estimating the sex of individuals from the age of six, which is the age at which the canine crown completes its formation (Moorrees et al. 1963).

On the other hand, while the information about modern human populations, Neanderthals and pre-Neanderthals is relatively abundant (e.g., Wolpoff 1979; Smith 1980; Trinkaus 1980; Arsuaga et al. 1997; Rosas 1997; Lorenzo et al. 1998; Rosas et al. 2002; García-Campos et al. 2020) the scarcity and geographically scattered pre-Middle Pleistocene fossil record prevents a proper understanding of extinct hominins variability (e.g. McHenry 1991, 1994; Richmond and Jungers 1995; Reno et al. 2003, 2010; Harmon 2009, 2006). In this context, it is particularly interesting to attempt an assessment of the variability of the hominin sample from Gran Dolina-TD6.2 site, from the Sierra de Atapuerca archaeological complex.

The TD6.2 level of the Gran Dolina cavity has provided a large number of archaeological and paleontological remains which have allowed to document the presence of human activity in this hill range for at least the last million years (Carbonell et al. 2008; Rodríguez et al. 2011). This has made of this site one of the most important references for Quaternary research (Carbonell et al. 1999). The human fossil remains found in Gran Dolina-TD6.2 have been studied by several authors (e.g., Bermúdez de Castro et al. 1997, 1999, 2003, 2008, 2015; Arsuaga et al. 1999; Lorenzo et al. 1999; Carbonell et al. 2005; Gómez-Robles et al. 2012; Martinón-Torres et al. 2012, 2019; Martín-Francés et al. 2018, 2020). Concerning the taxonomy and phylogenetic position of the population to which these remains belong, initial studies showed that this population exhibited a unique combination of primitive characters (in their dental morphology) and derived traits (in their facial morphology) which led to the definition of a new species: *Homo antecessor* (Bermúdez de Castro et al. 1997), the oldest species described so far in the Early Pleistocene of Europe. Later studies highlighted the expression of certain features shared with other Eurasian populations and, in particular, with those that lived during the Middle and early Later Pleistocene (Martinón-Torres 2006; Bermúdez de Castro et al. 2015; Martinón-Torres et al. 2019). This unique mosaic of skeletal and dental characteristics suggested that this species might be phylogenetically close to the divergence between Neanderthals and modern humans (Bermúdez de Castro et al. 2015). In 2020, in an innovative study carried out by Welker and colleagues, the dental enamel proteomes of *H. antecessor* were analyzed. This research provided evidence that the TD.2 hominids belonged to a close sister lineage to subsequent Middle and Late Pleistocene hominins, including modern humans, Neanderthals and Denisovans (Welker et al. 2020). Regarding the paleodemography of this population, the study of the maxillar, mandibular and dental samples from this site resulted in a minimum number of eight individuals, although given the small area excavated so far, it is suspected that this number could be higher (Bermúdez de Castro et al. 2006). The high percentage (75 %) of immature individuals in the hypodigm of TD6.2 is noteworthy (Bermúdez de Castro et al. 2015). Despite the various research lines developed with this fossil sample (e.g., Bermúdez de Castro et al. 1997, 2003, 2008, 2015; Arsuaga et al. 1999; Bermúdez de Castro et al. 1999), there were no studies in which the sexual dimorphism of this population was assessed. This is mainly because most individuals included Gran Dolina-TD6.2 sample has not completed their development, which complicates their sexual estimation. In this preliminary study, microtomographic techniques have been employed to analyze two human maxillary permanent canines from Gran

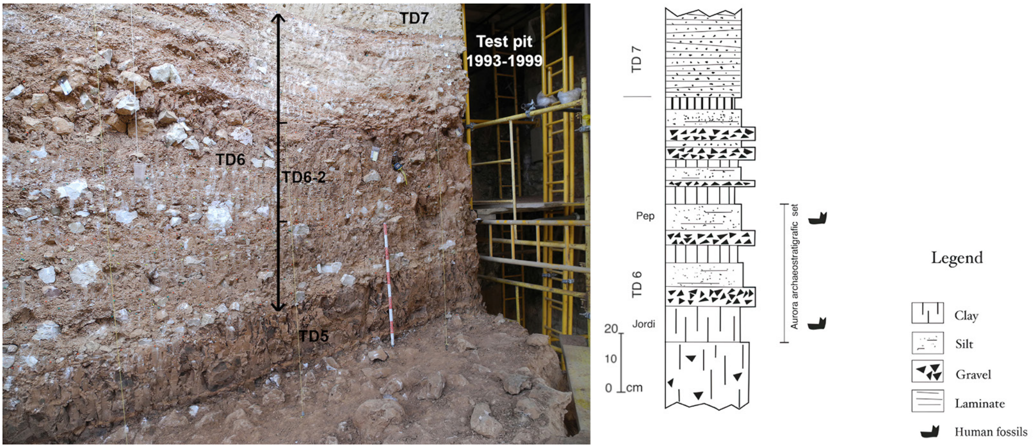

Fig. 1 ***- Stratigraphy of the*** **Gran Dolina** ***site. On the left, the sub-unit TD6.2 is indicated in the image of the Gran Dolina site (photo taken by M. A. Martín). On the right, the main lithostratigraphic units described in the section uncovered of the site (image taken from Campaña*** **et al.** ***2017).***

Dolina-TD6.2 for trying to evaluate the degree of variability of their dental tissue proportions and whether this variability can be attributed to sexual dimorphism.

Several studies have shown that the dental tissue proportions of permanent teeth are a dimorphic feature, not only in modern humans but also in other hominoid species (e.g., Schwartz and Dean 2001; Schwartz et al. 2005; Saunder et al. 2007; Feeney et al. 2010; García-Campos et al. 2018a,b, 2020; Sorenti et al. 2019). Particularly, female individuals tend to have smaller canines and a distinctive histological pattern characterized by the relative predominance of the enamel component and a smaller dentine-pulp complex than the males from the same population (Saunder et al. 2007; Feeney et al. 2010; García-Campos et al. 2018a,b, 2020; Sorenti et al. 2019). In modern humans, the differences observed in the volumes and three-dimensional surfaces of permanent canines' dental tissues have turn out to be a useful tool to estimate the sex (García-Campos et al. 2018a,b) with rates of success comparable to those of other traditional metric and non-metric methods based on the cranial and postcranial skeleton (e.g., Ateş et al. 2006; Acharya and Mainali, 2008; Hassett 2011; Zorba et al. 2013). This sexually dimorphic pattern has been also employed for sex estimation in past populations. In a study by García-Campos et al. (2020), dental histology was successfully used to estimate the sex and the degree of sexual dimorphism present in the Middle Pleistocene population of the Sima de los Huesos (SH) site of the Sierra de Atapuera (Spain), as well as in the dental sample from the Neanderthal site of Krapina (Croatia).

In order to evaluate the degree of variation of *H. antecessor* teeth we employed the Person Variability Coefficient (CV) on one hand, and a Principal Component Analysis and the Euclidean Distance assessment on the other. We compared our results with those obtained in previous studies about from Sima de los Huesos site (Spain), the Neanderthal site of Krapina (Croatia), and a large forensic sample of known sex (García-Campos et al. 2020).

