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Inter- and intrapopulation variability of dental tissue proportions of European and African modern human populations' permanent canines

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Abstract Numerous studies have shown that human dentition traits vary both between and within populations. However, there is still little knowledge about how dental tissue proportions differ between modern human groups. In this study, two samples of European and African individuals were compared to assess the possible differences and similarities present in the dental tissue dimensions of their permanent canines. For this purpose, the volumes and surface areas of the coronal dentine and pulp complex and the enamel cap of 127 canines were measured by microcomputed tomography. The results show the existence of interpopulation variability in the dental tissue pattern of both samples, which is mainly due to the presence of a larger enamel component in the African population, while dentine seems to play a less critical role in the differences described between both dental samples. We also observed a similar pattern of sexual dimorphism in the dental tissue proportions of European and African canines, but in this case, the intrapopulation variability was mainly due to the presence of a greater dentine component in males. Therefore, because the dimensions of dental tissues vary at both inter- and intrapopulation levels in modern human groups, our results highlight the importance of selecting comparative samples that are geographically mixed and sex-balanced for future paleoanthropological investigations on dental tissue patterns of extinct and extant species to avoid overestimating or underestimating any possible similarities or differences.

Key words: sexual dimorphism, geographic variation, microcomputed tomography, canines, dentine, enamel

Introduction

Several studies have shown that human populations vary not only in tooth shape but also in tooth size (e.g. Hanihara and Ishida, 2005; Harris and Lease, 2005; Hanihara, 2008). However, despite the many works undertaken, little is known today about how dental tissue proportions vary among the different extant populations even though this feature has aroused interest in recent years both in the field of paleoanthropology and in the study of sexual dimorphism in current human populations.

Due to their hardness, mineralized dental tissues tend to be preserved well in sedimentary deposits. As a consequence, a large fossil record of hominid teeth exists, which has allowed us to study the variability present in human phylogeny through the assessment of dental traits. In particular, enamel thickness has been widely used in paleoanthropological studies to infer the taxonomic nature and the phylogenetic relationships between different fossil populations (e.g. Smith et al., 2006a, 2012; Olejniczak et al., 2008a; García-Campos et al., 2019). Studies on the permanent dentition have shown that representatives of the genus *Homo* mostly exhibit a thick to hyperthick enamel, with a few exceptions, such as 'classic' Neanderthals (OIS 4 and 3), who have proportionally thinner enamel (e.g. Olejniczak et al., 2008a; Smith et al., 2012; Zanolli, 2015; Zanolli et al., 2018; García-Campos et al., 2019; Lockey et al., 2020; Martín-Francés et al., 2020), allowing us to differentiate members of the modern human lineage by their greater

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Table 1. Sample of permanent canines (maxillary and mandibular) included in this study

	European (<i>N</i> = 60)		African (<i>N</i> = 67)		Total (<i>N</i> = 127)	
	Males	Females	Males	Females	Males	Females
Maxillary	15	13	16	14	31	27
Mandibular	19	13	18	19	37	32
Total	34	26	34	33	68	59

enamel thickness.

Furthermore, numerous authors have observed the existence of a sexually dimorphic pattern in the permanent dentition of modern humans (e.g. Schwartz and Dean, 2005; Smith et al., 2006b; Saunders et al., 2007; Feeney et al., 2010), pointing to the canines as the dental piece with the highest degree of dimorphism (e.g. Işcan and Kedici, 2003; Schwartz and Dean, 2005; Ateş et al., 2006; Karaman, 2006; Zorba et al., 2014; Peckmann et al., 2015). In particular, the study of the dimensions of dental tissues has become increasingly relevant for the study of intrapopulation variability (e.g. Saunders et al., 2007; Feeney et al., 2010; García-Campos et al., 2018a, 2018b). The results obtained from the various studies have shown differences between the dental tissue proportions of males and females: while males appear to present a larger dentine–pulp complex, females have relatively thicker enamel (e.g. Schwartz and Dean, 2005; Smith et al., 2006b; Saunders et al., 2007; Feeney et al., 2010; García-Campos et al., 2018a, 2018b).

However, although the analysis of dental tissue dimensions is becoming increasingly common in phylogenetic and sexual dimorphism studies, very little is known about how dental tissue dimensions range among extant human populations (Harris et al., 2001; Grine, 2004; Feeney et al., 2010). In this study, through application of computerized axial microtomography (micro-CT), we have tried to assess the inter- and intrapopulation variability of the three-dimensional (3D) dental tissue proportions of a sample of permanent canines (maxillary and mandibular) belonging to modern human samples from European (Spain) and African (South Africa and Sudan). Therefore, the present study aims: (1) to evaluate the possible similarities and differences in the dental tissue proportions of permanent canines between modern European and African populations; and (2) to analyze the sexual dimorphism present in the permanent canine dental tissues of individuals from Europe and Africa.

Materials and Methods

In the present study, we used a sample of 127 maxillary and mandibular canines from 43 European individuals (19 females and 24 males) and 48 African individuals (22 females and 26 males) of known sex and age (Table 1).

The sample was selected from the anthropological collections of the Escuela de Medicina Legal de Madrid (Spain) and the University of Pretoria (South Africa), and from a collection of dental extractions performed in different clinics in Sudan. A detailed description of the samples can be found in L'Abbé et al. (2005), Elamin and Liversidge (2013), and García-Campos et al. (2018a, 2018b). The individuals who compose the collection of the

Escuela de Medicina Legal de Madrid are Spanish (of different regional origin) and of European ancestry. The bone material in the University of Pretoria collection comes from donations and unclaimed bodies from three South African hospitals, and the Sudanese dental sample comes from extractions carried out at the Elrazi Dental School and the Ribat National Hospital, both in Sudan. From these latter collections, dental pieces belonging to individuals of African descent were selected.

