



Modern human molar enamel thickness and enamel–dentine junction shape

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Summary This study examines cross-sections of molar crowns in a diverse modern human sample to quantify variation in enamel thickness and enamel–dentine junction (EDJ) shape. Histological sections were generated from molars sectioned buccolingually across mesial cusps. Enamel cap area, dentine area, EDJ length, and bi-cervical diameter were measured on micrographs using a digitizing tablet. Nine landmarks along the EDJ were defined, and X and Y coordinates were digitized in order to quantify EDJ shape. Upper molars show greater values for the components of enamel thickness, leading to significantly greater average enamel thickness than in lower molars. Average enamel thickness increased significantly from M1 to M3 in both molar rows, due to significantly increasing enamel cap area in upper molars, and decreasing dentine area in lower molars. Differences in EDJ shape were found among maxillary molars in combined and individual populations. Sex differences were also found; males showed significantly greater dentine area, EDJ length, and bi-cervical diameters in certain tooth types, which resulted in females having significantly thicker average enamel. Differences in enamel thickness and EDJ shape within molars were also found among populations, although few consistent trends were evident. This study demonstrates that enamel thickness and EDJ shape vary among molars, between sexes, and among populations; these factors must be considered in the categorization and comparison of ape and human molars, particularly when isolated teeth or fossil taxa are included. Human relative enamel thickness encompasses most

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values reported for fossil apes and humans, suggesting limited taxonomic value when considered alone.

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Introduction

Enamel thickness studies

Many anthropological studies have focused on aspects of tooth enamel thickness due to its purported taxonomic and phylogenetic value for the interpretation of human evolution.^{1–4} Other studies have examined the functional implications of enamel thickness and enamel distribution.^{5–9} Related morphological variation, such as trends in enamel thickness throughout the molar row, differences between sexes, and differences among populations, have also been considered.^{3,5,7,10,11} These studies facilitate refined interpretation of the distribution of dental tissues, and ultimately they suggest that a number of factors must be considered when making comparisons of enamel thickness between or among apes and humans (Primates: Superfamily Hominoidea).

Enamel thickness has been previously assessed using linear measurements of exposed enamel in worn or naturally fractured teeth.^{2,12,13} Martin¹⁴ demonstrated, however, that it is difficult to accurately measure enamel thickness based on exposed enamel. Martin^{14,15} measured thickness in buccolingual molar sections cut through mesial cusp tips, which were scaled for body size (using a surrogate measurement local to each molar) to make comparisons across taxa, resulting in a measure of relative enamel thickness (RET). Other scholars have quantified dental tissue proportions using lateral (flat-plane) radiography^{16,17} and medical computed tomography,^{18,19} although it has been demonstrated that these methods of visualization do not result in accurate measurements of enamel thickness.^{20,21} More recently, multiple forms of high-resolution computed microtomography have yielded accurate measurements of dental tissue thicknesses.^{22,23} Despite recent advances in three-dimensional medical imaging, the most widely-available enamel thickness data result from recent large histological studies of dental development.^{24–27}

An emerging trend in recent studies is an emphasis on documenting changes in enamel thickness throughout the molar row (i.e., metameria variation), which is important for the interpretation of data on isolated fossil teeth where only one or a few teeth, but not an individual's entire dentition, are available for study.^{2,3,7} The most widely available data for interpretation of trends in hominoid

permanent teeth come from studies of human molars.^{5,7,28,29} However, sample sizes in each of these studies were generally about ten or less per tooth type, resulting in limited statistical capability for the detection of differences using conventional parametric techniques such as Analysis of Variance (ANOVA).^{3,30,31} For example, Grine^{5,7} found that enamel thickness increases along the molar row in modern human molars, but significant differences among permanent molars were not detected. Smith et al.³ employed non-parametric trend analyses in a similarly sized sample of chimpanzee and orangutan molars, and found significant increasing trends in average enamel thickness in mesial sections of both taxa, thus confirming statistically that tooth position must be considered in comparative studies of enamel thickness.

Although studies of enamel thickness variation are becoming more common, little is known about variation in enamel thickness between sexes or among con-specific populations.^{2,10,11,29} Hlusko et al.² did not find a significant difference in linear enamel thickness between male and female baboon molars, but when scaled for tooth size, female baboons had relatively more enamel than males. Among humans, Schwartz and Dean¹¹ examined enamel and dentine proportions in canines and third molars, and found that males showed a greater dentine area than females, which was significantly different in third molars. Sex differences in enamel thickness are likely to be taxon-specific, however, evidence available at present does not facilitate testing whether sexual dimorphism in human and baboon enamel thickness is comparable. Moreover, little is known about population-level enamel thickness variation. Grine^{5,7} studied human molars from geographically diverse populations, and found similar values between groups and low levels of variation in the mixed population sample. Nonetheless, samples of molars from geographically diverse populations have not been compared on a large scale, including analyses of variation within the molar row.

In addition to enamel thickness and its variation throughout the molar row, several studies suggest that the dentine component of the molar crown, or the shape of the enamel–dentine junction (EDJ), may be indicative of species-level affiliation.^{32–35} Although it has been shown that EDJ shape in maxillary molars may distinguish species from one another with relatively high resolution,³⁵ it remains unknown whether this aspect of morphology, like

enamel thickness, may differ between molar types, between sexes, or between populations within a species. A large sample of human molars representing different populations thus presents an opportunity to study EDJ shape in light of these possible sources of variation.

It is also unclear whether enamel thickness and the shape of the EDJ may be correlated, and the sample studied here may illuminate the relationship between these two aspects of morphology. For example, Martin¹⁴ suggested that relatively tall dentine horn tips might be associated with thin enamel in *Gorilla* molars, as both characters are related to folivory (see also Shimizu³⁶ and Ulhaas et al.³⁷ for discussions of these characters in cercopithecoid primates). Because the EDJ begins to take shape earlier in development than enamel or dentine deposition (i.e., the zones of maturation at the future dentine horn tips are identifiable before the commencement of hard tissue secretion), the macromorphology of a tooth is likely to be influenced by the locations of the dentine horn tips. Examination of tissue thickness and shape simultaneously in a large sample of a single taxon will facilitate exploration of the relationships of the coronal dentine and enamel components of the molar crown.

This study aims to examine variation in enamel thickness among molar types, between sexes, and among populations in a large sample of regionally diverse human molars. An additional aim is to quantify two-dimensional (2D) EDJ shape and to assess the degree of morphological variation in this component of the tooth crown. These data represent the largest 2D comparative sample of modern humans from diverse populations for the interpretation of fossil apes and humans. Despite the advent of sophisticated methods of characterizing the molar crown in three dimensions,^{4,6,22,23} information from 2D planes of sections (virtual or physical) facilitates complementary analyses of linear and relative enamel thickness.^{2,4,8,22,23,38} By utilizing the largest-known collection of histological sections of modern human molars, this study aims to employ the most appropriate statistical analyses possible.

Materials and methods

Micrographs of histological sections were generated from several collections of modern human molar teeth, which were prepared previously for studies of crown formation.^{24,26,27} The sample was composed of upper and lower permanent molar teeth from four human populations: South African, North American, Northern England, and medieval

Table 1 Modern human molars included in this study

Row	Tooth	SA	NA	NE	Dan	Combined
Max	M1	25	—	10	2	37
	M2	13	—	9	3	25
	M3	13	24	13	1	51
Mand	M1	17	—	10	28	55
	M2	11	—	15	19	45
	M3	5	5	13	21	44
Totals		84	29	70	74	257

Row: maxillary or mandibular molar positions. SA, South African population; NA, North American population; NE, Northern England population; Dan, medieval Danish population.

Denmark (Table 1). Sex was known for all South African and North American individuals, and also for a few individuals from Northern England. Approximately 530 histological sections were generated from 435 molars of 372 individuals; 257 of these sections were chosen for the study of enamel thickness and 247 of these were used for the study of EDJ shape. Teeth that had not completed crown formation of the mesial cusps or that showed evidence of marked enamel hypoplasia were excluded from the study because measurements of enamel thickness are likely to be affected.

Components of enamel thickness

Several aspects of each cross-section were measured using a digitizing tablet interfaced with SigmaScan software (SPSS Science, Inc.): area of the enamel cap (c), length of the enamel–dentine junction (e), dentine area (b), and the bi-cervical diameter (BCD) (Fig. 1). Average enamel thickness (AET) was calculated as (c/e) , and relative enamel thickness (RET) was calculated as $100 \times [(c/e)/\sqrt{b}]$ (following Martin^{14,15}). As noted by Martin¹⁴ and Smith et al.,³ RET is not appropriate for intra-specific comparisons because it controls for average tooth size within a species, and it was included here only for comparison of this human sample with previously published hominoid species. Slight reconstructions were made prior to measurement in sections that showed light to moderate wear or a minimal amount of missing cervical enamel. Sections that showed heavy wear or two missing cervices were excluded. When multiple planes of section were available, the section with the lowest RET was used in the analysis, as obliquity necessarily causes an overestimate.^{14,39} In rare instances when both left and right molar analogues within the maxillary or mandibular row were available, the section with the lower RET value was chosen to maintain independence of observations.