Materials

Gran Dolina site is a large cavity, 27 meters deep and with a maximum width of 17 meters, located in the so-called Trinchera del Ferrocarril of the Sierra de Atapuerca archaeological complex (Burgos, Spain). The stratigraphic sequence

***Fig. 2** - Permanent canines of Gran Dolina-TD6.2 included in the study. The upper row shows the maxilla of individual H3 which includes the upper canine ATD6-69, the frontal view on the left and the lower and lateral views on the right. In the lower row, the left maxillary canine of individual H1, ATD6-13 is observed (buccal, mesial and occlusal view).*

of the Gran Dolina cave is divided into eleven levels numbered in an increasing order from the base to the top: TD1-TD11 (Parés and Pérez-González 1999). In the TD6.2 (Fig. 1) nearly 170 human fossils belonging to at least 8 individuals were found (Bermúdez de Castro et al. 1997; Carbonell et al. 2010). Regarding the geochronology of this level, the analysis of ESR dating applied to quartz grains from TD6 yielded a date that ranges between 600 ± 90 ka and 950 ± 90 ka (Moreno et al. 2015). In a new thermoluminescence study Arnold and Demuro (2015) a weighted mean age of 840 ± 60 ka was obtained for this level. Finally, a recent ESR analysis performed directly on the human remains provided a final estimated age range of 720- 950 ka for the fossils from this site (Duval et al. 2018). In conclusion, taking into account the results obtained from all of these studies, as well as the biostratigraphic information from this level (Cuenca-Bescós et al. 1999; Cuenca-Bescós et al. 2015), the TD6 hominis can be confidently assigned to MIS (Marine Isotope Stage) 21.

The Gran Dolina-TD6.2 dental sample comprises 46 permanent and eight deciduous teeth, which includes two upper (ATD6-13 and ATD6-69) and two lower (ATD6-1 and ATD6-6) permanent canines. The canines ATD6-1, ATD6-6 and ATD6-13 belong to individual H1 (the holotype of *H. antecessor*) and the canine ATD6-69, included within the maxilla ATD6-69, belongs to individual H3 (Bermúdez de Castro et al. 2015, see Fig. 2). In this study, two upper canines (ATD6-69 and ATD6-13) were analyzed. These teeth were selected for their good state of conservation. The canine ATD6-69 has not reached the occlusal plane and therefore does not present wear facet. In addition, the crown of this tooth has a linear hypoplasia that is not very marked. On the other hand, the canine ATD6-13 presents an oval wear facet on its occlusal surface, but it does not reach the dentine.

As a comparative sample, we employed the specimens analyzed by García-Campos et al. (2020). This sample includes a total of 86 maxillary canines from: the Sima de los Huesos site from Spain (n = 16), the Krapina site from Croatia (n = 12) and a sample of modern humans with different geographical origin (n = 58). We considered the results obtained from those teeth with a wear degree equal or lower than 3 (Molnar 1971) and only one antimere were assessed. The sexual estimations of the fossil samples was taken from García-Campos et al. (2020) who used a combination of two approaches: the Mean method and a Hierarchical cluster analysis. The final sex estimation was established through a comparison of the results of both approaches. The modern human sample was composed by forensic samples of known sex. For more details on the sexual estimation techniques see García-Campos et al. (2020).

Methods

The isolated tooth TD6-13 was scanned using the Scanco Medical AG Micro-Computed Tomography 80 housed at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH) in Burgos. Scans were performed employing two 0.1 mm Copper filters and using a voltage of 70 kV and an amperage of 114 μA. The resultant slice thickness was 18 micrometers (μm). ATD6-69, which is included in a maxillary fragment, was scanned using a Phoenix v/tome/x s (GE Measurement & Control) available in the same research centre. In this case, the scan was performed with two 0.1 mm Copper filters, 100-120 kV voltage and 110-140 μA amperage, resulting isometric voxel of 37 μm. The subsequent image processing was performed using the Amira 6.0.0 software (Visage Imaging, Inc.). Dental tissues (enamel and dentine-pulp complex) were semi-automatically segmented using the Watershed Segmentation Tool and through manual editing. Following the protocol described in García-Campos et al. (2018a,b, 2019, 2020), we considered the cervical line as the fundamental morphological feature to isolate the crown and the root.

Next, on the virtually isolated crowns, we quantified the following absolute variables: the volume of the enamel cap (Ve, in mm^3); the volume of the crown dentine including the crown pulp (Vcdp, in mm^3); the surface area of the enamel-dentine junction (EDJS, in mm^2); the outer surface of the enamel cap (OES, mm^2); and the basal surface of the crown (BS, in mm^2). These values were subsequently used to compute the 3-D average enamel thickness index (3DAET = Ve/EDJS, mm); the 3-D relative enamel thickness index (3DRET = 3DAET/) x 100, scale-free); the crown volume (Vc = Ve + Vcdp, mm^3); the percentage of crown volume that is dentine and pulp (Vcdp/Vc = Vcdp/Vc x100, percentage scale); and relative outer enamel complexity ratio (OES/EDJ, free-scale). Due to ATD6-69 has no already finished the root formation the volume of the root dentine including the pulp (Vr, mm^3) was not assessed. These variables were described by Olejniczak et al. (2008a,b) and Skinner et al. (2008). They were previously employed by García-Campos et al. (2018a,b) to estimate the sex in modern human samples, reaching accuracy rates of up to 92.3%. Likewise, they were also used to estimate the sex of Neanderthal and pre-Neanderthal fossil samples (García-Campos et al. 2020).

Statistical analyses were performed using the SPSS software (v. 18.0, SPSS Science, Inc.). A descriptive statistical analysis was applied considering the data obtained in this study from the maxillary canines of *H. antecessor*, as well as from SH, Krapina and a modern human sample

***Tab. 1** - Descriptive statistics for the measurements and indices associated included in this study. The data from SH, KRA and RMH have been obtained from García-Campos* et al. *(2020). The crown measurements were assessed in the slightly worn upper canines (1-3 wear stage following Molnar, 1971).*

SAMPLE	SUB-SAMPLE	N	VC (mm³)	BS (mm²)	VE (mm³)	VCDP (mm³)	OES (mm²)	EDJS (mm²)	3DAET (mm)	3DRET (SCALE FREE)	VCDP/VC (%)	OES/EDJS (SCALE FREE)
			MEAN (SD)									
HA	ATD6-13	-	371.17	72.30	143.24	227.43	258.80	196.43	0.73	12.01	157.88	1.32
	ATD6-69	-	355.49	51.04	165.36	190.13	243.98	159.75	1.04	18.00	114.98	1.53
	Total	2	363.33 (11.09)	61.67 (15.03)	154.65 (15.15)	208.69 (26.24)	251.39 (10.48)	178.09 (25.94)	0.89 (0.22)	15.00 (4.24)	136.43 (30.33)	1.43 (0.15)
SH	Females*	3	287.60 (9.68)	46.14 (2.25)	130.35 (8.52)	157.26 (1.62)	208.93 (5.66)	149.64 (2.55)	0.87 (0.05)	16.13 (0.76)	54.71 (1.47)	1.40 (0.02)
	Males*	3	364.59 (18.59)	59.39 (4.07)	157.67 (9.67)	206.92 (18.17)	241.87 (16.49)	185.75 (5.81)	0.85 (0.04)	14.37 (0.93)	56.71 (2.97)	1.30 (0.12)
	Total	9	327.56 (35.34)	51.87 (6.37)	146.81 (14.25)	180.75 (23.62)	226.75 (17.52)	166.39 (16.41)	0.88 (0.05)	15.68 (1.19)	55.10 (2.08)	1.37 (0.08)
KRA	Females*	5	379.45 (15.05)	52.58 (1.98)	160.86 (7.57)	218.60 (9.91)	250.26 (3.15)	180.37 (3.40)	0.89 (0.04)	14.81 (0.65)	57.61 (1.15)	1.39 (0.03)
	Males*	1	524.26	64.83	215.3	308.96	314.14	229.46	0.94	13.88	58.93	1.37
	Total	6	403.59 (60.63)	54.62 (5.31)	169.93 (23.23)	233.66 (37.94)	260.91 (26.23)	188.56 (20.27)	0.90 (0.04)	14.65 (0.69)	57.83 (1.16)	1.39 (0.03)
RMH	Females	27	223.94 (35.93)	33.08 (3.72)	109.96 (20.04)	113.98 (18.57)	174.43 (18.64)	115.25 (11.32)	0.95 (0.12)	19.71 (2.52)	50.94 (3.36)	1.51 (0.07)
	Males	29	286.86 (57.05)	43.82 (5.61)	128.80 (34.77)	158.07 (26.95)	204.31 (29.61)	142.43 (17.81)	0.90 (0.17)	16.61 (2.97)	55.54 (4.64)	1.43 (0.08)
	Total	56	256.52 (57.21)	38.64 (7.21)	119.72 (29.93)	136.81 (32.05)	189.90 (28.94)	129.33 (20.24)	0.92 (0.15)	18.10 (3.15)	53.32 (4.66)	1.47 (0.08)

* We take into account the sexual estimates of the fossil samples by García-Campos *et al.* (2020).

by Garcia-Campos et al. (2020). The mean and standard deviation of each population were assessed, as well as of the male and female subsamples within each group. We take into account the sexual estimates of the fossil samples and the actual sex in the case of forensic samples (see García-Campos et al. 2020).