The sample was selected to obtain a similar representation within each subsample of European and African individuals, as well as females and males. In this study, only one antimer of each tooth was included. However, some individuals may be represented by a maxillary and a mandibular dental piece. Only those canines that present a degree of wear similar to or lower than category 3 (Molnar, 1971) were included in the sample ($n = 112$). This category is characterized by the presence of a dentine spot on the occlusal surface. For the measurement of the basal surface of the crown, canines with a wear degree of 4 ($n = 127$) were analyzed, since this variable is not affected by occlusal tooth wear. We also excluded teeth with dental pathologies (such as caries) or large fractures that significantly affected the dental tissues. In those pieces where small fractures produced by the conservation processes were observed, a virtual reconstruction process was conducted.

The scanning of the sample was performed in three different facilities located in Spain, Italy, and South Africa. The micro-CT systems used in this study are: (1) a GE Phoenix v|tome|x, housed at the Microscopy Laboratory of the National Center for Research on Human Evolution (CENIEH), Burgos, Spain; (2) a CTP-Mlab at the Multidisciplinary Laboratory of the International Center for Theoretical Physics (ICTP) in Trieste, Italy; and (3) a Nikon XTH 225 ST located at the Nuclear Energy Corporation of South Africa (NECSA). Scans were made with two 0.1 mm copper filters and using a voltage of 100–120 kV and a current of 100–140 μ A. The resultant slice thickness ranges between 12 and 50.8 μ m. The scanning parameters applied in each case are shown in Table 2.

The subsequent image processing was performed with Amira 6.0.0 software (Visage Imaging, Inc.). Dental tissues (enamel, dentine–pulp complex) were semi-automatically segmented using the watershed segmentation tool and through manual editing. A non-local means filter was also applied. Small fractures and cracks were virtually filled in. Once the segmentation process was carried out, we isolated the crown from the root. For that purpose, we follow the protocol proposed by García-Campos et al. (2018a, 2018b), which is based on the results obtained in a previous study by Benazzi et al. (2014).

Table 2. Parameters of the equipment used in the sample scanning process

Equipment	Filters	Voltage (kV)	Current (μ A)	Voxel size (μ m)
GE Phoenix v tome x	(2 \times) Copper 0.1 mm	100–120	110–140	17–21
ICTP-Mlab micro-CT	(2 \times) Copper 0.1 mm	100–120	110–140	12–21
Nikon XTH 225 ST	(2 \times) Copper 0.1 mm	100	100	48.8–50.8

The volumes and 3D surfaces of the different coronal dental tissues were then measured. The variables described by Kono (2004) and Olejniczak et al. (2008a, 2008b) were evaluated. The variables included are: the coronal volume (V_c , in mm^3), the volume of the enamel cap (V_e , in mm^3), the volume of the coronal dentine including the coronal pulp (V_{cdp} , in mm^3), the surface area of the enamel–dentine junction (SEDJ, in mm^2), and the outer enamel surface area (OES, in mm^2). Subsequently, these variables were employed to compute the 3D average enamel thickness index ($3DAET = V_e/SEDJ$, in mm); the 3D relative enamel thickness index ($3DRET = 3DAET / \sqrt[3]{V_{cdp}} \times 100$, dimensionless); the relative coronal dentine and pulp complex volume ($RDV = V_{cdp}/V_c \times 100$, percentage); and the relative outer enamel complexity ratio ($OES/SEDJ$, dimensionless). Additionally, we also assessed the ratio of enamel-thickness to dentine-thickness ($3DRED = 10 \times \sqrt[3]{V_e/V_{cdp}}$, in mm^3) described by Yi et al. (2021). The 3DRED index has proven to be very useful when comparing samples with different voxel sizes because it is less sensitive to the variations of this parameter (Yi et al., 2021). Finally, the basal surface area of the crown (BS, in mm^2) was measured following the protocols described by García-Campos et al. (2018a, 2018b).

In this paper, a comparative study of the interpopulation (between European and African individuals; and between African and European females, and African and European males independently) and intrapopulation (between male and female individuals in each population) variability has been carried out. The maxillary and mandibular canines were analyzed separately. The statistical analyses were conducted using SPSS v. 18.0 software (SPSS Science, Inc.). First, descriptive statistics were calculated for each variable. Next, normality was assessed employing the Shapiro–Wilks test. Finally, to analyze possible differences between groups, we used the Student’s *t*-test (when the sample was normally distributed) and the Mann–Whitney *U*-test (when the sample was not normally distributed). The means were determined to be statistically different at a significance level of 0.05.

Results

Interpopulation variability

The results of the statistics performed to assess interpopulation variability are shown in Table 3. Significant differences have been observed between the European and African samples in maxillary and mandibular canines in the following variables: V_c , V_e , and OES, with the African sample presenting higher mean values than the European sample in all cases (Table 3). However, significant differences were found neither in the V_{cdp} nor in the SEDJ or

the BS between the two populations (Table 3). Likewise, the results obtained from the relative variables (or indexes) analyzed showed that there are significant differences between the European and African samples in maxillary and mandibular canines in the following variables: 3DAET and OES/SEDJ, with the African sample presenting higher average values than the European sample in all cases (Table 3). Additionally, there are significant differences in the 3DRET among the mandibular canines. However, no significant differences were seen in the RDV or the 3DRED. Likewise, the 3DRET does not show significant differences in the maxillary canines of both populations (Table 3).