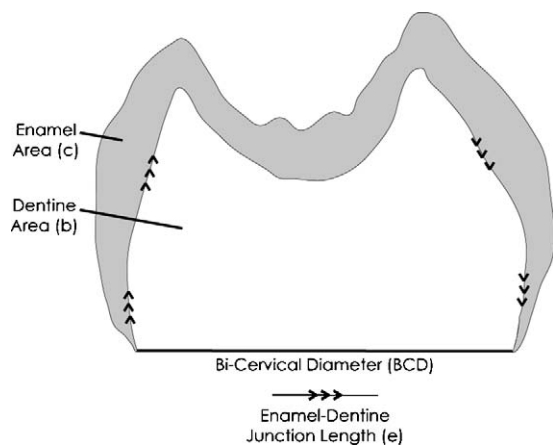


Figure 1 Schematic of a human molar showing the components of average and relative enamel thickness. The area of the enamel cap is represented as c , the area of the dentine under the enamel cap is represented as b , and the length of the enamel–dentine junction is represented as e . The bi-cervical diameter is recorded as measurement BCD. The average enamel thickness (AET) may be calculated as (c/e) , and relative enamel thickness (RET) may be calculated as $[(c/e)/\sqrt{b}] \times 100$.

Several statistical tests were employed to examine differences in c , e , b , AET, and BCD between upper and lower molars, throughout the molar row, between sexes, and among populations represented by sample sizes greater than three. The Mann–Whitney U -test⁴⁰ was employed to examine differences between maxillary and mandibular analogues. As noted above, previous studies of enamel thickness used ANOVA in order to test for differences among tooth types.^{5,7,10,28} ANOVA is insensitive to directional change, testing only whether sample means are significantly different from one another, but without testing the hypothesis that directional change among ordered samples exists (e.g., M1–M3) (reviewed in Jonckheere³⁰ and Smith et al.³). Conover's³¹ adaptation of the Jonckheere–Terpstra test was applied in order to test the significance of trends throughout the molar row for each component variable of RET (c , e , b), as well as for AET and BCD. Tests were performed separately for maxillary and mandibular molars. When a significant trend was found, the Kruskal–Wallis test was applied with molar type as the factor, and Conover's³¹ post hoc comparisons were made to illuminate which molar pairs accounted for the significant differences. The Mann–Whitney U -test was used to examine sex differences between equivalent molars. Lastly, differences between populations were examined using the Kruskal–Wallis test with population as the factor for those positions represented by more than two populations. For molar positions represented by only two populations (upper M1 and upper M2),

the Mann–Whitney U -test was used to examine differences. All analyses were run with SPSS software (v. 13.0, SPSS Science, Inc.), with the exception of post hoc comparisons for the Kruskal–Wallis test, which were performed with custom software.

Enamel–dentine junction shape

Quantification of EDJ shape differences in the molar cross-sections was achieved by locating nine landmarks and semi-landmarks on micrographs of each molar (Fig. 2). This method follows that of Olejniczak et al.,³⁵ who studied only maxillary molars; their protocol was adapted here for examining mandibular molars by reflecting the landmark notation about the vertical and horizontal axes, such that the first landmark, at the lingual cervix in maxillary molars, was made to lie at the buccal cervix in mandibular molars. Although the position of landmarks may be affected by the degree of 'enamel sleeving', (i.e., the thin extension of enamel defining the cervix), this tends to vary more between buccal and lingual cusps than within a cusp type.²⁵ Given that cusp-specific EDJ length relates to crown formation time,²⁵ and that these teeth show relatively little variation in cusp-specific crown formation times,^{26,27} it is unlikely that marked variation in enamel sleeving greatly increases variation in the location of these landmarks.

Euclidean Distance Matrix Analysis (EDMA-II) was employed to explore shape differences in the EDJ of molar cross-sections while controlling for size differences between teeth.⁴¹ An *a priori* scaling factor based on biological grounds is recommended for EDMA-II analyses⁴¹ in order to uniformly scale each specimen so that shape, but not size, is compared. The distance between landmark 1 and landmark 9, which represents the BCD, was accordingly scaled to a distance of 100 units. Martin¹⁴ suggested that BCD may be a useful surrogate for tooth size, and subsequent studies by Schwartz²⁹ and Grine⁵ have demonstrated that this distance has a significant positive relationship with tooth size. The Cartesian coordinates of each landmark in Fig. 2 were collected. Once the coordinates of each landmark were translated, rotated, and scaled to the BCD length of 100 units (procedures implemented in the objective-c programming language; source code is available from the second author), the software package WinEDMA, v1.0.1 beta⁴² was used to perform shape difference calculations. WinEDMA calculates the mean distance between pairs of landmarks and determines whether inter-landmark distances are significantly different between two samples; many significant inter-landmark distances point towards a significant overall shape difference between the

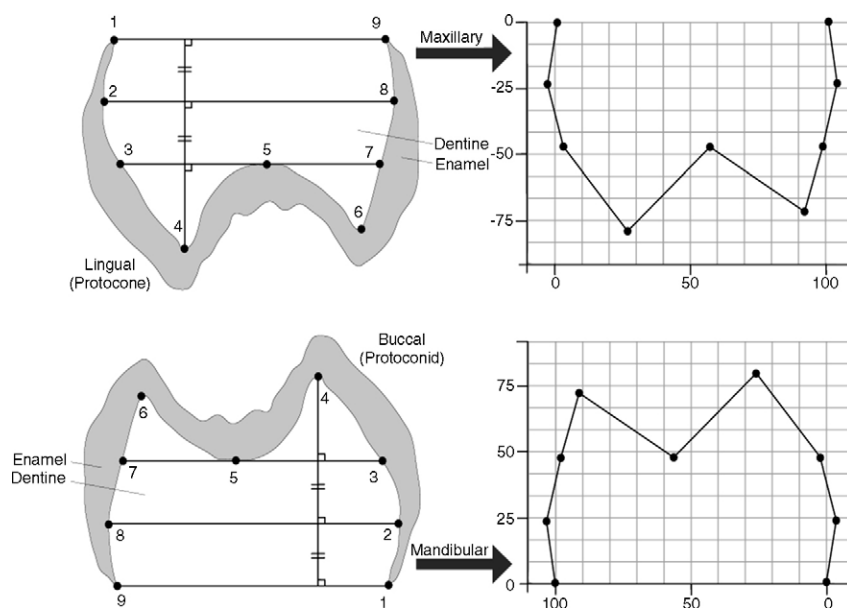


Figure 2 Landmarks are defined as follows for maxillary molars (with mandibular terms following in parenthesis): (1) tip of the lingual (buccal) enamel cervix; (2) lingual (buccal) intersection of the EDJ and a line parallel to the bi-cervical diameter and bisecting the length between the bi-cervical diameter and landmark 5; (3) lingual (buccal) intersection of the EDJ and a line parallel to the bi-cervical diameter and running through landmark 5; (4) protocone (protoconid) dentine horn tip; (5) lowest point of the EDJ between the two horn tips; (6) paracone (metaconid) dentine horn tip; (7) buccal (lingual) intersection of the EDJ and a line parallel to the bi-cervical diameter and running through landmark 5; (8) buccal (lingual) intersection of the EDJ and a line parallel to the bi-cervical diameter and bisecting the length between the bi-cervical diameter and landmark 5; (9) tip of the buccal (lingual) enamel cervix. Landmark 1 was made to lie at (0, 0) and landmark 9 at (100, 0) in every specimen examined in order to account for differences in tooth size.

samples. The null hypothesis tested by EDMA-II is that the two samples have equivalent shapes (i.e., inter-landmark differences do not differ significantly). In the present study, each analysis was bootstrapped 1000 times in order to calculate confidence intervals.

Shape comparisons were made between each tooth type within a molar row (i.e., M1 versus M2, M1 versus M3, and M2 versus M3 for both maxillary and mandibular samples) within each group studied, as well as for the entire combined sample. EDJ shape in each molar type was also compared between males and females. Finally, a third set of comparisons was run in order to examine relative shape differences between the four study samples at each tooth position (e.g., South African mandibular M1 versus Danish mandibular M1). EDJ shape comparisons were not made between upper and lower molar analogues because the scaling factor employed (BCD) shows different patterns in upper molars versus lower molars; the former are characterized by a relatively broader BCD in buccolingual sections,⁵ despite a strong correlation of BCD and dentine area in each molar row individually. Comparing upper and lower molars would thus be a comparison of differently scaled molars.

Two sets of data are output by WinEDMA in order to guide interpretation of the results. The Z-statistic is the overall measure of shape difference, and its 10% confidence intervals indicate significance; if the confidence intervals do not contain zero, then the shapes are considered to be significantly different at the $\alpha = 0.10$ level. The second set of information output by WinEDMA is the shape difference matrix, from which each inter-landmark distance is compared between the two samples; this table facilitates interpretation of which landmarks are responsible for overall shape differences.

Results

Components of enamel thickness

Table 2 shows the results of the Mann–Whitney *U*-test for differences between upper and lower molar analogues (raw values and descriptive statistics are given in Appendix A). Significance was achieved in almost all instances, with upper molars consistently showing greater values than corresponding lower molars. In light of these results, maxillary and mandibular molars were treated separately for the other analyses.