Because of the sample size, we could not apply a comparative statistical analysis to assess the magnitude of the differences described; nevertheless, we performed other approaches to evaluate the magnitude of the variability of *H. antecessor* upper canines.

Firstly, to evaluate the variability of each variable independently, the Pearson´s Coefficient of Variation ($V=(\delta_x/\mu_x) \times 100$) was then assessed. The CV is considered to be very highly correlated with sexual dimorphism since when the difference between male and females means increases it causes a proportional increase in the standard deviation of the pooled-sex sample (Fleagle et al. 1980). For this reason, this coefficient has previously been used by other authors to study the internal variability of the fossil samples (e.g. Kay 1982; Leutenegger and Shell 1987; Arsuaga et al. 1997; Bermúdez de Castro et al. 2001). In order to avoid that differences in sample size may interfere in the comparison of the intra-population variability between modern human and fossil samples, a bootstrapping with replacement was employed. It was simulated 1000 random datasets with a sample size of nine individuals from the original modern human sample using R statistical software. Then, we calculated the CV in each dataset. The mean value obtained from the random samples, as well as the 95% confidence interval of their distribution, were compared with the value of the fossil samples.

Subsequently, a Principal Component Analysis (PCA) was applied to assess the variability of all variables as a whole. We only included absolute and relative variables measured in teeth with a wear degree equal or lower than 3 (Molnar, 1971). Once the PCA results were obtained, the centroids of each group were located and the Euclidean Distance (d) between the centroids of the groups formed by male and female individuals within each population was assessed. The Euclidean Distance between the canines ATD6-13 and ATD6-69 was also calculated.

Results

The results of the measurement of the dental tissues volumes and surface areas (Tab. 1 and Fig. 3) show that the canine ATD6-13 displays higher crown dimensions than ATD6-69. The marked canine size variation is also reflected in the absolute tissue dimensions. In ATD6-69, the enamel outer surface (OES) and the crown dentine-pulp complex dimensions (Vcdp, EDJS) are also smaller, partially due to the lower size of its crown, whereas in ATD6-13 these variables are larger. Despite this, ATD6-69 canine has absolutely (Ve) and relatively (3DAET, 3DRET, and OES/EDJS) greater enamel cap dimensions than ATD6-13. Lastly, ATD6-13 displays a higher percentage of crown volume that is a dentine-pulp complex.

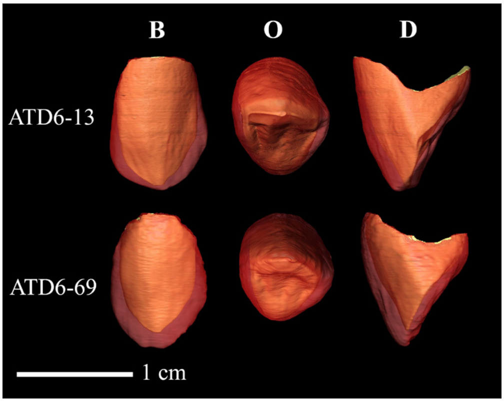

***Fig. 3** - Virtual reconstruction of the analysed teeth. In this figure are represented: the upper left canine ATD6-13 (H1) and the upper right canine ATD6-69 (H3). The right canine ATD6-69 has been mirrored in the image. Views: Buccal (B), occlusal (O) and distal (D).*

The Pearson´s Coefficient of Variation (CV) results obtained from *H. antecessor* (HA), Sima de los Huesos (SH), Krapina (KRA) and the recent modern human (RMH) samples are presented in Figure 4. For all absolute variables recorded, except for the crown basal surface (BS), the CV values of the HA maxillary canines fall below the mean value obtained from the 1000 recent modern human random samples, but near to the values obtained for SH and KRA. Among them, the CV values for the variables Vc, Ve and OES fall below to the recent modern humans 95% confidence interval. The CV value obtained for the BS of HA dental pieces overtakes the mean of RMH variation, although it falls within the 95% confidence interval. On the other hand, CV of the all relative variables recorded (3DAET, 3DRET, Vcdp/Vc, OES/EDJS) in HA maxillary canines are clearly higher than the values obtained in SH, KRA and RMH samples, even surpass the 95% confidence interval of the RMH variation range.

Regarding the results of the Principal Component Analysis, they are provided in Figure 5. The PCA analysis generated two principal components which explain 90.14% of the total variability observed in the sample. The results of the PCA allow us to observe that, in general terms, in each population the female individuals are displaced to the left quadrants with regard to the male individuals. These quadrants comprise the negative values for the first component which are obtained when the dental pieces exhibit higher values for the variables 3DAET, 3DRET and OES/EDJS, as well as lower values for the absolute variables and the Vcdp/Vc index. ATD6-13 and ATD6-69 appear separated in the PCA, being the first displaced to the upper left quadrant. The value for the Euclidean Distance calculated using the coordinates of the two points that represent the two maxillary canines of Gran Dolina-TD6.2 in the PCA was 2.73. This value is more than the double of those obtained through the comparison of the centroids of the point clouds formed by the female and male individuals from the recent modern human sample (d = 1.11), the Sima de los Huesos sample (d = 1.21) or the Krapina sample (d = 1.85).

Discussion

Several studies have documented that dental tissue proportions in the permanent dentition are sexually dimorphic not only in modern humans but also in other species of hominoids (e.g., Schwartz and Dean 2001; Schwartz et al. 2005; Saunders et al. 2007; Feeney et al. 2010; García-Campos et al. 2018a,b, 2020; Sorenti et al. 2019). These differences appear to have both a genetic and a hormonal origin (e.g., Alvesalo 1997, 2009; Zilberman and Smith 2001; Guatelli-Steinberg et al. 2008; Pentinpuro et al. 2014, 2017). On one hand, the quantitative and qualitative differences in the transcriptional products of the amelogenin genes, present on both the X and Y chromosomes, influence the proportions in which hard dental tissues are present (Salido et al. 1992; Schwartz and Dean 2005). Likewise, genetic alterations of these genes cause different dental tissue defects (Hu et al. 2012; Cho et al. 2014). On the other hand, sex hormones not only seem to play an essential role in the development of dental tissues, but also may be behind of the changes in secondary dentin deposition produced over the lifetime of the individual (Zilberman and Smith 2001; Guatelli-Steinberg et al. 2008; Alvesalo 2009; Ribeiro et al. 2012, 2013; Pentinpuro et al. 2014, 2017).

For this reason, the study of the dental tissue volumes and surface areas of permanent canines has been previously employed to estimate the sex and degree of sexual dimorphism of modern human populations (e.g., Saunders et al. 2007; Feeney et al. 2010; García-Campos et al. 2018a,b, 2020; Sorenti et al. 2019) as well as of some Middle Pleistocene human groups of Europe, such those from Sima de los Huesos (SH) and Krapina (Croatia) (García-Campos et al. 2020). The demographic structure of both SH and Krapina is characterized by the predominance of subadult and/or juvenile individuals (Bocquet-Appel and Arsuaga 1999), which makes difficult to obtain conclusive sexual estimates from their cranial and postcranial remains (Bermúdez de Castro et al. 2001; Rosas et al. 2002; Arsuaga et al. 2014). However, the assessment of the dental tissue proportions of their permanent canines has allowed not only the confirmation of the sex allocation of individuals previously assigned in the literature but also to estimate the sex of the youngest individuals, which were not assessed in previous studies (García-Campos et al. 2020). In total, employing this methodology it was possible to estimate the sex of 15 out of the 17 individuals of the SH sample, as well as of all the Krapina individuals of which permanent canines were available (García-Campos et al. 2020). As in the case of Sima de los Huesos and Krapina samples, the Gran Dolina-TD6.2 population is composed mainly of immature individuals. This is a limitation that must be addressed when carrying out paleodemographic studies on this fossil sample.

