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Dental tissue proportions and enamel thickness in Neandertal and modern human molars

Anthony J. Olejniczak [a,*], Tanya M. Smith [a], Robin N.M. Feeney [a], Roberto Macchiarelli [b], Arnaud Mazurier [c], Luca Bondioli [d], Antonio Rosas [e], Javier Fortea [f], Marco de la Rasilla [f], Antonio Garcia-Tabernero [e], Jakov Radovčić [g], Matthew M. Skinner [a], Michel Toussaint [h], Jean-Jacques Hublin [a]

[a] *Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany*
[b] *Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, UMR 6046 CNRS, Université de Poitiers, 40, avenue du Recteur Pineau, 86022 Poitiers Cedex, France*
[c] *Etudes Recherches Matériaux, 40, avenue du Recteur Pineau, 86022 Poitiers Cedex, France*
[d] *Museo Nazionale Preistorico Etnografico ''Luigi Pigorini'', Sezione di Antropologia, P.le G. Marconi 14, 00144 Rome, Italy*
[e] *Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, C/José Gutierrez Abascal 2, 28006 Madrid, Spain*
[f] *Área de Prehistoria, Universidad de Oviedo, Teniente Alfonso Martínez, 33011 Oviedo, Spain*
[g] *Croatian Natural History Museum, Demetrova 1, 10000 Zagreb, Croatia*
[h] *Direction de l'Archéologie, Ministère de la région Wallone, 5100 Namur, Belgium*

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Abstract

The thickness of dental enamel is often discussed in paleoanthropological literature, particularly with regard to differences in growth, health, and diet between Neandertals and modern humans. Paleoanthropologists employ enamel thickness in paleodietary and taxonomic studies regarding earlier hominins, but variation in enamel thickness within the genus *Homo* has not been thoroughly explored despite its potential to discriminate species and its relevance to studies of growth and development. Radiographic two-dimensional studies indicate that Neandertal molar enamel is thin relative to the thick enamel of modern humans, although such methods have limited accuracy. Here we show that, measured via accurate high-resolution microtomographic imaging, Neandertal molar enamel is absolutely and relatively thinner than modern human enamel at most molar positions. However, this difference relates to the ratio of coronal dentine volume to total crown volume, rather than the quantity of enamel per se. The absolute volume of Neandertal molar enamel is similar to that of modern humans, but Neandertal enamel is deposited over a larger volume of coronal dentine, resulting in lower average (and relative) enamel thickness values. Sample sizes do not permit rigorous intragroup comparisons, but Neandertal molar tissue proportions evince less variation than the modern human sample. Differences in three- and two-dimensional enamel thickness data describing Neandertal molars may be explained by dimensional reduction. Although molar tissue proportions distinguish Neanderthals from recent *Homo sapiens*, additional study is necessary to assess trends in tissue proportions in the genus *Homo* throughout the Pleistocene.

Keywords: Relative enamel thickness; Molar tissue volumes; Microtomography

Introduction

Molar enamel thickness measured in a controlled plane of section or using volumetric data effectively distinguish relatively thin-enameled extant African apes from thickly-enameled hominin taxa, including modern humans (e.g., Martin,

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* Corresponding author.
E-mail address: olejniczak@eva.mpg.de (A.J. Olejniczak).

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1985; Grine and Martin, 1988; Kono, 2004; Tafforeau, 2004; Smith et al., 2005, 2006a; Olejniczak et al., 2008). Enamel thickness has been similarly quantified in only a small number of fossil hominins (Grine and Martin, 1988; Macchiarelli et al., 2004, 2006; Smith et al., 2006b), and, with the exception of *Ardipithecus ramidus* (White et al., 1994), hominins are generally considered to be a thick-enameled clade. Despite this characterization, enamel thickness variation within the genus *Homo* is poorly understood. Some researchers have noted that Neandertal molars have a derived condition of thinner enamel than fossil *Homo sapiens* and modern human molars (e.g., Zilberman and Smith, 1992; Zilberman et al., 1992; Molnar et al., 1993; Smith and Zilberman, 1994; Ramirez Rozzi, 1996; Grine, 2004), indicating that the observed range of enamel thickness within the genus *Homo* may be broader than is commonly stated, and that Neandertals occupy the thin end of this range.

Thinner enamel in Neandertals has been used to support their specific distinction from relatively thicker-enameled *Homo sapiens* (Grine, 2004), as well as inferences about life history and general health (Zilberman and Smith, 1992; Molnar et al., 1993; Smith and Zilberman, 1994; Ramirez Rozzi, 1996), where thinner enamel in Neandertals has been linked to both suboptimal health and a faster developmental trajectory than modern humans. With the exception of two studies (Olejniczak and Grine, 2005; Macchiarelli et al., 2006), Neandertal enamel thickness has been studied by means of lateral flat plane radiographs, a method inadequate for measuring enamel thickness accurately (Grine et al., 2001). Olejniczak and Grine (2005) studied a microtomographic cross-section of the highly worn maxillary third molar of the Shanidar 3 Neandertal individual, concluding that its enamel thickness fell within the range of values for recent modern human molars. Conversely, a 3D microtomographic study of a mandibular permanent first molar from Abri Bourgeios-Delaunay (Macchiarelli et al., 2006) yielded a relative enamel thickness lower than the mean value for recent modern human molars reported by Kono (2004). Despite small methodological differences between microcomputed tomography studies, the data presented by Kono (2004) and Macchiarelli et al. (2006) are comparable, lending support to the idea that Neandertal molars are characterized by thinner enamel than modern humans when 3D data are considered.

Thinner molar enamel in Neandertals thus has yet to be confirmed using a sample large enough to provide analytical resolution of differences between Neandertals and modern humans coupled with imaging techniques allowing 3D measurements to be recorded. Microcomputed tomography (μCT) has been demonstrated to accurately portray internal dental surfaces (Rossi et al., 2004; Tafforeau, 2004; Coppa et al., 2006; Olejniczak and Grine, 2006; Skinner et al., 2008), facilitating nondestructive studies of enamel thickness in fossil hominin molars (e.g., Macchiarelli et al., 2004, 2006; Smith et al., 2006b). This imaging technique also allows 3D measurements to be recorded across the entire tooth crown (e.g., Kono, 2004; Tafforeau, 2004; Olejniczak et al., 2008) rather than limiting enamel thickness analyses to a single plane of section. Moreover, μCT facilitates the study of anatomical regions otherwise inaccessible to the observer, such as pulp chamber morphology (Peters et al., 2000; Oi et al., 2004; Amano et al., 2006).