Table 2 Results of the Mann–Whitney *U*-test for differences in components of enamel thickness between upper and lower molars in modern humans

Tooth		<i>b</i>	<i>c</i>	<i>e</i>	AET	RET	BCD
M1	Z	−1.692	−4.622	−0.800	−4.869	−3.667	−7.234
	<i>p</i> -value	0.091	0.000	0.424	0.000	0.000	0.000
M2	Z	−4.811	−5.865	−4.517	−4.566	−1.342	−6.576
	<i>p</i> -value	0.000	0.000	0.000	0.000	0.180	0.000
M3	Z	−5.008	−5.463	−4.239	−4.650	−0.381	−7.090
	<i>p</i> -value	0.000	0.000	0.000	0.000	0.703	0.000

Component variables: *b*, dentine area under the enamel cap; *c*, area of enamel cap; *e*, length of enamel–dentine junction; AET (average enamel thickness) is calculated as (*c*/*e*); RET (relative enamel thickness) is calculated as [(*c*/*e*)/√*b*] × 100; BCD, bi-cervical diameter, defined as the distance between buccal and lingual cervices. Significant *p*-values are in bold.

Table 3 shows the results of the Kruskal–Wallis post hoc comparisons and Jonckheere–Terpstra test for trends in the molar row. For upper molars, dentine area (*b*) showed a non-significant decreasing trend, enamel cap area (*c*) showed a significantly increasing trend, enamel–dentine junction length (*e*) and bi-cervical diameter (BCD) both showed significantly decreasing trends, and average enamel thickness (AET) (and RET) showed significant increases from M1 to M3. For lower molars, dentine area (*b*), enamel–dentine junction length (*e*), and bi-cervical diameter (BCD) showed significant decreasing trends, while enamel cap area (*c*) showed a non-significant increasing trend, and average enamel thickness (AET) showed a significant increasing trend. Post hoc comparisons revealed

Table 3 Results of Kruskal–Wallis post hoc comparisons for differences in the components of enamel thickness between molar types, with the directionality of significant trends indicated

Row	Var	M1 vs. M2	M2 vs. M3	M1 vs. M3	JT
Max	<i>b</i>	=	=	=	=
	<i>c</i>	<	=	<	+
	<i>e</i>	=	=	=	−
	AET	<	=	<	+
	BCD	=	>	>	−
Mand	<i>b</i>	>	=	>	−
	<i>c</i>	=	=	=	=
	<i>e</i>	>	=	>	−
	AET	<	=	<	+
	BCD	>	=	>	−

Row: maxillary or mandibular; Var: *b*, dentine area under the enamel cap; *c*, area of enamel cap; *e*, length of enamel–dentine junction; AET (average enamel thickness) is calculated as (*c*/*e*), BCD, bi-cervical diameter. Significant post hoc results are given with the directionality of differences indicated, non-significant results are indicated with '='; JT indicates the results of the Jonckheere–Terpstra test for trends: = indicates no significant trends were found; +, indicates that the variable increases from M1 to M3, −, indicates a decrease from M1 to M3.

that the majority of significant differences occurred between M1 and M2, as well as between M1 and M3. Differences between M2 and M3 were only found for the bi-cervical diameter (BCD) of upper molars.

Table 4 shows the results of the Mann–Whitney *U*-test for differences in enamel thickness components between the sexes. In upper M2, males showed significantly greater dentine area (*b*) and enamel–dentine junction length (*e*) than females. This resulted in a significantly lower M2 relative enamel thickness (RET) in males than in females. In upper M3, females showed significantly greater enamel cap area (*c*), which led to significantly greater average enamel thickness (AET). Bi-cervical diameter (BCD) in male upper M1 and M2 was also significantly greater than in females. In lower molars, female enamel cap area (*c*) was greater (but not significantly so) in M1 and M2, which, when coupled with (non-significantly) lower dentine area (*b*) and enamel–dentine junction length (*e*), led to significantly greater values of average enamel thickness (AET) (and RET) in females for lower M1 and M2. Descriptive statistics for these variables sorted by tooth type and sex are given in Appendix B.

Table 5 shows the results of the Mann–Whitney *U* and Kruskal–Wallis tests for differences between and among human populations. No differences in the components of enamel thickness were found in upper molars, although bi-cervical diameter (BCD) in upper M3 was significantly different. Post hoc tests revealed that both the South African and North American samples showed a greater BCD than the Northern England population (Table 6). Several significant differences were found among populations for lower M3. This was consistently the result of significantly greater values of dentine area (*b*), enamel cap area (*c*), enamel–dentine junction length (*e*), and average enamel thickness (AET) in the South African, North American, and Northern England samples relative to the medieval Danish population. No significant differences were found

Table 4 Results of the Mann–Whitney *U*-test for differences in the components of enamel thickness between males and females

Row	Tooth		<i>b</i>	<i>c</i>	<i>e</i>	AET	RET	BCW
Max	M1	<i>Z</i>	−1.553	−0.721	−1.720	0.000	−0.777	−2.219
		<i>p</i> -value	0.120	0.471	0.086	1.000	0.437	0.027
	M2	<i>Z</i>	−2.049	−0.732	−2.342	−1.464	−2.049	−2.489
		<i>p</i> -value	0.040	0.464	0.019	0.143	0.040	0.013
	M3	<i>Z</i>	−0.051	−2.079	−0.436	−2.695	−1.412	−0.719
		<i>p</i> -value	0.959	0.038	0.663	0.007	0.158	0.472
Mand	M1	<i>Z</i>	−0.390	−1.854	−0.098	−2.049	−2.245	−0.976
		<i>p</i> -value	0.696	0.064	0.922	0.040	0.025	0.329
	M2	<i>Z</i>	−1.278	−0.183	−1.826	−2.191	−2.191	−1.095
		<i>p</i> -value	0.201	0.855	0.068	0.028	0.028	0.273
	M3	<i>Z</i>	−0.425	−0.106	−0.212	−0.319	−0.531	−1.699
		<i>p</i> -value	0.671	0.915	0.832	0.750	0.595	0.089

Codes are as given in Table 2. Significant *p*-values are in bold.

Table 5 Results of the Mann–Whitney *U* and Kruskal–Wallis tests for differences in the components of enamel thickness between and among human populations

Row	Tooth	Comp	Stat	<i>b</i>	<i>c</i>	<i>e</i>	AET	BCD
Max	M1	SA vs. NE	M–W					
			<i>Z</i>	−0.365	−0.365	−0.365	−0.110	−1.680
			<i>p</i> -value	0.715	0.715	0.715	0.913	0.093
	M2	SA vs. NE	M–W					
			<i>Z</i>	−0.167	−0.301	−0.634	−0.701	−1.703
			<i>p</i> -value	0.867	0.764	0.526	0.483	0.089
M3	SA, NA, NE	K–W						
		Chi-square	2.374	4.288	3.210	2.175	6.490	
		<i>p</i> -value	0.305	0.117	0.201	0.337	0.039	
Mand	M1	SA, NE, Dan	K–W					
			Chi-square	2.966	3.727	1.017	4.522	5.823
			<i>p</i> -value	0.227	0.155	0.601	0.104	0.054
	M2	SA, NE, Dan	K–W					
			Chi-square	0.258	4.103	0.136	5.193	0.947
			<i>p</i> -value	0.879	0.129	0.934	0.075	0.623
M3	All 4	K–W						
		Chi-square	18.417	18.451	10.720	11.341	2.715	
		<i>p</i> -value	0.000	0.000	0.013	0.010	0.438	

Row: maxillary or mandibular. Comp: populations being compared; SA, South African; NA, North American; NE, Northern England; Dan, medieval Danish. Stat: M–W = Mann–Whitney *U*-test between two groups; K–W, Kruskal–Wallis test among three or more groups. Codes for variables are as in Tables 2 and 3. Significant *p*-values are in bold.

Table 6 Results of Kruskal–Wallis post hoc comparisons for differences in the components of enamel thickness between populations

Row	Tooth	Var	1 vs. 2	1 vs. 3	1 vs. 4	2 vs. 3	2 vs. 4	3 vs. 4
Max	M3	BCD	=	>	–	>	–	–
Mand	M3	<i>b</i>	=	=	>	=	>	>
		<i>c</i>	=	=	>	=	>	>
		<i>e</i>	=	=	>	=	>	>
		AET	=	=	>	=	>	>

Codes are as in Tables 2 and 3. Populations compared: 1, South African; 2, North American; 3, Northern England, 4, medieval Danish. Significant post hoc results are given with the directionality of differences indicated, non-significant results are indicated with ‘=’, and instances where comparisons were not possible are indicated by ‘–.’

among the three 20th century populations (SA, NA, and NE). Descriptive statistics for these variables sorted by tooth type and population are given in Appendix C.

Enamel–dentine junction shape

Fig. 3 depicts the average EDJ shape for maxillary and mandibular molars in the combined populations sample. Table 7 shows the results of the shape comparisons among molars in the combined and individual populations. Among maxillary molars in the combined sample, M1 and M2 are not significantly different in dentine shape. The maxillary M3 is significantly different compared to both M1 and M2; its shape is distinguished from maxillary M1 and M2 by its relatively taller dentine horn tips. Third

maxillary molars are also characterized by the relatively lingual placement of their horn tips and lingual lateral wall (landmarks 3 and 4), although this is a characteristic that separates both the M1 and M3 from the M2. The buccal lateral wall (landmarks 7 and 8) does not display such marked differences among maxillary molars. No significant differences in dentine shape were found among mandibular molars in the combined sample, although the M1 tends to have taller dentine horns than the M2 and M3.