The sample of *H. antecessor* included in this study is composed of two permanent canines: the left maxillary canine ATD6-13, belonging to individual H1, holotype of the species (Bermúdez de Castro et al. 1997); and the left maxillary canine ATD6-69 of individual H3. The individual H1 is identified by a set of isolated permanent teeth, as well as a fragment on the right side of a mandibular body with the molar series in-situ and a small and deteriorated fragment on the left side of a maxilla with the canine and first premolar in-situ (Arsuaga et al. 1999, see Fig. 2). The H1 teeth are very large in the context of the variability known for the European Pleistocene fossil record (Bermúdez de Castro et al. 1999; Martinón-Torres et al. 2019). In particular, the size of the maxillary canine of H1 is at the upper limit of the range of variation of the genus *Homo* (Bermúdez de Castro et al. 1999; Martinón- Torres et al. 2019). For this reason, H1 was previously estimated to represent a young male individual with an age at death of 12.9 years old according to current standards (Bermúdez de Castro et al. 1999). Likewise, the remarkable size difference between the teeth of the mandibles ATD6-5 (H1) and ATD6-96 (H7) makes Carbonell et al. (2005) suggest that the former was probably a male, whereas the latter mandible belonged to a female. On the other hand, the individual H3 is identified by the specimen ATD6-69, which consists of an important part of the left side of the face, the alveolar process of the maxilla, the anterior portion of the palate and the vomer (Arsuaga et al. 1999, see Fig. 2). The incisor, canine, first and second premolars, first permanent molar on the right side and the first premolar and the complete molar series on the left side are preserved in-situ (Bermúdez de Castro et al. 2006; Martín-Francés et al. 2018, 2020). Except for the alveolar width, the facial dimensions of ATD6-69 are small (Arsuaga et al. 1999). This fact has been associated with the age of death of H3, which according to current standards, could be between 10 and 12 years old (Bermúdez de Castro et al. 1999). However, the results obtained in various studies suggest that the 85% of maxillar size is reached by the age of 6 (Enlow and Bang 1965; Sperber et al. 2001; Vardimon et al. 2010), which opens the door to the hypothesis that the size of this individual maxilla may be due to the effect of intersexual variability.

The analysis of the two upper canines of Gran Dolina-TD6.2, belonging to individuals H1 (ATD6-13) and H3 (ATD6-69), reveals that the H1 canine has larger crown dimensions (Tab.1 and Fig. 3). Previous studies have already described differences in size between ATD6-13 and ATD6-69 canines (Bermúdez de Castro et al. 1999; Martinón-Torres et al. 2019). The canine ATD6-69 is in process of eruption, which has prevented that the mesiodistal (MD) and buccolingual (BL) diameters of its crown could be measured employing traditional techniques. However, once the canine ATD6-69 was virtually reconstructed in this study, it was possible to measure the MD and BL diameters of its crown. As it was expected, the values obtained (MD = 8.57 mm, BL = 9.73 mm) are lower than those observed by Bermúdez de Castro et al. (1999) in ATD6-13 (MD = 8.9 mm, BL = 11.0 mm). This is consistent with the results obtained from the evaluation of the volume and surface areas of the crown (Vc, BS, OES, EDJS) of both dental pieces. Interestingly, despite individual H1 upper canine has larger crown dimensions than individual H3, it displays lower volume and relative enamel dimensions (3DAET, 3DRET and OES/EDJS). This could be potentially attributed to the slight dental wear of individual H1 canine (degree of wear 2 according to Molnar, 1971) whereas the crown of H3 is intact (Bermúdez de Castro et al. 1999). However, as it is explained below, these differences are too large to be only explained by the effect of dental wear.

The results obtained from the Pearson´s Coefficient of Variation (CV) show that, for the most of the absolute variables recorded, the CV values of the *H. antecessor* maxillary canines fall below the mean value obtained from the 1000 recent modern human random samples, but near to the values obtained for SH and KRA (Fig. 4). However, for all relative variables recorded (3DAET, 3DRET, Vcdp/Vc, OES/EDJS) and the area of the crown basal surface (BS), the CV values of Gran Dolina-TD6.2 teeth are clearly higher than the values obtained in SH,

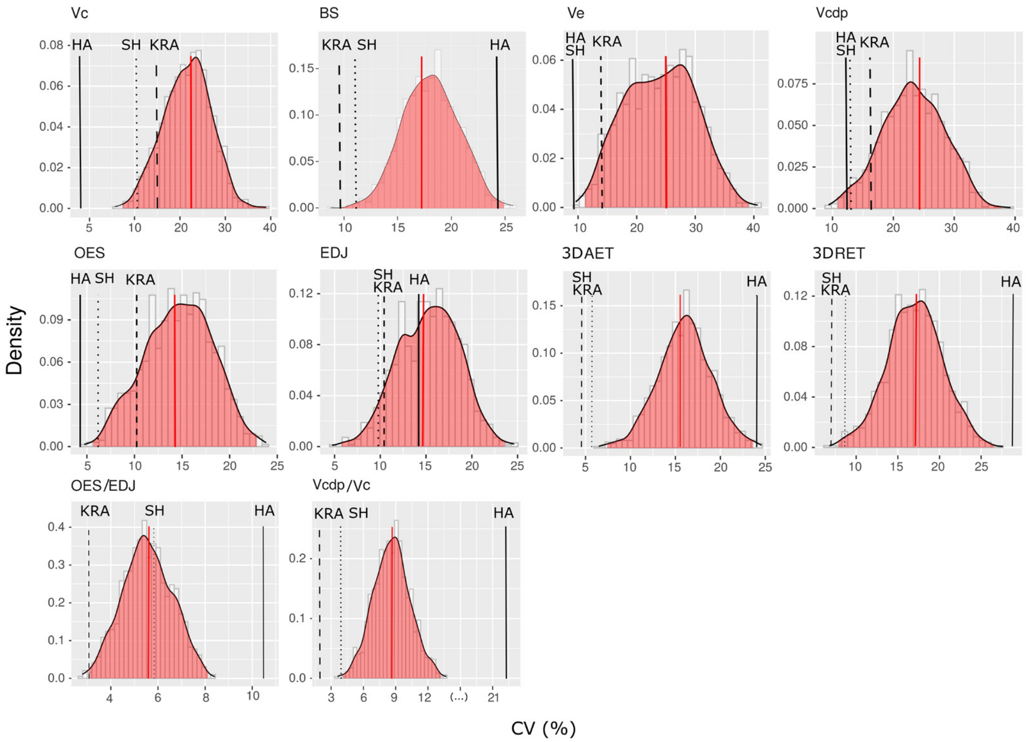

***Fig. 4** - Frequency histograms of coefficients of variation (CV, percentage scale) of each absolute variable and associated indices evaluated in upper canines, calculated from 1000 random samples of individuals belonging to the recent modern human sample of the same size that the SH fossil-sample. The vertical red line marks the CV mean value of the whole recent modern human sample and the red shaded area shows 95% confidence interval of this distribution. On the other hand, the black line indicates the CV value Gran Dolina-TD6.2 (HA) hominid dental sample. Finally, the dashed black lines indicate the CV the mean value of the Sima de los Huesos (SH) and Krapina (KRA) sample.*

KRA and RMH samples, even surpassing the 95% confidence interval of the RMH variation range (Fig. 4). Likewise, as it can be appreciated in the scatter plot (Fig. 5), the two canines of Gran Dolina-TD6.2 appear clearly separated in the PCA. The canine ATD6-69 falls within the positive values of Principal Component 1 (PC1), but is closer to the ordinate axis than ATD6-13, which holds higher values for the first component. For the Principal Component 2 (PC2), ATD6-69 falls within the positive area, whereas ATD6-13 holds negative values. The assessment of Euclidean Distance between both dental pieces resulted in a value of 2.73, more than double of those obtained through the comparison of the centroids of the point clouds formed by the female and male individuals from the recent modern human sample (d = 1.11), the Sima de los Huesos sample (d = 1.21) or the Krapina sample (d = 1.85).