To complete the study of interpopulation variability, the values obtained in the subsamples composed of European and African individuals were compared within each sex and for each dental class. In total, four two-by-two comparisons were performed. In this way the values obtained from European males were contrasted with those of the African males, while the values of the European females were contrasted with those of the African ones, in maxillary and mandibular canines, respectively. The results obtained in the comparison between sexes of different populations are shown in Table 4. We observe significant differences mainly in the maxillary and mandibular canines of the females of European and African origin in the following variables: V_c , V_e , V_{cdp} , and OES, with the African female sample presenting higher mean values than the European female sample in all the absolute dimensions (Table 4). Additionally, significant differences were appreciated only in V_e and BS in the mandibular canines of males. Furthermore, the results showed that there are significant differences in the female individuals of European and African populations (in maxillary and mandibular canines) in the following relative variables: 3DAET, OES/SEDJ, and 3DRET (only in mandibular canines), with the mean values being higher in the African female sample (Table 4). In the male individuals, there were significant differences only between African and European mandibular canines in 3DAET and OES/SEDJ (Table 4). African male individuals present higher mean values for the indices related to enamel dimensions but these differences are not statistically significant.

Intrapopulation variability

To analyze intrapopulation variability, we perform four two-by-two comparisons (Table 5). The values obtained for male and female individuals’ teeth in each population were compared, just like for each dental class (maxillary and mandibular canines separately). Significant differences were found between male and female individuals (in maxillary and mandibular canines) in both European and African

Table 3. Results of descriptive statistics (mean and standard deviation (SD)), Shapiro–Wilks (SW) normality analysis, Levene’s homoscedasticity test and comparative statistics (Student’s *t*-test and Mann–Whitney *U*-test) applied to the 3D variables measured in maxillary and mandibular canines of European and African populations

		European			African			SW		Levene	Comparative	
		<i>N</i>	Mean	SD	<i>P</i> -value	Mean	SD	<i>P</i> -value	<i>P</i> -value	<i>P</i> -value		
								EU	AF			
Absolute variables	Vc	Max	26	238.09	53.31	30	272.50	56.48	0.321	0.083	0.993	0.023
		Mand	24	192.58	39.20	32	225.74	38.53	0.138	0.030	0.990	0.006*
Ve	Max	26	109.87	27.49	30	128.25	29.74	0.015	0.029	0.705	0.009*	
	Mand	24	85.28	18.11	32	105.32	19.51	0.380	0.030	0.357	0.000*	
Vcdp	Max	26	128.22	30.60	30	144.25	31.89	0.726	0.384	0.910	0.061	
	Mand	24	107.30	24.87	32	120.42	24.16	0.362	0.257	0.693	0.052	
SEDJ	Max	26	125.91	20.46	30	132.29	19.91	0.872	0.192	0.890	0.243	
	Mand	24	117.75	16.91	32	122.29	16.67	0.233	0.333	0.805	0.320	
OES	Max	26	181.23	28.35	30	197.42	27.74	0.165	0.077	0.792	0.036	
	Mand	24	163.84	21.86	32	178.88	21.69	0.151	0.068	0.770	0.013	
BS	Max	28	38.36	7.52	30	39.02	6.85	0.492	0.463	0.616	0.730	
	Mand	32	36.36	5.78	37	38.93	6.74	0.516	0.757	0.337	0.096	
Relative variables												
3DAET	Max	26	0.87	0.13	30	0.97	0.15	0.164	0.148	0.334	0.013	
	Mand	24	0.72	0.11	32	0.86	0.13	0.885	0.433	0.252	0.000	
3DRET	Max	26	17.48	3.10	30	18.64	3.14	0.670	0.320	0.549	0.172	
	Mand	24	15.42	2.56	32	17.67	2.98	0.584	0.359	0.250	0.005	
RDV	Max	26	53.77	4.89	30	52.93	4.49	0.768	0.070	0.808	0.510	
	Mand	24	55.55	4.59	32	53.24	4.57	0.432	0.375	0.699	0.067	
OES/SEDJ	Max	26	1.44	0.07	30	1.50	0.08	0.831	0.353	0.289	0.014	
	Mand	24	1.39	0.07	32	1.47	0.08	0.053	0.620	0.209	0.001	
3DRED	Max	26	9.53	0.63	30	9.63	0.58	0.648	0.088	0.830	0.522	
	Mand	24	9.29	0.57	32	9.59	0.58	0.575	0.473	0.597	0.064	

The absolute and relative variables are: coronal volume (Vc), volume of the enamel cap (Ve), volume of the coronal dentine including the coronal pulp (Vcdp), surface area of the enamel–dentine junction (SEDJ), outer enamel surface area (OES), basal surface area of the crown (BS), 3D average enamel thickness index (3DAET), 3D relative enamel thickness index (3DRET), relative coronal dentine and pulp complex volume (RDV), relative outer enamel complexity ratio (OES/SEDJ), and the ratio of enamel thickness to dentine thickness (3DRED). Max, maxillary; Mand, mandibular. *Indicates when the Mann–Whitney test was applied; in all other cases Student’s *t*-test was employed. Significant results are indicated in bold.

samples. These differences were observed in the following variables: Vc, Vcdp, SEDJ, OES and BS, with the male sample presenting higher mean values than the female sample in all cases (Table 5). Additionally, significant differences were appreciated in Ve in the maxillary canines of the European individuals. Furthermore, the results obtained from the relative variables showed that there were significant differences in European individuals between males and females (in maxillary and mandibular canines) in the following variables: 3DRET, RDV, OES/SEDJ, and 3DRED, the mean values being higher in the female subsamples, except for the RDV (Table 5). In the African population, there were significant differences between male and female maxillary and mandibular canines in 3DRET and OES/SEDJ. The maxillary canines also exhibited significant differences in RDV and 3DRED (Table 3). As in the case of the European population, African females had greater values in those variables related to the enamel component and lower relative dimensions in those of the dentine component.