Variation within the molar row in individual populations revealed few consistent results (Table 7, Fig. 4). The South African population did not demonstrate any significant differences in dentine shape between maxillary or mandibular molar positions. Maxillary M2 and M3 were found to be significantly different in the Northern England sample. The Northern England and Danish samples both demonstrated significant differences in mandibular EDJ shape between M1 and M3, and between M2 and M3, but not between M1 and M2.

When known-sex individuals from populations were combined, males and females were not found to be significantly different in terms of EDJ shape at any molar position (Table 8, Fig. 4). Among upper molars, M2 shows the greatest (non-significant) differences, caused primarily by a relatively taller buccal horn tip in males. In the maxillary M1 and M3, males also have lingual lateral walls and dentine horn tips that are located towards the buccal aspect of the tooth compared to females (landmarks 2, 3, 4, and 6). In the lower molar row, there is a trend toward greater differences between male and female EDJ shape from the M1 to the M3, such that the M3 shows the greatest differences between the sexes. This is supported by the increasing absolute value of the Z-statistic from M1 to M3 (Table 8). In the mandibular M3, (non-significant) differences are largely attributable to taller dentine horn tips in females (landmarks 4 and 6), whereas the mandibular M1 shows the opposite condition (taller dentine horn tips in males).

EDJ shape differences between populations are summarized in Table 9 and Fig. 4. Seven comparisons showed significant differences, which were only found within M1 and M3. Among maxillary molars, the South African population tends to have lower dentine horn tips than the Northern England sample, although the maxillary M2 could not distinguished statistically. Significant differences in maxillary M3 shape were also found between the South African and North American populations. In the lower row, significant differences were found between the Northern England and Danish populations in M1 and M3, as well as between the Danish and South

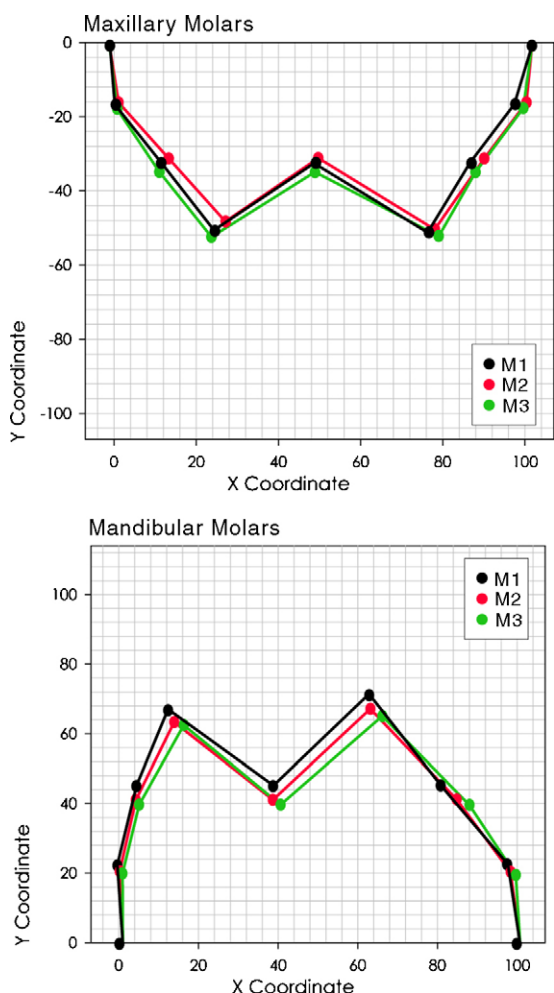


Figure 3 Plot depicting the average shapes of the enamel–dentine junction (EDJ) in human molars. Maxillary molars are plotted above and mandibular molars are plotted below as illustrated in Fig. 2. First molars are indicated in black, second molars in red, and third molars in green.

Table 7 Results of EDMA-II shape comparisons between tooth types, H_0 : there is no difference in mean shape

Comparison	Z	10% Lower	10% Upper	Reject H_0 ?
Combined groups				
Maxillary M1 vs. M2	0.036	-0.035	0.062	No
Maxillary M1 vs. M3	-0.029	-0.024	-0.046	Yes
Maxillary M2 vs. M3	-0.053	-0.081	-0.035	Yes
Mandibular M1 vs. M2	0.050	-0.048	0.059	No
Mandibular M1 vs. M3	0.079	-0.079	0.097	No
Mandibular M2 vs. M3	0.035	-0.040	0.054	No
SA				
Maxillary M1 vs. M2	0.054	-0.047	0.103	No
Maxillary M1 vs. M3	-0.043	-0.061	0.052	No
Maxillary M2 vs. M3	-0.068	-0.106	0.039	No
Mandibular M1 vs. M2	0.048	-0.066	0.069	No
Mandibular M1 vs. M3	0.048	-0.065	0.068	No
Mandibular M2 vs. M3	0.097	-0.101	0.148	No
NE				
Maxillary M1 vs. M2	0.047	-0.043	0.072	No
Maxillary M1 vs. M3	-0.061	-0.102	0.056	No
Maxillary M2 vs. M3	-0.085	-0.123	-0.067	Yes
Mandibular M1 vs. M2	-0.039	-0.057	0.042	No
Mandibular M1 vs. M3	-0.073	-0.130	-0.048	Yes
Mandibular M2 vs. M3	-0.060	-0.124	-0.040	Yes
Dan				
Mandibular M1 vs. M2	0.060	-0.068	0.082	No
Mandibular M1 vs. M3	0.131	0.117	0.147	Yes
Mandibular M2 vs. M3	0.071	0.064	0.084	Yes

Comparison: populations being compared, SA, South African; NA, North American; NE, Northern England; Dan, medieval Danish. Z-statistic: measure of overall shape difference between the two samples; if the Z-statistic's 10% confidence interval does not contain 0, then the two shapes are considered to be significantly different, which is indicated as 'yes' in the reject H_0 column.

African M1, due in part to the relatively taller dentine horn tips in the Danish sample. In addition, the mandibular M3 is significantly different between the South African and Northern England samples, due to in part to relatively taller dentine horn tips in the former.

Discussion

Variation among molars

Significant differences in the components of enamel thickness between upper and lower molars, and among molars in the same molar row, demonstrate that tooth position must be taken into account when making comparisons of enamel thickness (also discussed in Macho,²⁸ Hlusko et al.,² Grine,^{5,7} and Smith et al.³). A similar result is implied by the comparisons of EDJ shape along the molar row. Differences between upper and lower molars are not surprising given differences in tooth dimensions; maxillary molars are known to be larger in buccolingual dimensions than mandibular molars. Grine⁵

noted in his study of human enamel thickness that dentine area and bi-cervical diameter were approximately 12% and 20% larger, respectively, in maxillary molars. This finding is comparable with the differences reported here. Because broader teeth have a larger cross-sectional enamel area as well, significantly greater values of average enamel thickness were also found in maxillary molars.

This study has demonstrated a statistically significant trend of increasing enamel thickness from M1 to M3 in modern humans, which is similar to the pattern observed in chimpanzee and orangutan molars.³ Increases in average enamel thickness from M1 to M3 in human mesial sections are related to increases in the area of the enamel cap and/or decreases in the area of the dentine and the enamel-dentine junction (EDJ) length. The significance of these patterns differed between upper and lower molars; enamel cap area showed a significant increase in upper molars and dentine area showed a significant reduction in the lower molar row. Grine^{5,7} reported that a posterior increase in "relative" enamel thickness (c/b) in humans is the result of a decrease in dentine area rather than an increase