The magnitude of the variability observed in the Gran Dolina-TD6.2 dental sample might make us think that the two teeth assessed in this study may belong to individuals from different taxa. Two- and three-dimensional assessment of dental tissues, and specifically of the enamel thickness, has been also used in taxonomic studies to infer the identity and phylogenetic

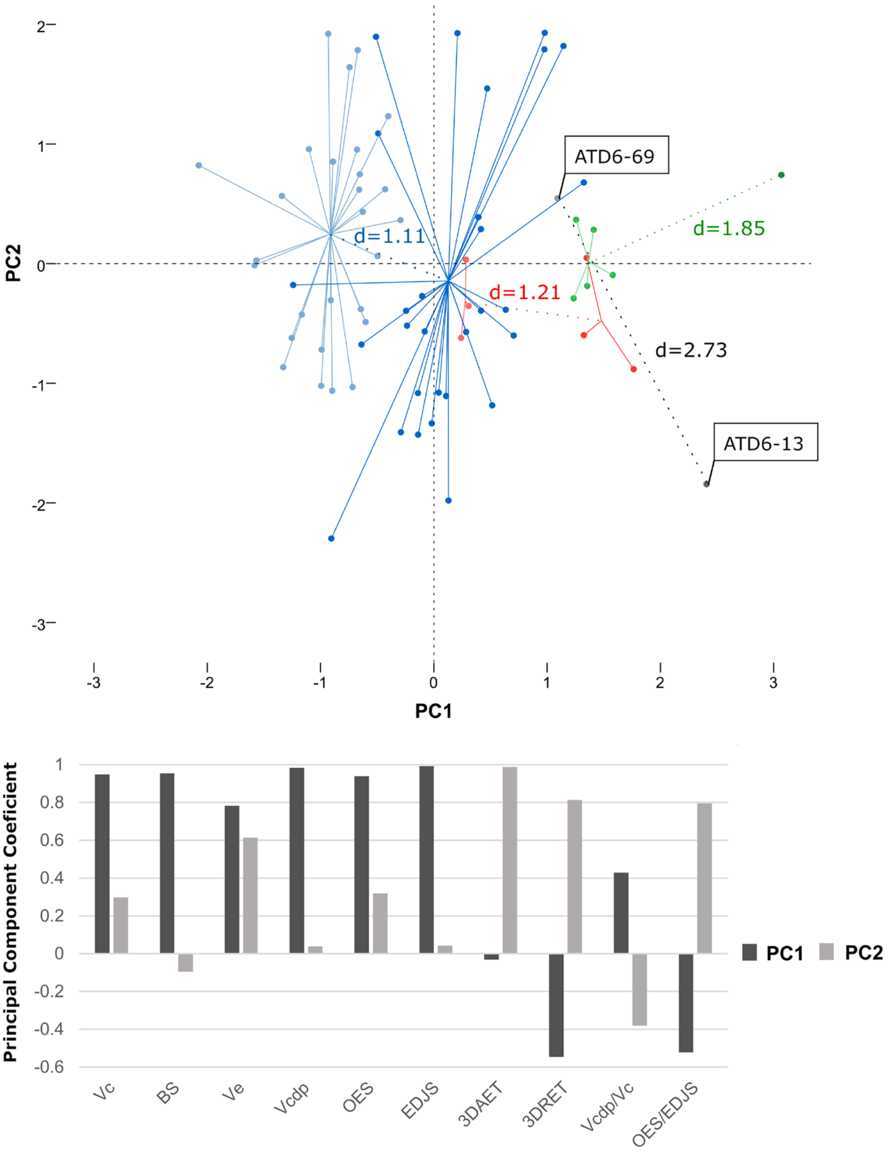

***Fig. 5** - Principal Component Analysis (PCA) applied to the maxillary canines from* Gran Dolina -TD6.2 *(in grey), Sima de los Huesos (in red), Krapina (in green) and the modern human (in blue) samples. Above, the scatter plot represents the first two components of the PCA (PC1 and PC2), which explain 90.14% of the total variability observed in the sample. In the graph, each point appears referenced concerning the centroid of each sub-sample. The values Euclidean distance (d) between the centroids of the groups formed by male and female individuals within each population can be also seen in the scatter plot. Male individuals in the Krapina sample are represented by a single tooth, whose coordinates were employed to calculate the Euclidean distance. The Euclidean distance between the canines ATD6-13 and ATD6-69 has been also assessed thought the values of their coordinates. Below, the coefficients of each of the variables and index evaluated for each component can be seen.*

relationships of past hominid species (e.g., Kono 2004; Olejniczak et al. 2008; Smith et al. 2012; Martín-Francés et al. 2018; García-Campos et al. 2019). In particular, the thinly enameled pattern has been identified as a distinctive Neanderthal lineage features (Olejniczak et al. 2008a; Bayle et al. 2009; Smith et al. 2012; Buti et al. 2017; García-Campos et al. 2019). However, neither taphonomic nor morphological evidence seem to support this scenario. On the one hand, ATD6-13 and ATD6-69, as well as the other dental and cranial remains associated with both teeth, were discovered in a small excavation area of only 6 m², a survey performed in 1994 in the Gran Dolina site (Bermúdez de Castro et al. 1999). Likewise, all these remains come from the same lithostratigraphic subunit, ATD6.2 (Bermúdez de Castro et al. 1997; Carbonell et al. 2010). On the other hand, both upper canines share some morphological traits that characterized the mosaic pattern typical from *H. antecessor* dentition, such as the asymmetry of the occlusal edge, the reduction mesial cutting edge and the degree of inclination of the distal one, or the loss of the cingulum and associated structures (Martinón-Torres et al. 2019). Therefore, the most parsimonious interpretation the results obtained here is that the wide variability observed in the histological pattern of the two canines from Gran Dolina-TD6.2 is result of the intra-population variability not of the inter-population variability.

The wide intra-population variability seen in *H. antecessor* canines has also been described in its posterior dentition by Martin-Francés et al. (2018, 2020). On one hand, Martín-Francés and colleagues describe that: "The individual TD6-H1 upper premolars (P 3: ATD6-7 and ATD6-13, and P 4: ATD6-8 and ATD6-9) exhibit thin enamelled crowns (…) On the contrary, the upper premolars (ATD6-69 specimens) belonging to individual H3 exhibit the thick pattern in their crowns". Likewise, similar but less marked differences could be appreciated in the molars of both individuals (Martín-Francés et al. 2018). These authors support that this high variability would be compatible with *H. antecessor* species being close to the last common ancestor of the Neanderthal and modern human lineages (Bermúdez de Castro et al. 2016), which might explain the presence of individuals with derived and primitive conditions in their dentition within the TD6.2 population. Another possibility is that the differences observed in the dental tissue proportions of H1 and H3 individuals might be due to the presence of sexual dimorphism. The differences appreciated between ATD6-13 and ATD6-69 concur with the histological pattern that tends to distinguish the dentition of males and females in recent modern humans (e.g., Feeney et al. 2010; García-Campos et al. 2018a,b, 2020; Saunders et al. 2007; Sorenti et al. 2019) as well as in other hominoid species (Schwartz and Dean 2001; Schwartz et al. 2005; García-Campos et al. 2020). Numerous studies have shown that female individuals tend to have smaller teeth, with a relative predominance of the enamel component and a smaller dentin-pulp complex than male individuals (Schwartz and Dean 2001, 2005; Schwartz et al. 2005; Smith et al. 2006; Saunders et al. 2007; Feeney et al. 2010; García-Campos et al. 2018a,b, 2020; Sorenti et al. 2019). Therefore, the presence of this pattern in Gran Dolina TD6.2 canines, premolars and molars would reinforce the idea that the variability found in the TD6.2 sample is likely due to sexual variation. If this is the case, the pattern observed in H1 dentition would be indicative that we are face on a male individual, while H3 would be a female individual, which would support the conclusions obtained by other authors (Bermúdez de Castro et al. 1999, 2006; Carbonell et al. 2005).