Given that Neandertal permanent molar enamel has been variously found to be both thinner than and within the range of modern human permanent molar enamel thickness, and that only three molars (two permanent and one deciduous) have been studied using microtomographic techniques with quantified accuracy relative to physically produced sections, the present study aims to assess the Neandertal enamel thickness condition relative to modern humans using advanced imaging techniques and a substantially larger sample than previous studies. The use of microtomographic techniques allows a detailed assessment of unworn (or slightly worn) Neandertal molars at a finer resolution than has been employed in previous enamel thickness studies.

Materials and methods

Forty-two Neandertal molars of 27 individuals from 11 sites (Abri Bourgeois-Delaunay, Abri Suard, La Quina, Le Moustier, Regourdou, and Roc de Marsal, France; Ehringsdorf, Germany; El Sidrón, Spain; Engis and Scladina, Belgium; and Krapina, Croatia) spanning oxygen isotope stages 6 to 3, and a comparative sample of recent modern human molars ($n = 46$), were subjected to high-resolution μCT scanning using both synchrotron and laboratory facilities (Table 1; Fig. 1). In some cases, multiple teeth from the same Neandertal individual were measured (e.g., Le Moustier, Regourdou). The recent modern human molar sample is largely of unknown provenance, although at least part of the sample derives from North American and European dental extractions (Paul Brown, pers. comm.). All of the teeth in the comparative sample are unworn and free from pathological conditions affecting the mineralized tissues. Maxillary molars were included in this study only if all four major cusps were well-defined in order to eliminate bias due to talon reduction in posterior modern human molars. One-half of the modern human mandibular molars showed reduced hypoconulid expression, but molars with a complete absence of a hypoconulid were not included in the study. Sex is known for 19 of the modern human molars (10 female, 9 male, 27 unknown). It is known that modern human average enamel thickness is greater at certain tooth positions in females than in males (e.g., Schwartz et al., 2001; Schwartz and Dean, 2005; Smith et al., 2006a). Nonetheless, as is the case in external crown measurements (Hillson, 1996), differences in molar enamel thickness between males and females are slight, and overlap between sexes is substantial (Smith et al., 2006a).

Isometric voxel dimensions for all virtual representations of teeth in this study were between 14 and 50 μm. The comparability of the laboratory and synchrotron μCT systems employed has been quantified; each system produces reliable enamel thickness measurements with low intersystem error (Olejniczak et al., 2007).

Volumetric enamel thickness data were recorded for 29 of the fossil specimens after digital tissue segmentation and

Table 1
Composition of the Neandertal and modern human molar sample[a]

Group	Locality	Maxillary			Mandibular			Total
		M^1	M^2	M^3	M_1	M_2	M_3	
Neandertal	Abri Bourgeois-Delaunay				1 (1)		1 (1)	2 (2)
Neandertal	Abri Suard[b]				3 (3)	1 (1)	2 (2)	6 (6)
Neandertal	Ehringsdorf				1			1
Neandertal	El Sidrón	1	4 (4)	3 (3)	2 (2)			10 (9)
Neandertal	Engis[b]	1 (1)			1 (1)			2 (2)
Neandertal	Krapina					2 (2)	1 (1)	3 (3)
Neandertal	La Quina						1 (1)	1 (1)
Neandertal	Le Moustier[b]	1	1	1 (1)	1	1	1 (1)	6 (2)
Neandertal	Regourdou[b]				1	2 (1)	2	5 (1)
Neandertal	Roc de Marsal[b]				2 (2)			2 (2)
Neandertal	Scladina[b]	1	1 (1)		1	1		4 (1)
Recent *H. sapiens*		6	6	15	1	9	9	46
Grand total		10	12	19	14	16	17	88

[a] Numbers in parentheses are the sample sizes used in volumetric (3D) analyses of Neandertal molars.
[b] Indicates that multiple teeth from the same individual were measured.

surface model construction. Segmentation was achieved via image filtration (median and anisotropic diffusion filters), as described by Olejniczak (2006), followed by region-growing assisted voxel thresholding. Surface models were produced using Slicer 3D software (Gering et al., 2001), which makes use of the well-known marching cubes algorithm (Lorensen and Cline, 1987) to extract a triangular polygon mesh isosurface from volumetric data; smoothing and decimation parameters were set to 20 and 1, respectively. This subsample of the full collection represents the unworn (or very lightly worn) molars; wear was determined by external examination of the molars supplemented by cross-sectional visualization of cusps, where flattened areas at wear facets can readily be seen. The following measurements were recorded:

1. The volume of the enamel cap, in mm^3.
2. The volume of coronal dentine, in mm^3. Following methods described in greater detail elsewhere (Olejniczak, 2006), the coronal dentine volume measurement is defined to include the coronal aspect of the pulp chamber. The molar enamel cervix is sinuous, and defining a single plane (above which is crown and below which is root) is difficult in light of areas of enamel that extend towards the root apex. The most apical plane of section through the cervix that shows a continuous ring of enamel was first located; this plane was then gradually moved apically until the most apical plane of section still containing enamel was located. The plane midway between that containing the most apical ring of continuous enamel and that containing the most apical extension of enamel was taken as the cervical plane, above which coronal measurements are recorded.
3. The surface area of the enamel-dentine junction (EDJ), in mm^2.
4. Average enamel thickness, in mm. This is the average straight-line distance between the EDJ and the outer enamel surface, calculated as the quotient of the enamel volume and EDJ surface area.
5. Relative enamel thickness, a scale-free measurement. This is the average enamel thickness scaled by the (cube root of the) coronal dentine volume in order to make scaled, size-free comparisons. The cube root of coronal dentine is used to make the result scale-free, so as to be appropriate for interspecies comparisons; the result is multiplied by 100 for ease of interpretation, setting the scale of results above 1.0.
6. The volume of the coronal aspect of the pulp chamber, in mm^3. In some cases we were unable to rule out the possibility of secondary dentine growth, and there is a tendency for fossil molars to collect matrix in the pulp chamber, which is approximately the same density as dentine. Thus, this measurement was possible in only 13 of the Neandertal molars and 17 of the modern human molars.