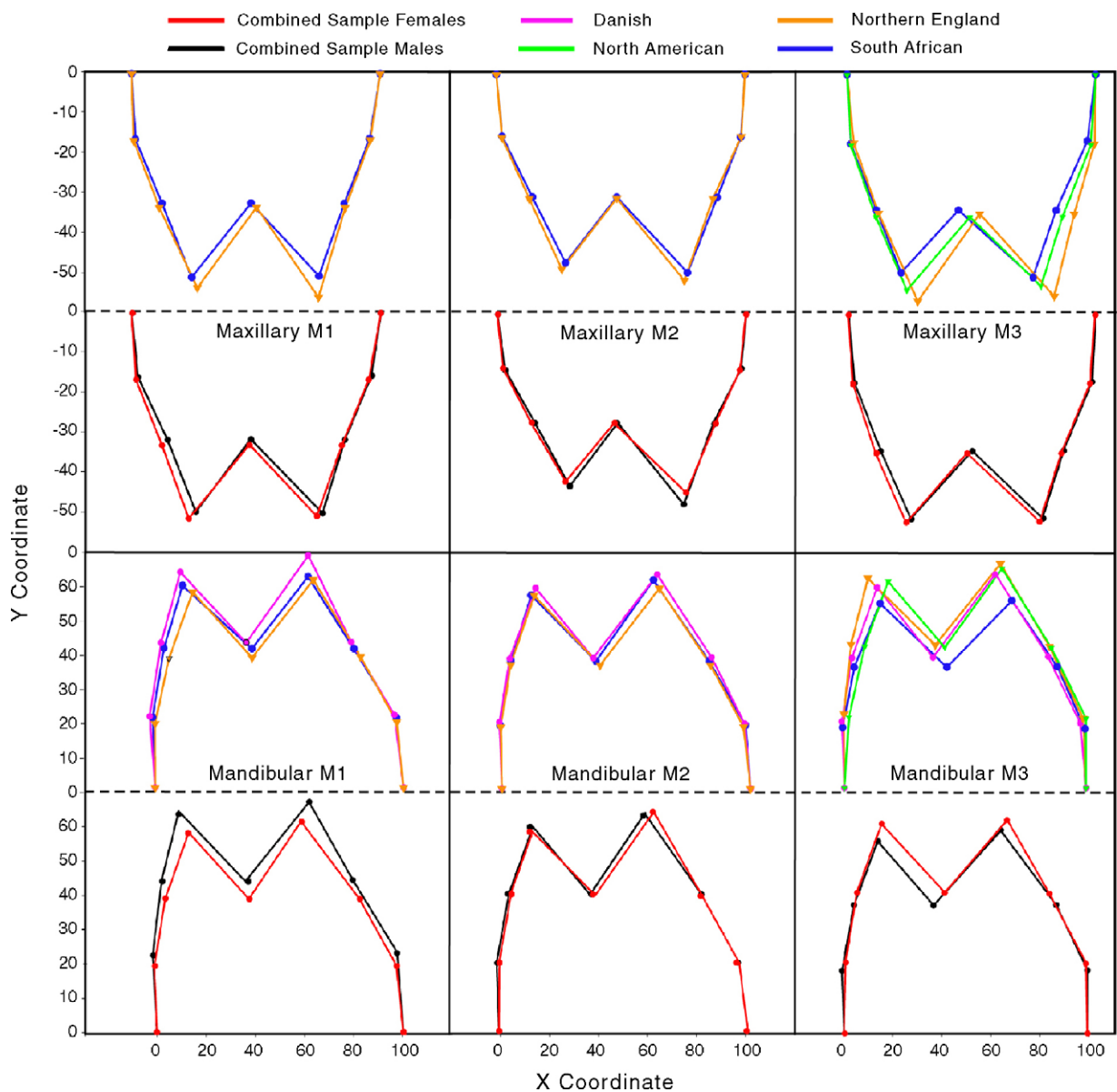


Figure 4 Plot depicting differences in the average shapes of the enamel–denture junction (EDJ) of maxillary and mandibular molars between females and males and among populations. Maxillary teeth are shown in the upper two rows, and mandibular teeth are in the lower two rows, with M1 on the left and M3 on the right. Females are in red, and males are in black. The four populations, medieval Danish, North American, Northern England, and South African are in purple, green, orange, and blue, respectively. Differences in sample sizes between groups at particular tooth positions can bias the bootstrapped EDMA Z-statistic, and result in slight difference in the position of landmarks between groups without associated statistical significance.

Table 8 Results of EDMA-II shape comparisons between sexes, H_0 : there is no difference in mean shape

Comparison	Z	10% Lower	10% Upper	Reject H_0 ?
Maxillary M1	0.032	-0.035	0.055	No
Maxillary M2	-0.039	-0.079	0.062	No
Maxillary M3	0.021	-0.038	0.049	No
Mandibular M1	0.042	-0.036	0.067	No
Mandibular M2	0.044	-0.067	0.078	No
Mandibular M3	-0.074	-0.105	0.121	No

Column headers are as in Table 7.

Table 9 Results of EDMA-II shape comparisons between groups, H_0 : there is no difference in mean shape

Comparison	Z	10% Lower	10% Upper	Reject H_0 ?
SA vs. NE				
Maxillary M1	-0.047	-0.085	-0.027	Yes
Maxillary M2	-0.029	-0.090	0.038	No
Maxillary M3	-0.098	-0.136	-0.053	Yes
Mandibular M1	0.045	-0.042	0.063	No
Mandibular M2	0.034	-0.034	0.056	No
Mandibular M3	-0.117	-0.174	-0.071	Yes
SA vs. NA				
Maxillary M3	-0.053	-0.079	-0.040	Yes
Mandibular M3	-0.113	-0.164	0.117	No
SA vs. Dan				
Mandibular M1	-0.056	-0.075	-0.047	Yes
Mandibular M2	-0.024	-0.059	0.037	No
Mandibular M3	-0.071	-0.113	0.118	No
NA vs. NE				
Maxillary M3	-0.056	-0.095	0.069	No
Mandibular M3	-0.075	-0.129	0.067	No
NA vs. Dan				
Mandibular M3	0.096	-0.064	0.147	No
Dan vs. NE				
Mandibular M1	0.077	0.060	0.104	Yes
Mandibular M2	0.041	-0.036	0.061	No
Mandibular M3	-0.094	-0.166	-0.072	Yes

Comparisons between human populations: SA, South African; NA, North American; NE, Northern England; Dan, medieval Danish for the specified tooth types. Column headers are as in Table 7.

in enamel cap area (although his data also show a slight increase in enamel cap area from M1 to M3). Smith et al.³ suggested that the distribution of these tissues within the molar row differs between apes and humans, and is perhaps related to posterior molar reduction in *Homo* (reviewed in Kieser⁴³).

This trend of molar reduction is confirmed in the current sample by the significantly decreasing bi-cervical diameter length found in both upper and lower molar rows. Among maxillary molars, the average bi-cervical diameter length in the M3 is approximately 6.6% less than the M1 average, and in mandibular molars, bi-cervical diameter in the M3 is approximately 6.0% less than this measurement in M1, suggesting a slightly greater molar breadth reduction in maxillary molars (data from Appendix A). LeBlanc and Black⁴⁴ found that occlusal area in the maxillary molar row decreased more than in mandibular molars for Greek and Turkish archaeological populations. Additional study of the relationships between overall dental reduction and changes in tissue proportions may be best conducted with 3D analyses,^{6,22} which may reveal the relationships between changes in occlusal area, 2D and 3D tissue distribution, and total crown volume.

Differences in EDJ shape in the combined samples do not directly correspond to differences in enamel

thickness. It is interesting that EDJ shape was significantly different between some of the molar types within a jaw, as a previous study found that samples in which maxillary M1–M3 were combined could reliably distinguish humans from other species.^{23,45} It thus appears that differences in EDJ shape between molars within a jaw are not so great as to overwhelm the ability of this character to distinguish higher-level taxa (e.g., species, genera) from one another. However, intra-species variation within the samples examined here does not follow a clear pattern along the molar row, so when examining isolated teeth it is prudent to assess the shape of the EDJ in light of known differences between teeth from different positions, as is the case in enamel thickness studies of single teeth.³

Variation between sexes

Data from known-sex individuals in this study suggest that differences in molar enamel thickness and dentine area exist between females and males. Significantly greater average (and/or relative) enamel thickness in females often appeared to be the result of slightly greater enamel cap area coupled with a lower dentine area and EDJ length. Greater dentine area in males was also reported in

several radiographic studies of enamel and dentine thickness^{46–50} and a histological study.¹¹ Evidence from studies of molar crown dimensions (mesiodistal and buccolingual widths) in modern humans demonstrates that males and females show overlapping dimensions,^{43,51} although males show slightly greater dimensions (~3–6%) than females (recently reviewed in Hillson⁵² and Schwartz and Dean,¹¹ and also demonstrated in this study). These lines of evidence have been used to suggest that sexual dimorphism in tooth dimension is due to differences in dentine proportions, not differences in enamel thickness. This suggestion is further supported by the findings of Hlusko et al.,² who showed that the linear thickness of lateral enamel in male and female baboons does not differ, although the scaled quantity of enamel is greater in females than in males.

In contrast, evidence from a histological study of canine formation by Schwartz et al.⁵³ shows that female hominoids have greater linear cuspal enamel thickness values than males, which is significant in humans and orangutans (see also^{54,55}). The present study demonstrates that females often have greater mean molar enamel cap area, and although this achieved significance in only one comparison (upper M3), it frequently contributes to greater average (and/or relative) enamel thickness. Schwartz and Dean¹¹ also showed that females have a greater mean enamel cap area in mandibular canines, although significant differences were not found in this study either. It is possible that absolute differences between female and male molar enamel cap area/thickness are often too small to detect statistically. Hillson⁵² similarly noted that absolute size differences between male and female crown dimensions are quite small, and may be influenced by observer error. If these differences in tissue proportions are confirmed by additional studies, it may be prudent to consider using different scaling methods for known mixed-sex samples.²

Studies of genetic anomalies have suggested that X and Y chromosomes may influence enamel and dentine development in different ways.^{11,49,56,57} It appears that enamel formation is related to promotion of the X chromosome, while the Y chromosome promotes both enamel and dentine growth. Alvesalo⁵⁵ and Lähdesmäki and Alvesalo⁵⁷ noted that Y chromosome genes may lead to sexual dimorphism in tooth development, which is consistent with the finding of greater dentine proportions in males. Schwartz and Dean¹¹ suggested that changing levels of sex hormones during development could relate to differences in the proportions of dental tissues in teeth forming at different times (as they found differences in the dentine area of later-forming

M3 but not in the earlier-forming canine). The current study has shown a significant degree of sexual dimorphism in dentine area in lower M2, and since the majority of the coronal dentine in this tooth develops during the first 3–6 years, this does not support the idea that the development of dimorphism in dentine proportions occurs as a result of changing hormone levels in later childhood.