Discussion

Interpopulation variability

Numerous publications describe how human populations vary in tooth size (e.g. Hanihara and Ishida, 2005; Harris and Lease, 2005). However, despite the several odontometric studies performed using samples of different geographic origin (e.g. Hanihara and Ishida, 2005; Schwartz and Dean, 2005; Olejniczak et al., 2008a, 2008b; Smith et al., 2012), little is still known about how each histological component contributes to these differences in tooth size, although it is true that the few studies carried out on dental tissue dimensions seem to support the existence of an interpopulation variability between modern human groups (Harris et al., 2001; Grine, 2004; Feeney et al., 2010).

The results obtained in this work show that the canines of the African individuals had significantly larger crowns (Vc) than those of the European individuals. They also reveal that the differences described in the dental size of European and African populations are mainly because of the

Table 4. Results of descriptive statistics (mean and standard deviation (SD)), Shapiro–Wilks (SW) normality analysis, Levene’s homoscedasticity and comparative statistics (Student’s *t*-test and Mann–Witney *U*-test) applied to the 3D variables measured in maxillary and mandibular canines of European and African populations according to sex

		European			African			SW	Levene	Comparative	
		<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>P</i> -value	<i>P</i> -value	<i>P</i> -value	
Males											
Absolute variables								EU	AF		
Vc	Max	13	269.55	49.41	16	300.92	60.43	0.577	0.910	0.341	0.144
	Mand	15	208.84	39.53	16	238.07	38.00	0.519	0.040	0.728	0.133*
Ve	Max	13	119.30	31.67	16	136.51	36.23	0.263	0.128	0.254	0.190
	Mand	15	89.60	20.91	16	108.54	21.46	0.761	0.071	0.621	0.019
Vcdp	Max	13	150.26	22.27	16	164.41	29.38	0.744	0.941	0.297	0.164
	Mand	15	119.24	23.00	16	129.54	22.35	0.976	0.617	0.978	0.216
SEDJ	Max	13	140.16	16.70	16	144.27	19.00	0.952	0.699	0.566	0.547
	Mand	15	125.84	15.61	16	130.93	15.02	0.733	0.618	0.859	0.362
OES	Max	13	197.04	28.06	16	210.21	30.39	0.264	0.772	0.467	0.240
	Mand	15	172.49	22.41	16	187.55	20.52	0.271	0.145	0.956	0.060
BS	Max	15	43.42	5.81	16	43.76	5.54	0.577	0.536	0.496	0.869
	Mand	19	38.98	5.39	18	43.92	4.68	0.407	0.207	0.346	0.005
Relative variables											
3DAET	Max	13	0.84	0.16	16	0.94	0.17	0.336	0.090	0.300	0.133
	Mand	15	0.71	0.13	16	0.83	0.14	0.906	0.212	0.436	0.018
3DRET	Max	13	15.89	2.79	16	17.20	3.08	0.408	0.211	0.469	0.243
	Mand	15	14.51	2.58	16	16.53	3.19	0.555	0.108	0.333	0.064
RDV	Max	13	56.20	4.64	16	55.00	4.72	0.662	0.149	0.651	0.497
	Mand	15	57.22	4.71	16	54.50	4.85	0.376	0.080	0.795	0.124
OES/SEDJ	Max	13	1.40	0.07	16	1.46	0.08	0.295	0.602	0.459	0.068
	Mand	15	1.37	0.07	16	1.44	0.09	0.397	0.211	0.495	0.030
3DRED	Max	13	9.21	0.59	16	9.37	0.60	0.576	0.129	0.608	0.499
Females											
Absolute variables											
Vc	Max	13	206.63	36.52	14	240.01	27.80	0.378	0.062	0.236	0.013
	Mand	9	165.48	19.00	16	213.40	36.04	0.663	0.185	0.106	0.001
Ve	Max	13	100.44	19.48	14	118.80	16.69	0.015	0.451	0.509	0.015*
	Mand	9	78.08	9.17	16	102.10	17.44	0.397	0.110	0.152	0.001
Vcdp	Max	13	106.18	20.06	14	121.21	14.20	0.321	0.399	0.271	0.033
	Mand	9	87.40	11.80	16	111.30	23.01	0.556	0.237	0.117	0.008
SEDJ	Max	13	111.65	12.38	14	118.60	9.47	0.989	0.062	0.294	0.113
	Mand	9	104.27	8.27	16	113.65	13.77	0.177	0.399	0.447	0.076
OES	Max	13	165.42	18.59	14	182.80	14.81	0.368	0.214	0.340	0.012
	Mand	9	149.43	10.96	16	170.21	19.76	0.550	0.151	0.203	0.008
BS	Max	13	32.52	4.33	14	33.59	3.13	0.182	0.558	0.134	0.467
	Mand	13	32.53	4.00	19	34.21	4.67	0.999	0.287	0.807	0.298
Relative variables											
3DAET	Max	13	0.90	0.11	14	1.00	0.12	0.071	0.700	0.939	0.024
	Mand	9	0.75	0.07	16	0.90	0.10	0.725	0.374	0.054	0.001
3DRET	Max	13	19.08	2.61	14	20.29	2.38	0.052	0.883	0.569	0.220
	Mand	9	16.94	1.75	16	18.81	2.32	0.218	0.844	0.272	0.046
RDV	Max	13	51.33	3.94	14	50.57	2.81	0.151	0.834	0.173	0.569
	Mand	9	52.77	2.78	16	51.98	4.03	0.307	0.007	0.437	0.213*
OES/SEDJ	Max	13	1.48	0.06	14	1.54	0.06	0.636	0.657	0.974	0.015
	Mand	9	1.43	0.03	16	1.50	0.06	0.289	0.145	0.014	0.002
3DRED	Max	13	9.84	0.53	14	9.93	0.37	0.107	0.889	0.167	0.600
	Mand	9	9.64	0.36	16	9.75	0.51	0.256	0.013	0.452	0.213*