The full sample of 42 fossil molars was also employed in a study of mesial cross-sectional enamel thickness using the techniques developed by Martin (1983, 1985). This planar technique allows slightly worn molars to be reconstructed and measured, thereby expanding the available sample. Historically mesial planes of section have been the most widely-used method of recording enamel thickness data, and the data produced here facilitate comparison with previously published values. Planes of section were produced using VoxBlast software (Vaytek, Inc.), following techniques described by Olejniczak (2006). Comparative data from four modern human groups were culled from a study of physical sections (Smith et al., 2006a). It has been demonstrated that molar sections produced manually and those produced virtually closely approximate one another, and comparisons between physically and virtually produced sections are justified (Olejniczak and Grine, 2006).

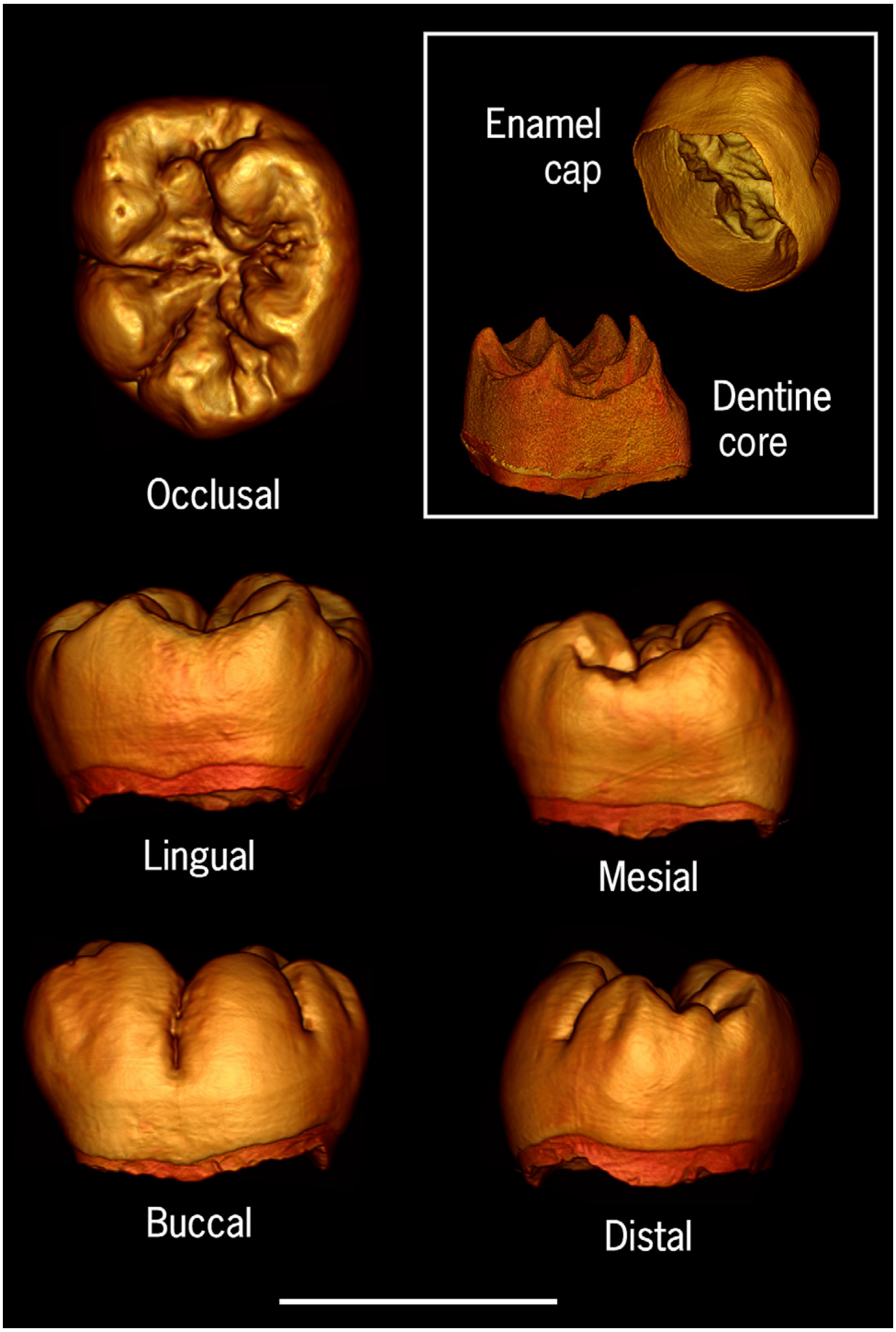

Fig. 1. Virtual reconstructions of a Neandertal mandibular left first molar crown (Abri Suard S5) in standard views. The inset box illustrates the results of the digital segmentation process allowing separation of the enamel cap from the underlying dentine core, facilitating the measurement of volumes and surface areas of each tissue separately. Scale = 1.0 cm.

Measurements on each mesial section were recorded on printed images using a digitizing tablet, and are defined following Martin (1983, 1985) as:

1. The area of the enamel cap, in mm^2.
2. The area of coronal dentine contained within the enamel cap, in mm^2.
3. The length of the EDJ, in mm.
4. Average enamel thickness, in mm. Defined as the average straight-line distance between the EDJ and the outer enamel surface, calculated as the quotient of enamel area and EDJ length.
5. Relative enamel thickness, a scale-free measurement. This is the average enamel thickness scaled by a surrogate for tooth size (coronal dentine area). The square root of the coronal dentine area is used in order to eliminate the

mm units from the result (as is appropriate in scaling equations); the result is multiplied by 100 to produce a scale above 1.0 for ease of comparison.

Differences between Neandertal and modern human values for each volumetric measurement were tested for significance using the Mann-Whitney *U* statistic. The modern human third molar sample is comprised of teeth with varying degrees of hypocone expression, and the reduced size of molars with small hypocones may inflate relative enamel thickness. In order to examine the influence of size variation due to differential cusp expression at a single tooth position, data collected for the relatively large sample of modern human maxillary third molars were examined using the nonparametric Spearman's rho statistic. Correlations between dentine volume, relative enamel thickness, and average enamel thickness were considered.