All sex differences were found within the South African population; data from other known-sex populations were for third molars only, which did not show significant differences in enamel thickness nor EDJ shape. When considered in light of differences between males and females, EDJ shape does not appear to be correlated with enamel thickness or the components of enamel thickness. Significant sex differences in average enamel thickness were found in three of six comparisons, while no differences in EDJ shape were found in these tooth positions. Although EDJ shape does not appear to be correlated with enamel thickness, differences between sexes among mandibular molars corroborate studies of other aspects of molar morphology and development suggesting that third molars show higher variance than second molars, which in turn show higher variance than first molars (e.g., variance in crown dimensions or occlusal area, reviewed in Scott and Lockwood⁵⁸ and Smith et al.³; variance in age at eruption, Garn et al.⁵⁹ and Bailit⁶⁰). Currently, it is unclear how these morphological and developmental patterns relate to one another. Additional research on the specific effects of hormones or gene products will hopefully further clarify the etiology of sexual dimorphism in dental development, differences in EDJ shape, and tissue proportions.

Variation among populations

The current study suggests that differences in the components of enamel thickness and EDJ shape may exist among regionally (and, to a degree, temporally) diverse modern human populations, which may result in significant differences in enamel thickness indices (*contra* Grine⁵). Differences among populations were found in both upper and lower M3, which is not unexpected in light of variation in other aspects of M3 morphology and development discussed above. However, EDJ shape varied between populations within M1 as well. Significant differences between populations were also found in an examination of dental developmental variables in this sample.²⁷ Smith et al.²⁷ found that the most common variable to differ among populations was linear cuspal enamel thickness, with the North American sample possessing the thickest cuspal

enamel (for M3) and the Danish sample possessing the thinnest enamel. This is consistent with the results of post hoc comparisons between groups in the present study; the Danish molars often showed the lowest average enamel thickness values and had the lowest values for the components of enamel thickness.

It is unclear to what degree these differences are due to environmental or genetic factors; numerous studies have considered the effects of genetic drift or genetic distances on dental metric differences between populations.^{43,61–63} Dental development in the Danish archaeological sample in particular may relate to the relatively poor health of the population, which was believed to have a fairly high incidence of leprosy.^{64,65} Although teeth with obvious signs of enamel hypoplasia were excluded from this study, this sample displayed a high incidence non-specific stress indicators in the enamel (accentuated lines).²⁴ Additional studies of well-documented populations from different environmental conditions may help to clarify this issue further.

Other factors that may contribute to differences found between populations may relate to differences in tooth size and occlusal morphology among populations. The Danish population had the smallest teeth of the combined sample as indicated by the length of the bi-cervical diameter. The South African molars generally showed the

largest bi-cervical diameter, which was significantly greater than both North American and Northern England for upper M3. This is consistent with studies of regional or racial differences among human molars.^{62,63,66–68} Harris and Rathbun⁶² reviewed a number of studies on population-specific differences between teeth, and noted that among a global sample, Subsaharan blacks and Europeans showed the highest and lowest averages of tooth dimensions, respectively (also reported by Harris and Lease⁶⁸ for the primary dentition). Lunt⁶⁶ reported that medieval Danes showed smaller teeth relative to a number of archaeological and modern populations. Recent work on dental metrics in a wide sample of populations suggests that the majority of odontometric variation is found within groups; less than 20% of the diversity is found between groups.⁶³ Very little is known about population-level variation in EDJ shape, although a recently developed three-dimensional technique to assess coronal EDJ shape using micro-computed tomography⁶⁹ may provide more insight into this potential source of variation.

When values for enamel thickness indices are compared to other studies of modern humans, the results presented here are similar (Table 10). Slight differences between studies may be due to differences in preparation techniques, imaging techniques, or the criteria used for excluding teeth. Martin^{14,15} used macro photographs of sectioned

Table 10 Averages for the components of average enamel thickness (AET) and relative enamel thickness (RET) in human molars

Row	Tooth	N	AET	Range	RET	Range	CV	Source	
Max	M1	37	1.22	0.98–1.50	18.75	13.95–23.86	11.1	This study	
		10	–	–	17	14–21	12.4	Grine ⁷	
		2	1.22	0.98–1.45	20.05	17.46–22.65	–	Martin ¹⁴	
	M2	25	1.40	1.13–1.76	21.59	16.49–28.03	14.5	This study	
		10	–	–	20	18–24	9.4	Grine ⁷	
		1	1.80	–	29.59	–	–	Martin ¹⁴	
	M3	51	1.38	1.18–1.95	21.80	17.02–30.01	13.2	This study	
		10	–	–	24	18–29	16.6	Grine ⁷	
		3	1.09	1.01–1.15	17.20	16.69–17.89	3.6	Martin ¹⁴	
Mand	M1	55	1.07	0.80–1.40	16.99	11.76–22.62	13.5	This study	
		10	–	–	18	14–23	15.0	Grine ⁷	
		2	1.28	0.92–1.63	23.92	17.36–30.48	–	Martin ¹⁴	
	M2	45	1.19	0.94–1.55	20.51	14.85–27.66	14.3	This study	
		10	–	–	22	18–27	12.6	Grine ⁷	
		2	1.44	1.40–1.47	30.29	28.29–32.29	–	Martin ¹⁴	
	M3	44	1.24	0.98–1.67	21.63	17.22–31.84	13.8	This study	
		144	1.20	0.88–1.59	25.39	20.8–31.3	8.5	Schwartz and Dean ¹¹	
		10	–	–	22	19–27	11.8	Grine ⁷	
			2	1.26	1.21–1.30	23.51	21.42–25.59	–	Martin ¹⁴

Codes are as in Tables 2 and 3. Range data represents minimum and maximum values. CV is calculated as the standard deviation of RET divided by the mean for samples greater than 2. Data from Schwartz and Dean¹¹ are a weighted average of known-sex averages from their Table 2.

Table 11 Relative molar enamel thickness (RET) in mesial sections of extant and fossil hominoids

Taxon and source	Maxillary			Mandibular		
	M1 (range)	M2 (range)	M3 (range)	M1 (range)	M2 (range)	M3 (range)
<i>Proconsul africanus</i> ⁷⁰	8.5	—	—	—	—	—
<i>Hylobates lar</i> ¹⁵	—	—	—	—	—	11.0
<i>Gorilla gorilla</i> ³	9.8 (9.1–10.1)	12.3 (11.6–13.0)	10.8 (9.8–11.8)	10.8 (9.0–12.6)	12.4 (9.7–15.2)	13.9 (12.8–15.1)
<i>Pan troglodytes</i> ³	10.3 (8.5–12.2)	11.4 (10.7–12.5)	12.8 (10.0–15.0)	12.6 (10.3–14.1)	12.9 (10.9–15.5)	15.0 (13.9–16.6)
<i>Dryopithecus laietanus</i> ⁷¹	12.7	—	—	—	—	—
<i>Pan paniscus</i> ⁷¹	—	—	—	—	—	13.6
<i>Proconsul major</i> ⁷¹	—	—	—	—	—	13.7
<i>Lufengpithecus hudienensis</i> ⁷²	—	—	—	14.1	—	—
<i>Rangwapithecus gordonii</i> ⁷²	—	—	—	—	—	14.9
<i>Oreopithecus bambolii</i> ⁷¹	13.0	—	—	—	—	—
<i>Pongo pygmaeus</i> ³	13.0 (9.8–16.3)	15.5 (11.2–18.1)	18.1 (15.3–19.9)	13.0 (8.6–15.8)	15.3 (12.5–18.5)	16.7 (9.8–22.5)
<i>Proconsul heseloni</i> ⁷³	—	—	—	—	—	17.0
<i>Sivapithecus sivalensis</i> ⁷¹	17.2 (16.3–18.2)	—	—	—	—	20.8
<i>Griphopithecus</i> sp. ⁷¹	—	19.0 (17.8–20.2)	—	17.2	18.4 (16.5–20.7)	22.0 (20.9–23.0)
<i>Sivapithecus paravada</i> ⁷⁴	—	—	—	18.9	—	—
<i>Afropithecus turkanensis</i> ⁷¹	—	—	—	—	20.9 (19.4–22.3)	—
<i>Australopithecus africanus</i> ⁷¹	21.6	21.3	—	—	—	—
<i>Homo sapiens</i> ^a	18.8 (14.0–23.9)	21.6 (16.5–28.0)	21.8 (17.0–30.0)	17.0 (11.8–22.6)	20.5 (14.8–27.7)	21.6 (17.2–31.8)
<i>Proconsul nyanzae</i> ⁷³	—	—	—	—	22.4	—
<i>Lufengpithecus lufengensis</i> ⁷²	—	—	—	—	24.1 (24.1–24.6)	—
<i>Graecopithecus freybergi</i> ³⁹	—	—	—	—	—	25.5
<i>Paranthropus robustus</i> ⁷¹	—	—	29.6	—	—	—

^a This study.

molar faces of several lightly to moderately worn teeth, while Grine^{5,7} used scanning electron micrographs of sectioned molar faces of unworn teeth, and Schwartz and Dean¹¹ used flatbed scanner images of histological sections of unworn teeth. During the present study, it was found that measurements of bi-cervical diameters taken from flatbed scanned sections differed by approximately 10% from low magnification microscopic overviews, as the scanned images did not allow the position of the enamel cervix to be determined accurately.