The absolute and relative variables are: coronal volume (Vc), volume of the enamel cap (Ve), volume of the coronal dentine including the coronal pulp (Vcdp), surface area of the enamel–dentine junction (SEDJ), outer enamel surface area (OES), basal surface area of the crown (BS), 3D average enamel thickness index (3DAET), 3D relative enamel thickness index (3DRET), relative coronal dentine and pulp complex volume (RDV), relative outer enamel complexity ratio (OES/SEDJ), and the ratio of enamel thickness to dentine thickness (3DRED). Max, maxillary; Mand, mandibular. *Indicates when the Mann–Whitney test was applied; in all other cases Student’s *t*-test was employed. Significant results are indicated in bold.

Table 5. Results of descriptive statistics (mean and standard deviation (SD)), Shapiro–Wilks (SW) normality analysis, Levene’s homoscedasticity test and comparative statistics (Student’s *t*-test and Mann–Whitney *U*-test) applied to the 3D variables measured in maxillary and mandibular canines of European and African populations

		Males			Females			SW		Levene	Comparative
		<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>P</i> -value	<i>P</i> -value	<i>P</i> -value	
European											
Absolute variables											
Vc	Max	13	269.55	49.41	13	206.63	36.52	0.577	0.378	0.616	0.001
	Mand	15	208.84	39.53	9	165.48	19.00	0.519	0.663	0.072	0.006
Ve	Max	13	119.30	31.67	13	100.44	19.48	0.263	0.015	0.250	0.048*
	Mand	15	89.60	20.91	9	78.08	9.17	0.761	0.397	0.069	0.134
Vcdp	Max	13	150.26	22.27	13	106.18	20.06	0.744	0.321	0.681	0.000
	Mand	15	119.24	23.00	9	87.40	11.80	0.976	0.556	0.076	0.001
SEDJ	Max	13	140.16	16.70	13	111.65	12.38	0.952	0.989	0.438	0.000
	Mand	15	125.84	15.61	9	104.27	8.27	0.733	0.177	0.087	0.001
OES	Max	13	197.04	28.06	13	165.42	18.59	0.264	0.368	0.387	0.002
	Mand	15	172.49	22.41	9	149.43	10.96	0.271	0.550	0.053	0.009
BS	Max	15	43.42	5.81	13	32.52	4.33	0.577	0.182	0.272	0.000
	Mand	19	38.98	5.39	13	32.53	4.00	0.407	0.999	0.118	0.001
Relative variables											
3DAET	Max	13	0.84	0.16	13	0.90	0.11	0.336	0.071	0.581	0.321
	Mand	15	0.71	0.13	9	0.75	0.07	0.906	0.725	0.054	0.402
3DRET	Max	13	15.89	2.79	13	19.08	2.61	0.408	0.052	0.998	0.006
	Mand	15	14.51	2.58	9	16.94	1.75	0.555	0.218	0.187	0.021
RDV	Max	13	56.20	4.64	13	51.33	3.94	0.662	0.151	0.629	0.008
	Mand	15	57.22	4.71	9	52.77	2.78	0.376	0.307	0.095	0.018
OES/SEDJ	Max	13	1.40	0.07	13	1.48	0.06	0.295	0.636	0.631	0.004
	Mand	15	1.37	0.07	9	1.43	0.03	0.397	0.289	0.024	0.007
3DRED	Max	13	9.21	0.59	13	9.84	0.53	0.576	0.107	0.789	0.009
African											
Absolute variables											
Vc	Max	16	300.92	60.43	14	240.01	27.80	0.910	0.062	0.017	0.002
	Mand	16	238.07	38.00	16	213.40	36.04	0.040	0.185	0.431	0.032*
Ve	Max	16	136.51	36.23	14	118.80	16.69	0.128	0.451	0.001	0.093
	Mand	16	108.54	21.46	16	102.10	17.44	0.071	0.110	0.200	0.359
Vcdp	Max	16	164.41	29.38	14	121.21	14.20	0.941	0.399	0.016	0.000
	Mand	16	129.54	22.35	16	111.30	23.01	0.617	0.237	0.913	0.030
SEDJ	Max	16	144.27	19.00	14	118.60	9.47	0.699	0.062	0.025	0.000
	Mand	16	130.93	15.02	16	113.65	13.77	0.618	0.399	0.475	0.002
OES	Max	16	210.21	30.39	14	182.80	14.81	0.772	0.214	0.010	0.004
	Mand	16	187.55	20.52	16	170.21	19.76	0.145	0.151	0.444	0.021
BS	Max	16	43.76	5.54	14	33.59	3.13	0.536	0.558	0.220	0.000
	Mand	18	43.92	4.68	19	34.21	4.67	0.207	0.287	0.694	0.000
Relative variables											
3DAET	Max	16	0.94	0.17	14	1.00	0.12	0.090	0.700	0.053	0.252
	Mand	16	0.83	0.14	16	0.90	0.10	0.212	0.374	0.104	0.125
3DRET	Max	16	17.20	3.08	14	20.29	2.38	0.211	0.883	0.181	0.005
	Mand	16	16.53	3.19	16	18.81	2.32	0.108	0.844	0.167	0.027
RDV	Max	16	55.00	4.72	14	50.57	2.81	0.149	0.834	0.013	0.004
	Mand	16	54.50	4.85	16	51.98	4.03	0.080	0.007	0.224	0.097*
OES/SEDJ	Max	16	1.46	0.08	14	1.54	0.06	0.602	0.657	0.228	0.003
	Mand	16	1.44	0.09	16	1.50	0.06	0.211	0.145	0.242	0.020
3DRED	Max	16	9.37	0.60	14	9.93	0.37	0.129	0.889	0.017	0.004
	Mand	16	9.43	0.63	16	9.75	0.51	0.065	0.013	0.219	0.097*