Results

Complete data sets of 3D and 2D measurements describing each Neandertal molar are given in Online Supplementary Materials Tables 1 and 2. Volumetric analyses performed on the combined sample of 29 unworn or lightly worn Neandertal molars (Table 2) reveal that, on average, Neandertal molars have a similar volume of enamel ($n = 29$; mean $= 225.47$ mm^3; range $= 154.04-302.07$ mm^3) to modern human molars ($n = 46$; mean $= 226.72$ mm^3; range $= 139.44-373.10$ mm^3); this difference is not statistically significant (Mann-Whitney $U = 585$; $Z = -0.892$; $p = 0.372$). Neandertal molars, however, have a significantly larger EDJ surface area ($n = 29$; mean $= 211.60$ mm^2; range $= 129.33-284.64$ mm^2) than modern humans ($n = 46$; mean $= 168.32$ mm^2; range $= 82.48-282.04$ mm^2; Mann-Whitney $U = 329$; $Z = -3.677$; $p < 0.001$). Average 3D enamel thickness of Neandertal molars ($n = 29$; mean $= 1.08$ mm; range: $0.82-1.63$ mm) is therefore less than that of modern humans ($n = 46$; mean $= 1.41$ mm; range $= 0.65-2.30$ mm) because their EDJ surface area is greater, despite the similar enamel volume in the two samples.

Coronal dentine volume (which includes the volume of the coronal aspect of the pulp chamber) is significantly greater in the Neandertal sample ($n = 29$; mean $= 345.65$ mm^3; range $= 244.62-502.38$ mm^3) than in modern human molars ($n = 46$; mean $= 233.04$ mm^3; range $= 103.53-372.37$ mm^3; Mann-Whitney $U = 178$; $Z = -5.32$; $p < 0.001$). When 3D average enamel thickness is divided by the cubic root of dentine volume, the 3D relative enamel thickness of Neandertal molars ($n = 29$; mean $= 15.55$; range $= 11.61-24.02$) is significantly less than that of modern human molars ($n = 46$; mean $= 23.56$; range $= 12.56-40.71$; Mann-Whitney $U = 162$; $Z = -5.494$; $p < 0.001$). Mean Neandertal relative enamel thickness falls below the range of the commonly cited "thick-enamel" category, which spans relative enamel thickness values 17.70 to 26.20 (Martin, 1983, 1985).

Interspecific enamel thickness comparisons of combined tooth-position samples are useful, although recent evidence demonstrates that comparisons at homologous tooth positions also elucidate important differences (Macho and Berner, 1993;

Table 2
Mean three-dimensional enamel thickness measurements

	Sample size (for pulp measurement)	Enamel volume (mm^3)	Coronal dentine (+pulp) volume (mm^3)	Coronal dentine volume (mm^3)	Coronal pulp volume (mm^3)	EDJ surface area (mm^2)	Average enamel thickness (mm)	Relative enamel thickness	Percent of coronal volume that is dentine
Maxillary M^1									
Neandertal	1 (0)	249.44	355.59	**	**	232.74	1.07	15.13	59%
Modern human	6 (1)	214.08	288.34	251.55	5.25	196.54	1.13	17.05	57%
Maxillary M^2									
Neandertal	5 (1)	235.65	332.87	399.41	13.64	221.09	1.07	15.54	58%
Modern human	6 (1)	251.90	255.22	282.14	1.94	175.72	1.46	23.36	50%
Maxillary M^3									
Neandertal	4 (0)	223.44	339.86	**	**	217.28	1.04	14.97	60%
Modern human	15 (10)	205.50	181.65	173.39	4.22	145.10	1.48	26.70	46%
Mandibular M$_1$									
Neandertal	9 (3)	232.73	345.45	375.84	16.39	207.37	1.17	16.77	60%
Modern human	1 (0)	215.65	289.83	**	**	205.32	1.05	15.87	57%
Mandibular M$_2$									
Neandertal	4 (4)	232.95	391.02	374.17	16.85	231.56	0.99	13.63	63%
Modern human	9 (1)	235.67	245.61	304.71	0.57	177.79	1.46	23.44	51%
Mandibular M$_3$									
Neandertal	6 (5)	198.47	328.54	312.07	13.96	189.40	1.06	15.43	62%
Modern human	9 (4)	246.00	248.16	223.27	4.47	169.68	1.45	23.79	50%
Neandertal mean	29	225.47	345.65	352.61	15.39	211.60	1.08	15.55	60%
Modern human mean	46	226.72	233.04	203.85	3.99	168.32	1.41	23.56	50%

Grine, 2002; Smith et al., 2005, 2006a). When examined per molar position (sample sizes and data given in Table 2), Neandertal molars have, on average, greater enamel volume than modern humans at some tooth positions (M^1, M^3, M_1), and less at other positions (M^2, M_2, M_3). At every tooth position where comparisons are possible, however, the average volume of coronal dentine and the average EDJ surface area in the Neandertal volumetric sample are greater than those of the modern human molars. Average enamel thickness and relative (size-scaled) enamel thickness were compared for each molar position represented by more than four molars via the Mann-Whitney U test (Online Supplementary Materials Table 3). At the mandibular second molar, average enamel thickness was not significantly different between groups, but at all other tooth positions where comparisons were possible significant differences were found for both measurements.

A pattern of increasing enamel thickness (both absolute thickness and relative thickness) from first to third molars is characteristic of modern human molars (Grine, 2002; Smith et al., 2006a), great ape molars (Smith et al., 2005), and lesser ape and ceboid molars (Olejniczak, 2006), but was not found in the Neandertal molars studied here (Fig. 2, Table 2). This could be due to relatively small samples at each tooth position masking trends throughout the jaw. In the only case where molars from multiple positions were examined from the same individual using 3D data (Abri Suard S36), the mandibular third molar does show small increases in both relative and average enamel thickness compared to the mandibular second molar.

Neandertal molars have significantly larger coronal pulp chambers than modern human molars (Mann-Whitney $U = 8.00$; $Z = -4.5$; $p < 0.001$), although no comparison was possible for the M_1 or M^3 positions, and pulp chamber volumes are highly variable (Table 2). Nonetheless, pulp chamber volume in both samples accounted for less than 6.0% of the total crown volume on average, not contributing substantially to the total dentine volume measured for calculation of the relative enamel thickness index.