Unfortunately, the small sample size of TD6.2 population prevents us from obtaining conclusive inferences based on the dental tissue pattern of their permanent canines. The discovery of new fossils at this level of Gran Dolina could help to better understand the intrapopulation variability of this sample and, therefore, confirm or refute these hypotheses. In any case, the results obtained in this study demonstrate, once again, the usefulness of the dental tissue proportions of permanent canines for the sexual dimorphism assessment in modern and past human populations. In particular, the study of enamel and dentine dimensions can be a particularly useful tool in palaeoanthropological contexts, where other bone structures are often fragmented or absent, and especially in those where their demographic structure has a greater representation of subadult individuals.

Acknowledgments

This study has been supported by the Dirección General de Investigación of the Spanish Ministerio de Economía y Competitividad (MINECO /FEDER) grant number: PGC2018-093925-B-C31 and The Leakey Foundation through the personal support of G. Getty (2013) and D. Crook (2014-2020) to M. M.-T. C. G-C and L. M-F are the recipients of a post-doctoral research grant at the Atapuerca Foundation. The micro-CT images were obtained in the Laboratory of Microscopy of the CENIEH-ICTS (Spain) in collaboration with CENIEH staff. We thank all the members of the Atapuerca research team, in particular those who excavate the Gran Dolina-TD6.2 site, for their dedicated work. We also acknowledge several people for providing access to the modern human sample included. The African sample from Sudan was provided by Dr Christopher Dean from the Anatomy Department at University College London. We are indebted to A. Oettlé, G. Krüger and E.N. L'Abbé for kindly authorizing access to the Pretoria Bone Collection (PBC) of the University of Pretoria, and to Dr. Clément Zanolli for interceding and making it possible. In the same way, we would like to acknowledge to Dr. Bernardo Perea Pérez, for authorizing access to the collections from Escuela de Medicinal Legal de la Universidad Complutense de Madrid.

References

Acharya AB, Mainali S (2008) Are dental indexes useful in sex assessment? J Forensic Odontostomatol 26:53–59

Alvesalo L (1997) Sex chromosomes and human growth. Hum Genet 101:1–5. https://doi.org/10.1007/s004390050575

Alvesalo L (2009) Human sex chromosomes in oral and craniofacial growth. Arch Oral Biol 54 Suppl 1:S18–24. https://doi.org/10.1016/j.archoralbio.2008.06.004

Antón SC (2003) Natural history of *Homo erectus*. Am J Phys Anthropol Suppl 37:126–170. https://doi.org/10.1002/ajpa.10399

Arnold LJ, Demuro M (2015) Insights into TT-OSL signal stability from single-grain analyses of known-age deposits at Atapuerca, Spain. Quat Geochronol 30:472–478. https://doi.org/10.1016/j.quageo.2015.02.005

Arsuaga JL, Carretero JM, Lorenzo C, et al (1997) Size variation in Middle Pleistocene humans. Science 277:1086–1088. https://doi.org/10.1126/science.277.5329.1086

Arsuaga JL, Martínez I, Arnold LJ, et al (2014) Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science 344:1358–1363. https://doi.org/10.1126/science.1253958

Arsuaga JL, Martínez I, Lorenzo C, et al (1999) The human cranial remains from Gran Dolina Lower Pleistocene site (Sierra de Atapuerca, Spain). J Hum Evol 37:431–457. https://doi.org/10.1006/jhev.1999.0309

Ateş M, Karaman F, Işcan MY, Erdem TL (2006) Sexual differences in Turkish dentition. Leg Med 8:288–292. https://doi.org/10.1016/j.legalmed.2006.06.003

Bayle P, Braga J, Mazurier A, Macchiarelli R (2009) Dental developmental pattern of the Neanderthal child from Roc de Marsal: a high-resolution 3D analysis. J Hum Evol 56:66–75. https://doi.org/10.1016/j.jhevol.2008.09.002

Bermúdez de Castro JM, Arsuaga JL, Carbonell E, et al (1997) A hominid from the lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. Science 276:1392–1395. https://doi.org/10.1126/science.276.5317.1392

Bermúdez de Castro JM, Carbonell E, Gómez A, et al (2006) Paleodemografía del hipodigma de fósiles de homininos del nivel TD6 de Gran Dolina (Sierra de Atapuerca, Burgos): estudio preliminar. Estudios Geológicos 62:145–154. https://doi.org/10.3989/egeol.0662114

Bermúdez de Castro JM, Martinón-Torres M, Martín-Francés L, et al (2015) *Homo antecessor*: The state of the art eighteen years later. Quat Int 433:22-31. https://doi.org/10.1016/j.quaint.2015.03.049

Bermúdez de Castro JM, Martinón-Torres M, Sarmiento S, *et al (*2003) Gran Dolina-TD6 versus Sima de los Huesos dental samples from Atapuerca: evidence of discontinuity in the European Pleistocene population? *J Archaeol Sci* 30:1421–1428. https://doi.org/10.1016/S0305-4403(03)00036-0

Bermúdez de Castro JM, Pérez-González A, Martinón-Torres M, et al (2008) A new early Pleistocene hominin mandible from Atapuerca-TD6, Spain. J Hum Evol 55:729–735. https://doi.org/10.1016/j.jhevol.2008.03.006

Bermúdez de Castro JM, Rosas A, Nicolás ME (1999) Dental remains from Atapuerca-TD6 (Gran Dolina site, Burgos, Spain). J Hum Evol 37:523–566. https://doi.org/10.1006/jhev.1999.0323

Bermúdez de Castro JM, Sarmiento S, Cunha E, et al (2001) Dental size variation in the Atapuerca-SH Middle Pleistocene hominids. J Hum Evol 41:195–209. https://doi.org/10.1006/jhev.2001.0491

Bocquet-Appel JP, Arsuaga JL (1999) Age Distributions of Hominid Samples at Atapuerca (SH) and Krapina Could Indicate Accumulation by Catastrophe. J Archaeol Sci 26:327–338. https://doi.org/10.1006/jasc.1998.0370

Buti L, Le Cabec A, Panetta D, et al (2017) 3D enamel thickness in Neandertal and modern human permanent canines. J Hum Evol 113:162–172. https://doi.org/10.1016/j.jhevol.2017.08.009

Campaña I, Benito-Calvo A, Pérez-González A, et al. (2017) Pleistocene sedimentary facies of the Gran Dolina archaeo-paleoanthropological site (Sierra de Atapuerca, Burgos, Spain). Quat Int 433:68–84. https://doi.org/10.1016/j.quaint.2015.04.023

Carbonell E, Bermúdez de Castro JM, Arsuaga JL, et al (2005) An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. Proc Natl Acad Sci USA 102:5674–5678. https://doi.org/10.1073/pnas.0501841102

Carbonell E, Bermúdez de Castro JM, Parés JM, et al (2008) The first hominin of Europe. Nature 452:465–469. https://doi.org/10.1038/nature06815

Carbonell E, Cáceres I, Ruiz ML et al (2010) Cultural cannibalism as a Paleoeconomic system in the European Lower Pleistocene: the case of level TD6 of Gran Dolina (Sierra de Atapuerca, Burgos, Spain). Curr Anthropol 4:539–549. https://doi.org/10.1086/653807

Carbonell E, Mosquera M, Rodríguez XP, et al (1999) Out of Africa: The Dispersal of the Earliest Technical Systems Reconsidered. Journal of Anthropological Archaeology 18:119–136. https://doi.org/10.1006/jaar.1998.0331

Cho ES, Kim K-J, Lee K-E, et al (2014) Alteration of conserved alternative splicing in AMELX causes enamel defects. J Dent Res 93:980–987. https://doi.org/10.1177/0022034514547272

Cuenca-Bescós G, Blain H-A, Rofes J, et al (2015) Comparing two different Early Pleistocene microfaunal sequences from the caves of Atapuerca, Sima del Elefante and Gran Dolina (Spain): Biochronological implications and significance of the Jaramillo subchron. Quat Int 389:148-158. https://doi.org/10.1016/j.quaint.2014.12.059

Cuenca-Bescós G, Laplana C, Canudo JI (1999) Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). J Hum Evol 37:353–373. https://doi.org/10.1006/jhev.1999.0306

Dirkmaat DC (ed) (2012) A companion to forensic anthropology. John Wiley & Sons, Ltd, Chichester, UK.