The absolute and relative variables are: coronal volume (Vc), volume of the enamel cap (Ve), volume of the coronal dentine including the coronal pulp (Vcdp), surface area of the enamel–dentine junction (SEDJ), outer enamel surface area (OES), basal surface area of the crown (BS), 3D average enamel thickness index (3DAET), 3D relative enamel thickness index (3DRET), relative coronal dentine and pulp complex volume (RDV), relative outer enamel complexity ratio (OES/SEDJ), and the ratio of enamel thickness to dentine thickness (3DRED). Max, maxillary; Mand, mandibular. *Indicates when the Mann–Whitney test was applied; in all other cases Student’s *t*-test was employed. Significant results are indicated in bold.

significantly greater enamel component of the latter, with the dentine component playing a less relevant role. The results of the comparative statistics performed on the maxillary and mandibular canines of both populations revealed significant differences in the dimensions of the enamel component (Table 3), both in the absolute (V_e , OES) and in the relative (3DAET, OES/SEDJ, 3DRET) variables. Nonetheless, even though the dentine component presents larger dimensions in the canines of the African sample, the differences, in this case, are not statistically significant (Table 3). These results may suggest that the differences in the dimensions of the different dental tissues are due to the effect of allometry. The canines of European individuals are smaller than those of Africans; if this size difference occurs proportionally in the enamel and dentine components, they would grow isometrically. This does not appear to be the case. One way to test it is to express the variables in relative terms. In doing so, we could observe that, for example, the OES/SEDJ ratio exhibits statistically different values in the canines of European and African individuals, which indicated that both surfaces have not increased proportionally in size. The same occurs when we observed the results for 3DAET and 3DRED, as well as for 3DRET in the mandibular canines. All this would indicate that teeth have increased in size in African canines in an allometric manner, with a higher increase of the enamel component compared to the dentine–pulp complex. As a result, the canines of European populations seem to have thinner dental enamel than African ones.

The few previous works carried out on this topic have yielded ambiguous results. In 2001, Harris and colleagues employed lateral radiographs of deciduous molars to assess the variability in enamel thickness among various human populations. They observed that the dental enamel was thinner in European populations than in sub-Saharan African ones. However, radiographs are problematic for assessing enamel thickness because the teeth cannot be accurately positioned before taking a radiograph (Grine et al., 2001). A few years later, Grine (2004) used buccolingual physical sections with the same objective. In this case, no significant differences were found in the average and linear relative enamel thickness (RAET, RLET) of permanent molars between populations; nevertheless, it could be seen that the absolute values of dental tissues for the European sample exceeded those of sub-Saharan Africans. On the contrary, Smith et al. (2006b) observed significant differences in the components of enamel thickness and EDJ shape among regionally diverse human groups (South Africa, North America, northern England, and medieval Denmark) through the study of cross-sections of molar crowns. Finally, in one of the few studies on anterior dentition tissue dimensions performed by micro-CT, Feeney et al. (2010) quantified the enamel and dentine dimensions employing planes extracted from digital models of the canines and premolars belonging to samples from Asia, Europe, and Africa. As in the present study, Feeney and colleagues measured significant differences in the dimensions of the coronal dentine–pulp complex, but with higher values in the European and Asian individuals compared with the African ones, although no significant differences were observed in

the enamel component.

It is important to take into account that in all these works the authors employed linear or 2D measurements of dental tissues taken in different longitudinal planes. Due to enamel not being homogeneously distributed in the dental crown of canines (García-Campos et al., 2020), several researchers have recommended employing 3D measurements to avoid errors in the estimation of the dental tissue proportions (e.g. Martin, 1985; Olejniczak et al., 2008b; Benazzi et al., 2014; García-Campos et al., 2018a, 2018b). All these, together with the results obtained in this work, highlight the need for further work to evaluate the 3D dimensions of dental tissues. This is especially important for samples of diverse geographical origin, to fill the knowledge gap that exists on the variability of these traits in modern human populations.

Our results have also shown that the differences between the canines of the European and African populations may be mainly due to the differences present in the canines of the females of both groups and with male individuals' values being more similar between the two subsamples, with a few exceptions (Table 4). Overall, the maxillary and mandibular canines of African females and males are larger in size than their European homologues; nevertheless, the differences are only statistically significant for females (Table 4). All the absolute dimensions evaluated in this study present significantly higher values in the maxillary and mandibular canines of African females compared with the European sample (except for SEDJ and BS). On the contrary, from a statistical point of view, these differences can only be appreciated in enamel cap volume (V_e) and the coronal surface area (BS) in the mandibular canines of males. Likewise, although African male and female individuals tend to present higher values for the indices related to enamel dimensions than European permanent canines of both sexes, these differences are only significant between African and European female individuals.

Intrapopulation variability

The results of this work showed that in both the European and African samples the total crown volume (V_c), as well as the basal surface of the crown (BS), are significantly larger in male individuals than in female individuals (Table 3). This is consistent with the conclusions obtained in previous studies. The sexual dimorphism present in the crown dimensions of permanent dentition has been addressed by a multitude of studies (e.g. Harris et al., 2001; Işcan and Kedici, 2003; Schwartz and Dean, 2005; Ateş et al., 2006; Karaman, 2006; Zorba et al., 2014; Peckmann et al., 2015). These works showed that, in general terms, the dentition of female individuals is smaller than that of male individuals within the same population, with these differences particularly noticeable in canines (e.g. Zilberman and Smith, 2001; Işcan and Kedici, 2003; Ateş et al., 2006; Schwartz and Dean, 2005; Viciano et al., 2011; Peckmann et al., 2015).