Correlations between 3D enamel thickness and dentine size measurements in modern human third molars are presented in Online Supplementary Materials Table 4. Relative enamel

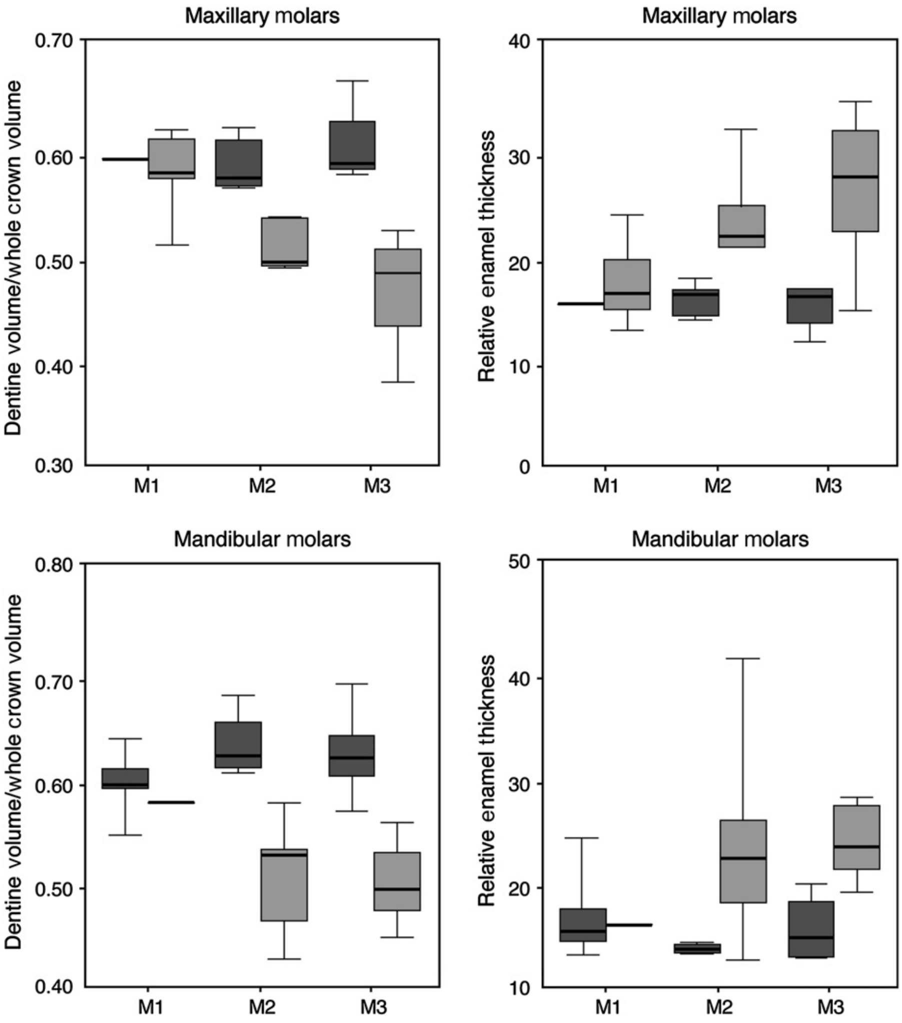

Fig. 2. Box plots depicting the percentage of the molar crown that is dentine (left) and relative enamel thickness (right) in maxillary (top) and mandibular (bottom) molars of Neandertals and extant humans based on 3D data. Neandertal values appear to the left of the human values in darker gray. The black line in each box represents the mean, the ends of boxes represent quartiles, and the ends of lines represent the range of the data. The increase in relative enamel thickness from the first to the third molar position in modern human molars corresponds to a reduction in dentine core volume.

thickness and the volume of coronal dentine show a significant negative correlation (rho = −0.721; $p < 0.001$), suggesting that tooth reduction (i.e., reduced hypocone expression) at a single molar position does inflate relative enamel thickness. Average enamel thickness also demonstrates a negative relationship with dentine volume (rho = −0.454; $p = 0.089$), although this correlation is not significant.

Data obtained from virtual mesial cross-sections (Neandertal $n = 42$; modern human $n = 257$; Table 3) indicate that, on average, Neandertal molars have less enamel area than modern human molars at each tooth position. Neandertal molars also have greater EDJ lengths than modern human molars, resulting in thinner enamel on average at every tooth position. Average coronal dentine area is also larger in Neandertal molars than in modern human molars at each tooth position. Thinner average enamel scaled by (the square root of) larger coronal dentine areas in Neandertal molars also results in relatively thinner molar enamel at each tooth position.

Thinner enamel in Neandertals, based on the 3D data presented above, is attributable to greater dentine volume per unit crown volume. Two-dimensional data presented in Table 3 show that Neandertal molars also evince a greater proportion of total crown area that is dentine than do modern human molars, but this difference is not as pronounced as in the 3D data. The overall mean Neandertal molar enamel volume ($n = 29$; 225.47 mm^3) is only 0.55% less than the mean modern human molar enamel volume ($n = 46$; 226.72 mm^3), whereas the mean Neandertal enamel area (21.97 mm^2) is 9.18% smaller than the mean modern human enamel area (24.19 mm^2). The overall mean Neandertal molar dentine volume ($n = 29$; 345.65 mm^3) is 48.32% greater than the mean modern human molar dentine volume ($n = 46$; 233.04 mm^3), whereas the mean Neandertal dentine area ($n = 29$; 41.65 mm^2) is 7.53% greater than the mean modern human dentine area ($n = 46$; 38.73 mm^2). Differences in 3D and 2D relative tissue quantities are depicted in Fig. 3.

Although both 3D and 2D data show that Neandertals have thinner enamel than modern humans, underlying tissue proportions (Fig. 3) reveal that this could be interpreted as the result of two different tissue conformations depending on which data are examined: a larger proportion of dentine per unit crown volume (3D), or a combination of less enamel area and greater dentine area (2D). Differences in data corresponding to two and three dimensions must be considered when describing enamel thickness within a taxon.