Finally, when values of relative enamel thickness are considered, it is clear that enamel thickness is highly variable both within and among apes and humans (Table 11). In particular, when small samples of fossils are considered in light of larger samples of modern hominoids, there is a large degree of overlap among taxa, and when trends in thickness from M1 to M3 are considered, few discrete categories of enamel thickness are apparent. For example, the range of relative enamel thickness values in modern humans encompasses almost all of the anthropoid primate taxa for which data are available,¹ and spans most of Martin's^{14,15,70} categories of enamel thickness. Therefore, relative enamel thickness appears to be of limited value

for distinguishing species of hominoids when tooth position is unknown. We suggest that, although enamel thickness itself does not offer a great level of resolution for species affiliation, when it is considered in light of other dental characteristics such as occlusal morphology, developmental rate and duration, and EDJ shape, a suite of dental features may yield high species-level discriminatory power.

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Appendix A. Raw data for the components of enamel thickness indices sorted by maxillary and mandibular molar positions

Row	Tooth	Variable	N	Minimum	Maximum	Mean	S.D.
Max	M1	<i>b</i>	37	32.46	59.44	42.87	6.25
		<i>c</i>	37	20.05	31.82	25.18	3.16
		<i>e</i>	37	17.66	24.11	20.64	1.51
		AET	37	0.98	1.50	1.22	0.12
		RET	37	13.95	23.86	18.75	2.08
		BCD	37	7.01	13.04	11.05	1.10
	M2	<i>b</i>	25	30.12	65.71	42.76	7.90
		<i>c</i>	25	23.12	36.64	28.61	4.07
		<i>e</i>	25	18.22	24.83	20.49	1.67
		AET	25	1.13	1.76	1.40	0.17
		RET	25	16.49	28.03	21.59	3.13
		BCD	25	8.99	12.99	11.26	1.13
	M3	<i>b</i>	51	27.39	55.87	40.97	7.46
		<i>c</i>	51	18.91	38.39	27.20	3.58
		<i>e</i>	51	16.02	23.15	19.72	1.70
AET		51	1.18	1.95	1.38	0.14	
RET		51	17.02	30.01	21.80	2.87	
BCD		51	8.16	11.88	10.37	0.94	
Mand	M1	<i>b</i>	55	27.45	50.82	40.16	5.02
		<i>c</i>	55	16.21	28.58	21.74	2.95
		<i>e</i>	55	16.73	22.94	20.32	1.28
		AET	55	0.80	1.40	1.07	0.13
		RET	55	11.76	22.62	16.99	2.29
		BCD	55	6.73	10.36	9.04	0.74

Appendix A (Continued)

Row	Tooth	Variable	N	Minimum	Maximum	Mean	S.D.
	M2	<i>b</i>	45	23.75	42.24	34.33	4.26
		<i>c</i>	45	16.81	29.13	22.05	2.59
		<i>e</i>	45	15.22	21.60	18.52	1.24
		AET	45	0.94	1.55	1.19	0.14
		RET	45	14.85	27.66	20.51	2.93
		BCD	45	6.25	10.09	8.65	0.76
	M3	<i>b</i>	44	24.40	45.98	33.09	5.11
		<i>c</i>	44	16.75	29.42	22.58	3.28
		<i>e</i>	44	15.90	22.26	18.27	1.36
		AET	44	0.98	1.67	1.24	0.15
		RET	44	17.22	31.84	21.63	2.99
		BCD	44	6.98	10.31	8.53	0.74

Codes are as in Tables 2 and 3. *N*, number of molars; values of *b* and *c* are in mm²; *e*, AET, and BCD are in mm; and RET is dimensionless.

Appendix B. Raw data for the components of enamel thickness sorted by sex for each molar position

Row	Tooth	Sex	Variable	N	Minimum	Maximum	Mean	S.D.		
Max	M1	Unknown	<i>b</i>	12	35.64	55.67	42.40	6.85		
			<i>c</i>	12	22.50	30.17	25.23	2.44		
			<i>e</i>	12	18.78	23.45	20.72	1.57		
			AET	12	1.07	1.33	1.22	0.08		
			RET	12	16.17	21.29	18.86	1.78		
			BCD	12	7.01	12.08	10.36	1.39		
		Female	<i>b</i>	10	32.46	46.43	40.49	4.36		
			<i>c</i>	10	20.05	29.63	24.40	3.05		
			<i>e</i>	10	17.66	21.95	19.90	1.44		
			AET	10	1.05	1.50	1.23	0.13		
			RET	10	15.95	23.86	19.39	2.60		
			BCD	10	10.41	11.50	10.97	0.41		
		Male	<i>b</i>	15	36.51	59.44	44.84	6.56		
			<i>c</i>	15	21.16	31.82	25.66	3.79		
			<i>e</i>	15	18.94	24.11	21.06	1.40		
			AET	15	0.98	1.42	1.22	0.14		
			RET	15	13.95	20.68	18.24	1.92		
			BCD	15	10.43	13.04	11.65	0.82		
		M2		Unknown	<i>b</i>	12	30.12	65.71	41.65	8.69
					<i>c</i>	12	23.12	33.18	27.83	4.05
					<i>e</i>	12	18.64	24.83	20.49	1.80
AET	12				1.13	1.71	1.36	0.18		
RET	12				16.49	28.03	21.35	3.50		
BCD	12				8.99	12.55	10.68	1.16		
Female	<i>b</i>			8	34.21	50.80	40.56	5.87		
	<i>c</i>			8	23.23	36.64	28.96	4.66		
	<i>e</i>			8	18.22	21.24	19.64	1.17		
	AET			8	1.18	1.76	1.47	0.18		
	RET			8	19.16	26.74	23.16	2.63		
	BCD			8	10.71	11.97	11.29	0.50		
Male	<i>b</i>			5	41.05	59.07	48.96	6.73		
	<i>c</i>			5	25.59	34.63	29.95	3.44		
	<i>e</i>			5	20.26	23.56	21.84	1.29		
	AET	5	1.26	1.59	1.37	0.13				
	RET	5	17.13	22.20	19.66	1.79				
	BCD	5	11.61	12.99	12.59	0.56				

Appendix B (Continued)

Row	Tooth	Sex	Variable	N	Minimum	Maximum	Mean	S.D.		
	M3	Unknown	<i>b</i>	6	27.39	48.91	36.02	8.94		
			<i>c</i>	6	18.91	27.74	23.33	3.34		
			<i>e</i>	6	16.02	21.54	18.74	2.23		
			AET	6	1.18	1.29	1.24	0.04		
			RET	6	18.42	22.63	21.02	1.98		
			BCD	6	8.16	11.84	9.39	1.70		
		Female	<i>b</i>	33	28.57	54.64	41.71	7.08		
			<i>c</i>	33	22.15	38.39	28.32	3.42		
			<i>e</i>	33	16.25	23.15	19.88	1.69		
			AET	33	1.21	1.95	1.43	0.15		
			RET	33	18.04	30.01	22.35	3.15		
			BCD	33	8.78	11.65	10.44	0.72		
		Male	<i>b</i>	12	30.43	55.87	41.41	7.48		
			<i>c</i>	12	22.49	30.30	26.06	2.38		
			<i>e</i>	12	17.62	22.49	19.77	1.38		
			AET	12	1.20	1.48	1.32	0.08		
			RET	12	17.02	24.85	20.69	2.05		
			BCD	12	9.55	11.88	10.66	0.78		
		Lower	M1	Unknown	<i>b</i>	38	27.45	50.82	40.06	5.60
					<i>c</i>	38	16.35	28.58	21.66	2.87
					<i>e</i>	38	16.73	22.94	20.43	1.45
AET	38				0.83	1.34	1.06	0.12		
RET	38				11.76	22.14	16.89	2.26		
BCD	38				6.73	10.36	8.99	0.81		
Female	<i>b</i>			10	35.13	46.45	40.08	3.95		
	<i>c</i>			10	16.21	28.39	23.09	3.59		
	<i>e</i>			10	18.11	21.15	20.04	0.81		
	AET			10	0.80	1.40	1.15	0.18		
	RET			10	13.31	22.62	18.21	2.62		
	BCD			10	8.41	9.92	9.05	0.54		
Male	<i>b</i>			7	34.73	44.44	40.86	3.06		
	<i>c</i>			7	18.22	22.87	20.27	1.68		
	<i>e</i>			7	19.01	20.85	20.11	0.62		
	AET			7	0.90	1.10	1.01	0.07		
	RET			7	13.95	16.98	15.78	1.10		
	BCD			7	8.35	9.81	9.34	0.51		
M2	M2			Unknown	<i>b</i>	34	23.75	42.24	34.18	4.48
					<i>c</i>	34	16.81	29.13	21.69	2.73
					<i>e</i>	34	15.22	21.60	18.54	1.36
					AET	34	0.94	1.55	1.17	0.14
					RET	34	14.85	27.66	20.22	3.14
					BCD	34	6.25	10.09	8.60	0.78
				Female	<i>b</i>	5	28.11	38.91	33.15	4.03
					<i>c</i>	5	21.53	27.73	23.64	2.46
					<i>e</i>	5	17.14	19.32	17.95	0.89
		AET	5		1.20	1.44	1.32	0.10		
		RET	5		20.36	25.11	22.93	1.92		
		BCD	5		7.56	9.68	8.65	0.78		
		Male	<i>b</i>	6	32.90	39.16	36.18	2.96		
			<i>c</i>	6	21.69	24.01	22.81	0.97		
			<i>e</i>	6	18.13	19.39	18.85	0.53		
			AET	6	1.17	1.24	1.21	0.03		
			RET	6	18.80	20.99	20.16	0.85		
			BCD	6	7.61	9.35	8.92	0.66		
		M3	M3	Unknown	<i>b</i>	26	24.40	45.98	31.45	5.20
					<i>c</i>	26	16.75	26.40	21.18	2.63
					<i>e</i>	26	16.05	22.26	18.02	1.41