Duval M, Grün R, Parés JM, et al (2018) The first direct ESR dating of a hominin tooth from Atapuerca Gran Dolina TD-6 (Spain) supports the antiquity of *Homo antecessor*. Quat Geochronol 47:120–137. https://doi.org/10.1016/j.quageo.2018.05.001

Enlow DH, Bang S (1965) Growth and remodeling of the human maxilla. Am J Orthod 51:446–464. https://doi.org/10.1016/0002-9416(65)90242-3

Feeney RN, Zermeno JP, Reid DJ, et al (2010) Enamel thickness in Asian human canines and premolars. Anthropol Sci 118:191–198. https://doi.org/10.1537/ase.091006

Fleagle JG, Kay RF, Simons EL (1980) Sexual dimorphism in early anthropoids. Nature 287:328–330. https://doi.org/10.1038/287328a0

García-Campos C, Martinón-Torres M, Martín-Francés L, et al (2018a) Contribution of dental tissues to sex determination in modern human populations. Am J Phys Anthropol 166:459–472. https://doi.org/10.1002/ajpa.23447

García-Campos C, Martinón-Torres M, Martínez de Pinillos M, et al (2018b) Modern humans sex estimation through dental tissue patterns of maxillary canines. Am J Phys Anthropol 167:914–923. https://doi.org/10.1002/ajpa.23715

García-Campos C, Martinón-Torres M, Martín-Francés L, et al (2019) Enamel and dentine dimensions of the Pleistocene hominins from Atapuerca (Burgos, Spain): A comparative study of canine teeth. C R Palevol 18:72–89. https://doi.org/10.1016/j.crpv.2018.06.004

García-Campos C, Modesto-Mata M, Martinón-Torres M, et al (2020) Sexual dimorphism of the enamel and dentine dimensions of the permanent canines of the Middle Pleistocene hominins from Sima de los Huesos (Burgos, Spain). J Hum Evol 144:102793. https://doi.org/10.1016/j.jhevol.2020.102793

Gómez-Robles A, Bermúdez de Castro JM, Martinón-Torres M, et al (2015) A geometric morphometric analysis of hominin lower molars: Evolutionary implications and overview of postcanine dental variation. J Hum Evol 82:34–50. https://doi.org/10.1016/j.jhevol.2015.02.013

Guatelli-Steinberg D, Sciulli PW, Betsinger TK (2008) Dental crown size and sex hormone concentrations: another look at the development of sexual dimorphism. Am J Phys Anthropol 137:324–333.https://doi.org/10.1002/ajpa.20878

Harmon E (2009) Size and shape variation in the proximal femur of *Australopithecus africanus*. J Hum Evol 56:551–559. https://doi.org/10.1016/j.jhevol.2009.01.002

Harmon EH (2006) Size and shape variation in *Australopithecus afarensis* proximal femora. J Hum Evol 51:217–227. https://doi.org/10.1016/j.jhevol.2006.01.009

Harris EF, Bailit HL (1988) A principal components analysis of human odontometrics. Am J Phys Anthropol 75:87–99. https://doi.org/10.1002/ajpa.1330750110

Hassett B (2011) Technical note: estimating sex using cervical canine odontometrics: a test using a known sex sample. Am J Phys Anthropol 146:486–489. https://doi.org/10.1002/ajpa.21584

Hillson S (1996) Dental Anthropology. Cambridge University Press

Hu JC-C, Chan H-C, Simmer SG, et al (2012) Amelogenesis imperfecta in two families with defined AMELX deletions in ARHGAP6. PLoS One 7:e52052. https://doi.org/10.1371/journal.pone.0052052

Kay RF (1982) *Sivapithecus simonsi*, a new species of miocene hominoid, with comments on the phylogenetic status of the *ramapithecinae*. Int J Primatol 3:113–173. https://doi.org/10.1007/BF02693493

Kono RT (2004) Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. Anthropol Sci 112:121–146. https://doi.org/10.1537/ase.03106

Işcan MY, Kedici PS (2003) Sexual variation in bucco-lingual dimensions in Turkish dentition. Forensic Sci Int 137:160–164. https://doi.org/10.1016/s0379-0738(03)00349-9

Johanson DC, Masao FT, Eck GG, et al (1987) New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. Nature 327:205–209. https://doi.org/10.1038/327205a0

Leutenegger W, Shell B (1987) Variability and sexual dimorphism in canine size of Australopithecus and extant hominoids. J Hum Evol 16:359–367. https://doi.org/10.1016/0047-2484(87)90066-2

Lorenzo C, Arsuaga JL, Carretero JM (1999) Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). J Hum Evol 37:501–522. https://doi.org/10.1006/jhev.1999.0341

Lorenzo C, Carretero JM, Arsuaga JL, et al (1998) Intrapopulational body size variation and cranial capacity variation in Middle Pleistocene humans: the Sima de los Huesos sample (Sierra de Atapuerca, Spain). Am J Phys Anthropol 106:19–33. https://doi.org/3.0.CO;2-8">10.1002/(SICI)1096-8644(199805)106:1<19::AID-AJPA2>3.0.CO;2-8

Martín-Francés L, Martinón-Torres M, Martínez de Pinillos M, et al (2020) Ectopic maxillary third molar in Early Pleistocene *Homo antecessor* from Atapuerca-Gran Dolina site (Burgos, Spain). Am J Phys Anthropol 171:733–741. https://doi.org/10.1002/ajpa.24010

Martín-Francés L, Martinón-Torres M, Martínez de Pinillos M, et al (2018) Tooth crown tissue proportions and enamel thickness in Early Pleistocene *Homo antecessor* molars (Atapuerca, Spain). PLoS One 13:e0203334. https://doi.org/10.1371/journal.pone.0203334

Martín-Francés L, Martinón-Torres M, Martínez de Pinillos M, et al 2021. Crown tissue proportions and enamel thickness distribution in early Pleistocene *Homo antecessor* maxillary premolars (Atapuerca, Spain). Unpublished manuscript.

Martinón-Torres M (2006) Evolución del aparato dental en homínidos: estudio de los dientes humanos del Pleistoceno de la Sierra de Atapuerca (Burgos). Universidad de Santiago de Compostela, Santiago de Compostela.