The Neandertal sites represented in the sample studied here span a substantial temporal and geographic interval. Sample sizes for each Neandertal site are too small to permit statistical comparison, although an examination of the 3D data recorded for specimens at each site shows less variation in tissue proportions and relative enamel thickness in Neandertals than in the recent modern human sample (Fig. 4, Table 4). The relatively young material from El Sidrón, Spain (OIS 3: Rosas et al., 2006), for instance, shows a similar pattern of tissue proportions and enamel thickness compared to much older material from Krapina and Scladina (OIS 5–6: Rink et al., 1995; Orlando et al., 2006). In terms of both tissue proportions and enamel thickness, the Neandertal molars from all sites occupy approximately one-half of the range of values occupied by modern human molars (Fig. 4; Table 4).

Table 3
Mean two-dimensional enamel thickness measurements in Neandertals and modern humans[a]

	Sample size	Total section area (mm^2)	Enamel area (mm^2)	Coronal dentine area (mm^2)	EDJ length (mm)	Average enamel thickness (mm)	Relative enamel thickness	Percent of coronal area that is dentine
Maxillary M^1								
Neandertal	4	69.09	23.46	45.63	22.75	1.03	15.23	66%
Modern human	37	68.05	25.18	42.87	20.64	1.32	18.75	63%
Maxillary M^2								
Neandertal	6	70.51	25.99	44.53	21.65	1.20	18.12	63%
Modern human	25	71.37	28.61	42.76	20.49	1.40	21.59	60%
Maxillary M^3								
Neandertal	4	72.29	26.25	46.04	21.49	1.22	18.00	64%
Modern human	51	68.17	27.20	40.97	19.72	1.38	21.80	60%
Mandibular M_1								
Neandertal	13	61.56	21.12	40.44	21.07	1.00	15.88	66%
Modern human	55	61.90	21.74	40.16	20.32	1.07	16.99	65%
Mandibular M_2								
Neandertal	7	63.14	20.64	42.50	20.17	1.02	15.69	67%
Modern human	45	56.38	22.05	34.33	18.52	1.19	20.51	61%
Mandibular M_3								
Neandertal	8	55.13	18.59	36.54	18.70	0.99	16.55	66%
Modern human	44	55.67	22.58	33.09	18.27	1.24	21.63	59%
Neandertal mean	42	63.62	21.97	41.65	20.75	1.06	16.44	65%
Modern human mean	257	62.92	24.19	38.73	19.60	1.24	20.06	62%

[a] Modern human cross-sectional data derive from Smith et al. (2006a).

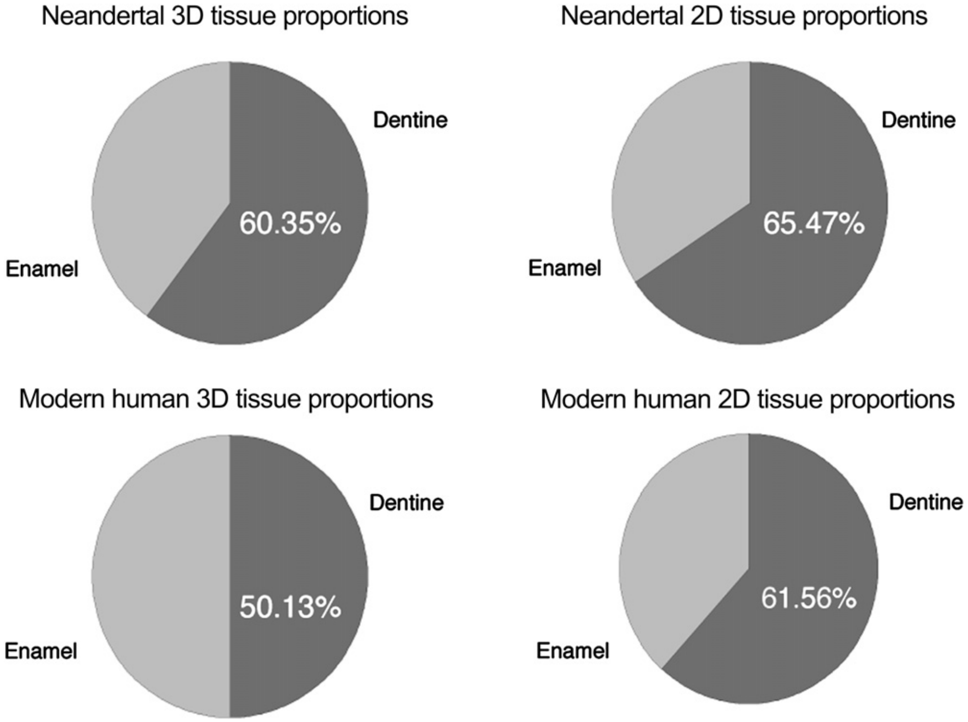

Fig. 3. Pie charts showing two- and three-dimensional relative tissue proportions in Neandertal and recent modern human molars. The three-dimensional data show that the relative volume of dentine per unit crown volume is greater in Neandertal molars than in modern human molars. Two-dimensional data, however, show a different pattern of tissue proportions in which Neandertal and modern human molars appear similar.