Appendix B (Continued)

Row	Tooth	Sex	Variable	N	Minimum	Maximum	Mean	S.D.
			AET	26	0.98	1.43	1.18	0.12
			RET	26	17.22	28.48	21.15	2.70
			BCD	26	6.98	10.31	8.53	0.79
		Female	<i>b</i>	14	27.35	40.37	35.20	4.35
			<i>c</i>	14	19.26	29.42	24.57	3.43
			<i>e</i>	14	15.90	21.21	18.61	1.32
			AET	14	1.08	1.67	1.32	0.19
			RET	14	18.67	31.84	22.44	3.77
			BCD	14	7.13	9.99	8.42	0.71
		Male	<i>b</i>	4	32.45	38.46	36.40	2.77
			<i>c</i>	4	22.33	26.62	24.71	2.10
			<i>e</i>	4	17.38	19.73	18.69	1.05
			AET	4	1.28	1.36	1.32	0.04
			RET	4	21.23	22.56	21.90	0.56
			BCD	4	8.42	9.53	8.95	0.50

Codes are as in Tables 2 and 3. *N*, number of molars; values of *b* and *c* are in mm²; *e*, AET, and BCD are in mm; and RET is dimensionless.

Appendix C. Raw data for the components of enamel thickness sorted by population for each molar position

Row	Tooth	Gcode	Variable	N	Minimum	Maximum	Mean	S.D.
Max	M1	SA	<i>b</i>	25	32.46	59.44	43.10	6.08
			<i>c</i>	25	20.05	31.82	25.16	3.50
			<i>e</i>	25	17.66	24.11	20.60	1.50
			AET	25	0.98	1.50	1.22	0.13
			RET	25	13.95	23.86	18.70	2.24
			BCD	25	10.41	13.04	11.38	0.76
		NE	<i>b</i>	10	36.56	55.67	43.15	7.18
			<i>c</i>	10	22.50	30.17	25.38	2.50
			<i>e</i>	10	18.78	23.45	20.89	1.67
			AET	10	1.07	1.33	1.22	0.08
			RET	10	16.17	21.29	18.67	1.90
			BCD	10	8.71	12.08	10.65	1.01
		Danish	<i>b</i>	2	35.64	41.62	38.63	4.23
			<i>c</i>	2	22.53	26.47	24.50	2.79
			<i>e</i>	2	19.38	20.35	19.87	0.69
			AET	2	1.16	1.30	1.23	0.10
			RET	2	19.47	20.16	19.82	0.49
			BCD	2	7.01	10.78	8.90	2.67
	M2	SA	<i>b</i>	13	34.21	59.07	43.79	7.30
			<i>c</i>	13	23.23	36.64	29.34	4.11
			<i>e</i>	13	18.22	23.56	20.48	1.61
			AET	13	1.18	1.76	1.43	0.16
			RET	13	17.13	26.74	21.82	2.87
			BCD	13	10.71	12.99	11.79	0.83
		NE	<i>b</i>	9	36.92	65.71	43.93	8.73
			<i>c</i>	9	23.12	33.18	28.52	4.34
			<i>e</i>	9	18.64	24.83	20.89	1.90
			AET	9	1.13	1.71	1.37	0.20
			RET	9	16.49	28.03	20.90	3.81
			BCD	9	9.66	12.55	11.10	1.00
		Danish	<i>b</i>	3	30.12	37.80	34.81	4.11
			<i>c</i>	3	23.57	28.49	25.75	2.51
			<i>e</i>	3	18.68	20.03	19.29	0.68
			AET	3	1.23	1.42	1.33	0.10
			RET	3	20.01	24.58	22.71	2.40
			BCD	3	8.99	10.09	9.44	0.57

Appendix C (Continued)

Row	Tooth	Gcode	Variable	N	Minimum	Maximum	Mean	S.D.	
	M3	SA	b	13	29.80	50.73	41.09	6.61	
			c	13	22.15	38.39	27.52	4.40	
			e	13	16.77	21.36	19.47	1.39	
			AET	13	1.20	1.95	1.41	0.22	
			RET	13	18.07	30.01	22.29	3.84	
			BCD	13	9.55	11.88	10.78	0.64	
		NA	b	24	30.00	55.87	42.77	7.77	
			c	24	23.49	33.30	28.18	3.06	
			e	24	17.38	23.15	20.26	1.67	
			AET	24	1.21	1.63	1.39	0.11	
			RET	24	17.02	28.06	21.53	2.55	
			BCD	24	9.22	11.65	10.54	0.70	
		NE	b	13	28.57	48.91	38.57	6.68	
			c	13	21.48	29.25	25.71	2.41	
			e	13	16.25	21.54	19.26	1.64	
			AET	13	1.24	1.52	1.34	0.09	
			RET	13	18.42	28.36	21.77	2.57	
			BCD	13	8.16	11.84	9.77	1.20	
		Danish	b	1	27.39	27.39	27.39		
			c	1	18.91	18.91	18.91		
			e	1	16.02	16.02	16.02		
	AET		1	1.18	1.18	1.18			
	RET		1	22.55	22.55	22.55			
	BCD		1	8.45	8.45	8.45			
	Mand	M1	SA	b	17	34.73	46.45	40.40	3.53
				c	17	16.21	28.39	21.93	3.22
				e	17	18.11	21.15	20.07	0.72
				AET	17	0.80	1.40	1.09	0.16
				RET	17	13.31	22.62	17.21	2.42
				BCD	17	8.35	9.92	9.16	0.53
			NE	b	10	32.13	49.37	42.31	6.17
				c	10	19.90	28.58	23.16	2.53
				e	10	17.65	22.94	20.59	1.72
AET				10	0.96	1.25	1.13	0.10	
RET				10	15.05	22.14	17.48	2.34	
BCD				10	8.70	10.08	9.44	0.44	
Danish			b	28	27.45	50.82	39.25	5.27	
			c	28	16.35	27.75	21.13	2.83	
			e	28	16.73	22.82	20.37	1.38	
			AET	28	0.83	1.34	1.04	0.12	
			RET	28	11.76	20.98	16.67	2.24	
			BCD	28	6.73	10.36	8.82	0.86	
M2		SA	b	11	28.11	39.16	34.80	3.66	
			c	11	21.53	27.73	23.19	1.75	
			e	11	17.14	19.39	18.44	0.82	
			AET	11	1.17	1.44	1.26	0.09	
			RET	11	18.80	25.11	21.42	1.98	
			BCD	11	7.56	9.68	8.80	0.69	
			NE	b	15	28.96	41.65	34.11	3.77
				c	15	17.93	29.13	22.08	3.19
				e	15	16.76	21.60	18.63	1.20
		AET		15	1.01	1.55	1.19	0.16	
		RET		15	17.46	27.66	20.38	2.97	
		BCD		15	7.74	9.67	8.71	0.44	

Appendix C (Continued)

Row	Tooth	Gcode	Variable	N	Minimum	Maximum	Mean	S.D.
		Danish	<i>b</i>	19	23.75	42.24	34.23	5.07
			<i>c</i>	19	16.81	25.20	21.38	2.34
			<i>e</i>	19	15.22	20.78	18.47	1.50
			AET	19	0.94	1.37	1.16	0.13
			RET	19	14.85	27.36	20.10	3.34
			BCD	19	6.25	10.09	8.51	0.98
	M3	SA	<i>b</i>	5	32.45	40.24	37.89	3.18
			<i>c</i>	5	22.33	28.89	25.91	2.38
			<i>e</i>	5	17.38	19.74	19.01	0.98
			AET	5	1.28	1.53	1.36	0.10
			RET	5	20.27	24.14	22.16	1.40
			BCD	5	8.09	9.99	9.04	0.78
		NA	<i>b</i>	5	31.07	40.37	36.52	3.43
			<i>c</i>	5	19.65	27.83	23.10	3.31
			<i>e</i>	5	18.17	21.21	19.13	1.31
			AET	5	1.08	1.31	1.20	0.10
			RET	5	18.67	20.64	19.91	0.89
			BCD	5	8.19	9.27	8.65	0.43
		NE	<i>b</i>	13	27.35	45.98	35.22	5.17
			<i>c</i>	13	19.26	29.42	24.49	2.73
			<i>e</i>	13	15.90	22.26	18.76	1.65
			AET	13	1.08	1.67	1.31	0.17
			RET	13	17.22	31.84	22.36	4.04
			BCD	13	7.13	10.31	8.61	0.90
		Danish	<i>b</i>	21	24.40	37.28	29.82	3.57
			<i>c</i>	21	16.75	26.40	20.48	2.35
			<i>e</i>	21	16.05	19.19	17.58	0.91
			AET	21	0.98	1.43	1.17	0.13
			RET	21	17.52	28.48	21.46	2.76
			BCD	21	6.98	9.66	8.34	0.65

Codes are as in Tables 2 and 3. *N*, number of molars; values of *b* and *c* are in mm²; *e*, AET, and BCD are in mm; and RET is dimensionless.

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