Furthermore, there is a growing interest in studying how the dimensions of each of the dental tissues contribute to the sexual dimorphism present in the overall dental size (e.g. Schwartz and Dean, 2005; Smith et al., 2006b;

Saunders et al., 2007; Feeney et al., 2010; García-Campos et al., 2018a, 2018b; Sorenti et al., 2019). Our results show that both African and European dental samples exhibit a pattern of sexual dimorphism in their dental tissue dimensions, which is similar to that described in previous works (Feeney et al., 2010; García-Campos et al., 2018a, 2018b; Sorenti et al., 2019). In particular, we have observed in both samples significant differences in the absolute variables (Vcdp, SEDJ) and the relative variables (RDV) associated with the dentine–pulp complex, with the mean values being higher in the male canines (maxillary and mandibular) in contrast to those of females (Table 5). Likewise, it was observed that the absolute dimensions of the enamel component (Ve, OES) tended to be significantly larger in male individuals; nevertheless, when we control the effect of size, it could be seen that the canines of European and African female individuals had significantly larger relative enamel dimensions (3DRET, 3DRED, OES/SEDJ; see Table 3). Therefore, we might conclude that regardless of their geographic origin, the permanent canines of human populations appear to exhibit a similar pattern of sexual dimorphism in the dimensions of their dental tissues.

The existence of a similar pattern of sexual dimorphism in the dimensions of their dental tissues regardless of their geographic origin seems logical if we consider that the pattern described here is not unique to modern humans but has also been observed in other hominoid species (Schwartz et al., 2001, 2005; Smith et al., 2012; García-Campos et al., 2020; 2021). This is the case of other primates such as *Pan troglodytes*, *Gorilla gorilla gorilla*, *Pongo pygmaeus*, or *Papio hamadryas* spp. (Schwartz et al., 2001; Hlusko et al., 2004), but also human fossil samples such as the Sima de los Huesos or Gran Dolina-TD6.2 (Sierra de Atapuerca, Spain) or the Neanderthal sample from Krapina (Croatia) (García-Campos et al., 2020, 2021). Sexual dimorphism of dental tissue dimensions is related to the role that both chromosomes and sex hormones seem to play in the regulation of dental tissue development. On the one hand, numerous studies on individuals with different abnormalities associated with the sex chromosomes show the existence of an influence of the genes linked to these chromosomes on dental size and tissues (e.g. Alvesalo and Tammissalo, 1981; Alvesalo et al., 1985, 1987, 1991). These conclusions were later supported by studies on the human amelogenin loci (Fincham et al., 1991; Salido et al., 1992). On the other hand, studies by Ribeiro et al. (2012, 2013) on opposite-sex twin pairs described the effect of intrauterine male sex hormone levels on the dental dimensions, which increases the tooth size of the female twin. The results of all these studies illustrate the complex adaptive system which underlines the sexual dimorphism present in the dental tissue dimensions, and which seems to act similarly in human populations regardless of their geographic origin.

The relevance of the composition of modern human comparative samples in taxonomic studies

The results of this work support the conclusions obtained in previous studies: dental traits, including dental tissue proportions, vary at inter- and intrapopulation levels. However, this is not always taken into consideration when se-

lecting comparative samples in taxonomic studies.

In most of the works in which the dimensions of dental tissues are compared between different taxa, the modern human samples employed are composed of individuals of different geographic origin (Schwartz and Dean, 2005; Olejniczak et al., 2008a, 2008b; Smith et al., 2012; Macchiarelli et al., 2013; García-Campos et al., 2020) or samples belonging to a single population (Saunders et al., 2007; Feeney et al., 2010; Zanolli and Mazurier, 2013; Zanolli et al., 2014; Martín-Francés et al., 2018). Nonetheless, it is important to note that most investigations employed European samples (e.g. Macho and Berner, 1993; Schwartz, 2000; Martín-Francés et al., 2018; Zanolli et al., 2018). This might produce an overrepresentation of European populations in taxonomy studies, and not adequately reflect the variability present in our species. As has been seen in this research, European populations have an absolute and relatively smaller enamel cap than African populations (Harris et al., 2001; Feeney et al., 2010; present study). Therefore, if we use in a taxonomic study a sample composed only of individuals of European origin, we could run the risk of underestimating the differences between our species and, for example, a sample of *H. neanderthalensis* (Figure 1). We would not obtain the same results if we used an African sample (Figure 1). Hence, the composition of the modern human comparative samples might have an impact on the results obtained. This may be especially relevant when we tried to assess fossil populations that present an intermediate pattern to that exhibited by modern humans and Neanderthals, which is usually the case of European Middle Pleistocene populations (Skinner et al., 2006; Smith et al., 2006b; García-Campos et al., 2019; Martín-Francés et al., 2020; Martínez de Pinillos et al., 2020).

The results of the present study therefore show the importance of selecting more representative comparative samples in taxonomic studies on dental tissue dimensions. The broad phenotypic diversity present in modern human populations makes it necessary to select samples geographically dispersed enough to be representative of the variability of our taxon, especially in those traits that present greater interpopulation variability in our species. Similarly, our results highlight the relevance of selecting sexually balanced samples. This work has focused on the study of canines; it would be necessary to carry out similar studies in which other dental pieces or samples of different geographic origins, such as those of Asian origin, are analyzed.