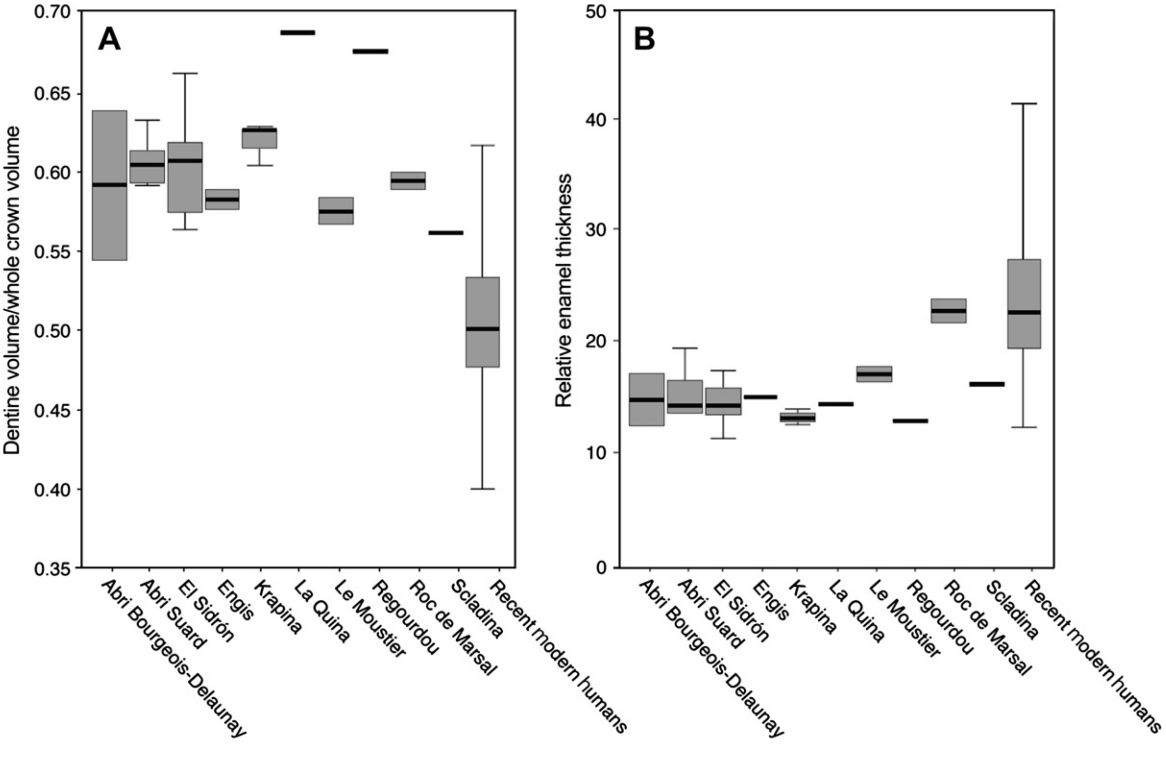

Fig. 4. Box plots depicting the percentage of the molar crown that is dentine (A) and relative enamel thickness (B) in Neandertal molars from the different localities studied here, and recent modern human molars, based on 3D data. The black line in each box represents the mean, the ends of boxes represent quartiles, and the ends of lines represent the range of the data. The range of variation for both variables is nearly double in modern humans compared to the Neandertal sample. While geographic and temporal variation likely contribute to variance within the Neandertal sample, the overall level of variation within Neandertal molars does not appear to be related to a specific geographic or temporal trend in enamel thickness or tissue proportions.

Table 4
Average 3D measurements at each Neandertal locality

	Sample size	Enamel volume (mm^3)	Coronal dentine (+pulp) volume (mm^3)	EDJ surface area (mm^2)	Average enamel thickness (mm)	Relative enamel thickness	Percent of coronal volume that is dentine
Abri Bourgeois-Delaunay	2	195.10	275.81	197.57	0.98	15.03	59%
Abri Suard	6	202.19	310.23	195.97	1.05	15.50	61%
El Sidrón	9	240.85	367.73	231.68	1.04	14.69	60%
Engis	2	241.87	336.59	228.67	1.06	15.21	58%
Krapina	3	265.41	428.30	260.22	1.01	13.46	62%
La Quina	1	222.11	485.91	192.52	1.15	14.67	69%
Le Moustier	2	228.29	306.48	194.61	1.17	17.30	57%
Regourdou	1	171.16	356.03	183.86	0.93	13.14	68%
Roc de Marsal	2	206.67	301.08	134.52	1.54	22.97	59%
Scladina	1	224.43	286.15	207.55	1.08	16.41	56%

Discussion

Our results demonstrate that Neandertal permanent molars are characterized by thinner enamel than modern human molars (contra Olejniczak and Grine, 2005). This finding is consistent with lateral radiograph analyses (e.g., Zilberman and Smith, 1992; Smith and Zilberman, 1994), preliminary evidence from the deciduous dentition (Zilberman et al., 1992; Macchiarelli et al., 2006; Mazurier and Macchiarelli, 2006), and the single permanent molar measured by Macchiarelli et al. (2006). This difference in enamel thickness is apparent when both 3D and 2D data are considered (Tables 2 and 3), although these disparate measurement techniques evince different underlying patterns of molar tissue proportions. Three-dimensional data show that the volume of dentine is greater in Neandertal molars than in modern human molars, while the volume of enamel is similar. Two-dimensional data show that Neandertal molars are characterized by the combination of less enamel area and greater dentine area than are modern human molars.

The 3D data presented here for modern humans come from a geographically limited sample (North American and European dental extractions), and it is unknown whether other human populations show similar differences in enamel thickness compared to Neandertals. The 2D data ($n = 257$) employed, however, derive from four geographically distinct populations, including European, North American, and African modern human groups (Smith et al., 2006a). These 2D measurements show differences in relative and average enamel thickness between Neandertals and modern humans, and only slight variation between modern human groups (Smith et al., 2006a). Differences between 2D and 3D data make it difficult to extrapolate one from the other, but 2D data indicate that our 3D results likely do not stem from having sampled a limited number of human populations.

Discrepancies between 3D and 2D data are an effect of dimensional loss in 2D, and may be explained in terms of a geometric analogy using two concentric spheres (Online Supplementary Materials Fig. 1): the inner sphere represents coronal dentine, and the space between the inner and outer spheres represents enamel. If the radius of the dentine sphere is decreased, representing the pattern of tissue proportions seen in modern humans, the radius of the outer sphere must also decrease, but to a lesser degree, in order to keep the volume of enamel constant. Cross-sectional measurements taken in a plane coursing through the center of the concentric spheres show an increase in enamel area and a decrease in dentine area relative to an analogous section through the Neandertal model, mimicking the condition seen in the actual data presented in Tables 2 and 3 (greater differences in the 2D relative enamel thickness data than in the 3D data; see Online Supplementary Materials Fig. 1).

This simplified model is complicated in actual molars by variation in enamel thickness across the tooth crown (e.g., Kono, 2004: their Fig. 15). Nonetheless, this example shows that cross-sections necessarily have less enamel area and greater dentine area when the volume of enamel is kept constant and the volume of coronal dentine is reduced, explaining differences in the pattern of tissue proportions in data of varying dimensions. Whether volumetric or cross-sectional data are preferred depends on the research question being addressed, but future studies of enamel thickness should take into account the implications of dimensional loss when 2D data are employed. For the purpose of the present study, which is focused on characterizing the whole-crown enamel thickness of Neandertal molars relative to that of modern humans, 3D data are most appropriate.