Martinón-Torres M, Bermúdez de Castro JM, Gómez-Robles A, et al (2012) Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). J Hum Evol 62:7–58. https://doi.org/10.1016/j.jhevol.2011.08.007

Martinón-Torres M, Bermúdez de Castro JM, Martínez de Pinillos M, et al (2019) New permanent teeth from Gran Dolina-TD6 (Sierra de Atapuerca). The bearing of Homo antecessor on the evolutionary scenario of Early and Middle Pleistocene Europe. J Hum Evol 127:93–117. https://doi.org/10.1016/j.jhevol.2018.12.001

McHenry HM (1991) Petite bodies of the robust australopithecines. Am J Phys Anthropol 86:445–454. https://doi.org/10.1002/ajpa.1330860402

McHenry HM (1994) Behavioral ecological implications of early hominid body size. J Hum Evol 27:77–87. https://doi.org/10.1006/jhev.1994.1036

Molnar S (1971) Human tooth wear, tooth function and cultural variability. Am J Phys Anthropol 34:175–189. https://doi.org/10.1002/ajpa.1330340204

Moorrees CF, Fanning EA, Hunt EE Jr (1963) Age variation of formation stages for ten permanent teeth. J Dent Res 42:1490–1502. https://doi.org/10.1177/00220345630420062701

Moreno D, Falguères C, Pérez-González A, et al (2015) New radiometric dates on the lowest stratigraphical section (TD1 to TD6) of Gran Dolina site (Atapuerca, Spain). Quat Geochronol 30:535–540. https://doi.org/10.1016/j.quageo.2015.05.007

Olejniczak AJ, Smith TM, Feeney RNM, et al (2008a) Dental tissue proportions and enamel thickness in Neandertal and modern human molars. J Hum Evol 55:12–23. https://doi.org/10.1016/j.jhevol.2007.11.004

Olejniczak AJ, Smith TM, Skinner MM, et al (2008b) Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus*. Biol Lett 4:406–410. https://doi.org/10.1098/rsbl.2008.0223

Parés JM, Pérez-González A (1999) Magnetochronology and stratigraphy at Gran Dolina section, Atapuerca (Burgos, Spain). J Hum Evol 37:325–342. https://doi.org/10.1006/jhev.1999.0331

Peckmann TR, Logar C, Garrido-Varas CE, et al (2016) Sex determination using the mesio-distal dimension of permanent maxillary incisors and canines in a modern Chilean population. Sci Justice 56:84–89. https://doi.org/10.1016/j.scijus.2015.10.002

Pentinpuro RH, Lähdesmäki RE, Niinimaa AO, et al (2014) Crown heights in the permanent teeth of 45,X and 45,X/46,XX females. Acta Odontol Scand 72:908–916. https://doi.org/10.3109/00016357.2014.921327

Reno PL, McCollum MA, Meindl RS, Lovejoy CO (2010) An enlarged postcranial sample confirms Australopithecus afarensis dimorphism was similar to modern humans. Philos Trans R Soc Lond B Biol Sci 365:3355–3363. https://doi.org/10.1098/rstb.2010.0086

Reno PL, Meindl RS, McCollum MA, Lovejoy CO (2003) Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. Proc Natl Acad Sci U S A 100:9404–9409. https://doi.org/10.1073/pnas.1133180100

Ribeiro DC, Brook AH, Hughes TE, et al (2013) Intrauterine hormone effects on tooth dimensions. J Dent Res 92:425–431. https://doi.org/10.1177/0022034513484934

Ribeiro D, Sampson W, Hughes T, et al (2012) Sexual dimorphism in the primary and permanent dentitions of twins: an approach to clarifying the role of hormonal factors. In: Townsend G, Kanazawa E, Takayama H. (eds) New Directions in Dental Anthropology, University of Adelaide Press, Adelaide, p. 46–64. 10.1017/UPO9780987171870.006

Richmond BG, Jungers WL (1995) Size variation and sexual dimorphism in *Australopithecus afarensis* and living hominoids. J Hum Evol 29:229–245. https://doi.org/10.1006/jhev.1995.1058

Rodríguez J, Burjachs F, Cuenca-Bescós G, et al (2011) One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quat Sci Rev 30:1396–1412. https://doi.org/10.1016/j.quascirev.2010.02.021

Rosas A (1997) A gradient of size and shape for the Atapuerca sample and Middle Pleistocene hominid variability. J Hum Evol 33:319–331. https://doi.org/10.1006/jhev.1997.0138

Rosas A, Bastir M, Martínez-Maza C, Bermúdez de Castro JM (2002) Sexual dimorphism in the Atapuerca-SH hominids: the evidence from the mandibles. J Hum Evol 42:451–474. https://doi.org/10.1006/jhev.2001.0536

Salido EC, Yen PH, Koprivnikar K, et al (1992) The human enamel protein gene amelogenin is expressed from both the X and the Y chromosomes. Am J Hum Genet 50:303–316

Saunders SR, Chan AHW, Kahlon B, et al (2007) Sexual dimorphism of the dental tissues in human permanent mandibular canines and third premolars. Am J Phys Anthropol 133:735–740. https://doi.org/10.1002/ajpa.20553

Schwartz GT, Dean C (2001) Ontogeny of canine dimorphism in extant hominoids. Am J Phys Anthropol 115:269–283. https://doi.org/10.1002/ajpa.1081

Schwartz GT, Dean MC (2005) Sexual dimorphism in modern human permanent teeth. Am J Phys Anthropol 128:312–317. https://doi.org/10.1002/ajpa.20211

Schwartz GT, Miller ER, Gunnell GF (2005) Developmental processes and canine dimorphism in primate evolution. J Hum Evol 48:97–103. https://doi.org/10.1016/j.jhevol.2004.10.005

Skinner MM, Gordon AD, Collard NJ (2006) Mandibular size and shape variation in the hominins at Dmanisi, Republic of Georgia. J Hum Evol 51:36–49. https://doi.org/10.1016/j.jhevol.2006.01.006

Skinner MM, Gunz P, Wood BA, Hublin J-J (2008) Enamel-dentine junction (EDJ) morphology distinguishes the lower molars of Australopithecus africanus and Paranthropus robustus. J Hum Evol 55:979–988. https://doi.org/10.1016/j.jhevol.2008.08.013

Smith FH 1980. Sexual differences in European Neanderthal crania with special reference to the Krapina remains. J Hum Evol 9:359–375. https://doi.org/10.1016/0047-2484(80)90048-2

Smith TM, Olejniczak AJ, Reid DJ, et al (2006) Modern human molar enamel thickness and enamel-dentine junction shape. Arch Oral Biol 51:974–995. https://doi.org/10.1016/j.archoralbio.2006.04.012

Smith TM, Olejniczak AJ, Zermeno JP, et al (2012) Variation in enamel thickness within the genus Homo. J Hum Evol 62:395–411. https://doi.org/10.1016/j.jhevol.2011.12.004

Sorenti M, Martinón-Torres M, Martín-Francés L, Perea-Pérez B (2019) Sexual dimorphism of dental tissues in modern human mandibular molars. Am J Phys Anthropol 169:332–340. https://doi.org/10.1002/ajpa.23822

Sperber GH, Sperber GHS, Guttmann GD, et al. 2001. Craniofacial Development (Book for Windows & Macintosh). PMPH-USA.

Stringer BC (1986) The credibility of *Homo habilis*. In: B Wood, H Martin, P Andrews (eds) Major topics in primate and human evolution. Cambridge University Press, Cambridge .

Trinkaus E (1980) Sexual differences in Neanderthal limb bones. J Hum Evol 9:377–397. https://doi.org/10.1016/0047-2484(80)90049-4

Vardimon AD, Shoshani K, Shpack N, et al (2010) Incremental growth of the maxillary tuberosity from 6 to 20 years-A cross-sectional study. Arch Oral Biol 55:655–662. https://doi.org/10.1016/j.archoralbio.2010.05.012

Welker F, Ramos-Madrigal J, Gutenbrunner P, et al (2020) The dental proteome of *Homo antecessor*. Nature 580:235–238. https://doi.org/10.1038/s41586-020-2153-8

Wolpoff MH (1979) The Krapina dental remains. Am J Phys Anthropol 50:67–114. https://doi.org/10.1002/ajpa.1330500110

Wood B (1992) Origin and evolution of the genus *Homo*. Nature 355:783–790. https://doi.org/10.1038/355783a0

Zilberman U, Smith P (2001) Sex- and age-related differences in primary and secondary dentin formation. Adv Dent Res 15:42–45. https://doi.org/10.1177/08959374010150011101

Zorba E, Vanna V, Moraitis K (2014) Sexual dimorphism of root length on a Greek population sample. Homo 65:143–154. https://doi.org/10.1016/j.jchb.2013.09.005

Editor, Giovanni Destro Bisol