Conclusions

The purpose of this work has been to assess the inter- and intrapopulation variability present in the dental tissue proportions of two modern human samples from Europe and Africa. Our results have shown that the dentine and enamel dimensions vary between different populations and at an intrapopulation level, but with a different pattern of variation. Whereas the interpopulation variability is mainly due to the presence of a greater enamel component in the African sample in contrast to the European one, with the dentine playing a less relevant role, the intra-population variability seems to be mainly due to the presence of a

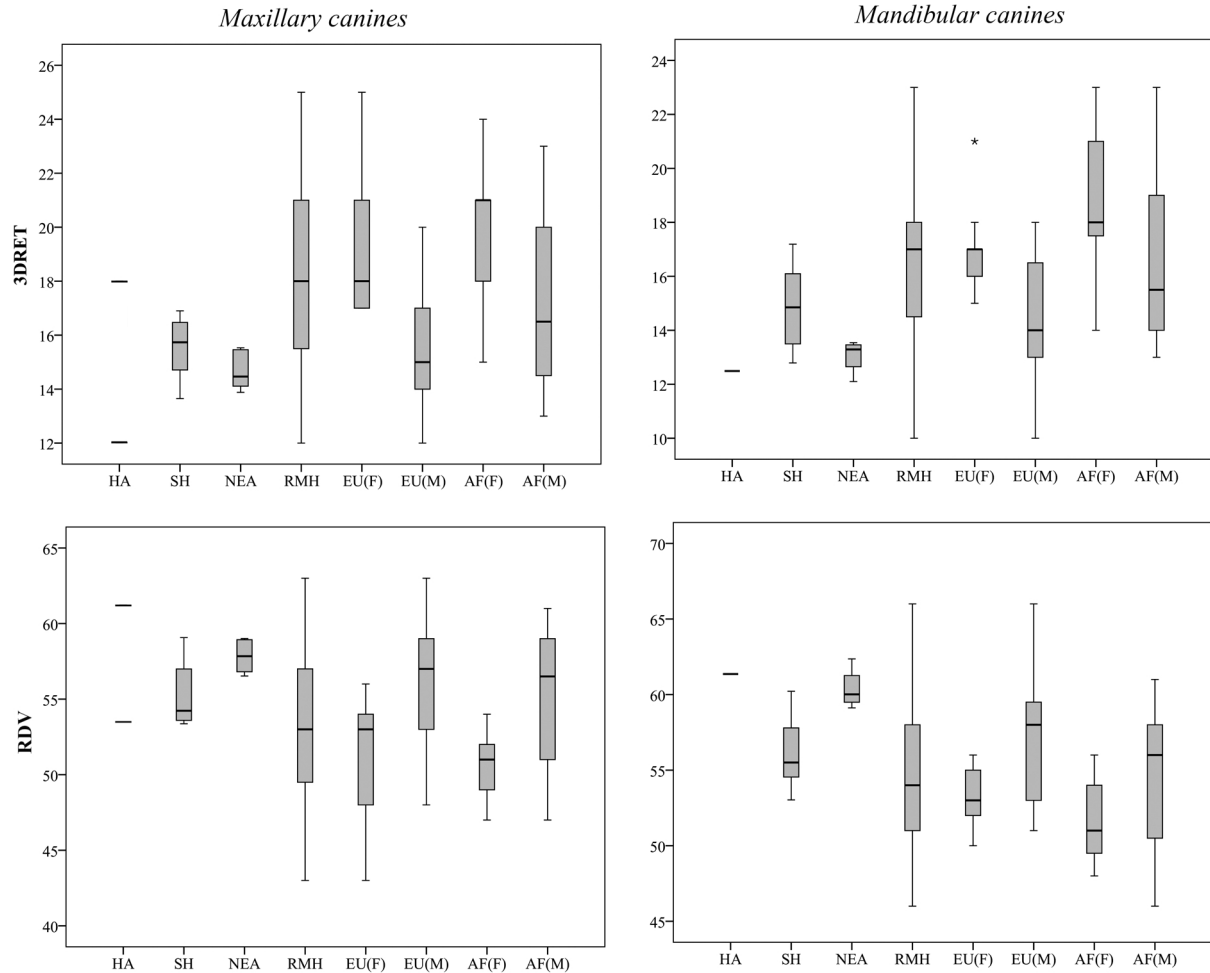


Figure 1. Box-and-whisker plot of the dental tissue proportions of the permanent canines of different fossil samples compared to human samples of different sexes and geographic origin. The groups are arranged in chronological order: *Homo antecessor* (HA), Sima de los Huesos (SH), Krapina (NEA), and recent modern humans (RMH). It also included data obtained from the subsample of females (F) and males (M) of African (AF) and European (EU) origin.

higher dentine component in males, regardless of the geographic origin of the samples. All this highlights the importance of correctly selecting comparative samples in taxonomic studies, in particular that these are geographically mixed and sex-balanced. Finally, this study was limited to the study of European and African samples. It is therefore necessary to carry out new studies that expand the information on the volumetric dimensions of enamel and dentine in other populations.

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Conflict of Interest

The authors declare no competing interests.

Author Contributions

S.B.-M., C.G.-C., and C.Z. designed the study and draft of the manuscript. S.B.-M. performed the statistical analysis. C.G.-C. performed the data acquisition. S.B.-M. and J.M.B.C. drafted the manuscript. E.G.-D., M.M.-M., M.M.-T., M.M.-P., L.M.-F., and A.O. critically revised the manuscript. C.G.-C., C.Z., M.M.-P., L.M.-F., and A.O. assisted in the creation and management of the anthropological collections.

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