The analogy presented above demonstrates a link between 2D and 3D patterns of molar tissue proportions, but does not offer a biological explanation for thinner enamel in Neandertal molars. Differences in enamel thickness between Neandertal and modern human molars may be related to other aspects of molar gross morphology (e.g., taurodontism, tooth size), dietary differences between these groups, or differences in growth and developmental patterns.

Although taurodontism is not universal among Neandertal molars, a relatively apical root furcation resulting in taller and apparently wider pulp chambers is more common in Neandertal than modern human molars (e.g., Adloff, 1907; Keene, 1966; Constant and Grine, 2001). According to traditional measurement techniques of relative enamel thickness, the coronal aspect of the pulp component of molars is included in the calculation of coronal dentine volume. Our results demonstrate that Neandertal molars have significantly larger coronal pulp chambers, but less than 6% of the total coronal dentine volume is attributable to the pulp chamber in both Neandertals and modern humans. Thinner enamel in Neandertals does not appear to be a function of expanding the volume of coronal dentine to accommodate a larger pulp chamber. Nonetheless, a link between taurodontism and enamel thickness may not be excluded based on the data collected here.

Homo sapiens individuals have smaller molar crowns than Neandertals in terms of buccolingual breadth and mesiodistal length (total crown volume, calculated as enamel volume plus coronal dentine volume, is also greater in Neandertal molars than modern human molars; Table 2). A reduction in modern human tooth size took place within the last 100,000 years (Brace et al., 1987), and a likely means of reducing tooth size is to decrease the quantity of the dentine component of the tooth crown (Grine, 2002, 2005). It may be the case that dental reduction in modern humans has preferentially reduced the volume of dentine, resulting in relatively thicker enamel (given that relative enamel thickness is scaled by the volume of dentine). Data from our study demonstrate that Neandertal molar crowns are comprised of 60.35% dentine, while only 50.13% of modern human molar crown volume is dentine, on average (Table 2); thick enamel in modern humans may simply be an artifact of dental reduction.

The data presented in this study, however, derive from recent modern humans and are, therefore, insufficient to assess whether a temporal trend of dental reduction is responsible for thicker enamel in modern humans. A representative sample of Middle and Upper Paleolithic *Homo sapiens* molars would facilitate a more rigorous examination of this hypothesis, where tooth size and enamel thickness could be compared over a temporal range. Unpublished data from the study of Smith et al. (2007a) show that modern human-like tissue proportions are apparent in the megadont molars from Jebel Irhoud (∼160 ka) described by Hublin and Tillier (1981). Calculation of tissue proportions from a small sample of large molars from South Africa dating to approximately 60 ka (Smith et al., 2006b) also yields modern human molar tissue proportions. Similarity between modern human molar tissue proportions and these large fossil *Homo sapiens* molars may indicate that dental size reduction is not responsible for thick enamel in modern humans, but a broader range of molars from fossil *Homo* individuals is required to fully address this hypothesis.

When a single tooth position is examined in isolation (modern human maxillary third molars), reduced dental size (e.g., reduced hypocone expression) shows a significant negative correlation with relative enamel thickness. A nonsignificant negative correlation between average enamel thickness and dentine volume was also detected. These results indicate that reduced dental morphology results in thicker enamel in millimeter units, and this thickness is further inflated when scaled by the quantity of dentine to produce the relative enamel thickness index. The sample of modern human molars employed in this study is biased towards larger samples of posterior molars (particularly third molars). When the effects of dentine volume reduction and tooth size reduction within the human maxillary third molar sample are considered, the differences detected between Neandertals and modern humans are, in part, a function of the study sample. Nonetheless, the range of relative enamel thickness in modern human maxillary third molars (14.54–34.10) shows little overlap with the range of values calculated for Neandertal maxillary third molars (11.61–16.60), suggesting that a difference in relative enamel thickness between taxa exists despite the compounding effects of reduced dental morphology (Online Supplementary Materials Fig. 2).

Although there is little evidence for substantially different dietary adaptations between Neandertals and modern humans, it may be considered whether more subtle dietary specializations, such as the exploitation of inland aquatic resources (Richards et al., 2001), result in different enamel thickness between the two groups. The most appropriate comparison groups for Neandertals, however, are penecontemporaneous *Homo sapiens* (e.g., late Pleistocene modern humans) or various populations of modern humans with traditional diets that may show differentiation in enamel thickness related to dietary specialization, not recent North American individuals. A nuanced analysis of the impact of dietary differences on enamel thickness within the genus *Homo* necessarily awaits larger samples of relevant materials.

The developmental mechanisms leading to differences in enamel thickness and dentine volume between Neandertal and modern human molars are poorly understood. Grine and Martin (1988) suggested that the quantity of enamel is the result of: (1) the rate of enamel secretion, (2) the duration of enamel secretion, and (3) the number of enamel secreting cells. Dean et al. (2001) and Macchiarelli et al. (2006) present secretion rate data for two Neandertal molars, which do not differ from modern human rates. The crown formation times of permanent first molars reported in Macchiarelli et al. (2006) and Smith et al. (2007b) fall more than one standard deviation below modern southern African and northern European mean values (Reid and Dean, 2006). Smith et al. (2007b) recently demonstrated that coronal enamel extension rates are greater, which is consistent with shorter molar crown formation times in Neandertals.

Additional histological work is necessary to determine precisely the developmental basis of differences between Neandertals and modern humans in terms of the rate and duration of enamel secretion. One hypothesis for the developmental basis of thinner and thicker enamel has recently been offered by Suwa and Kono (2005), and incorporated into Neandertal dental studies by Macchiarelli et al. (2006). Suwa and Kono (2005) posited that the relative steepness of EDJ topography results in differential tensile and compressive forces on migrating sheets of ameloblasts as they secrete enamel and, when a certain threshold of tension or compression is met, enamel secretion ceases. Neandertal molars appear to have steeper EDJ topography than modern human molars (Macchiarelli et al., 2006; see also Fig. 1), although rigorous topographic analysis has not been performed. If the Neandertal EDJ is steeper than that of modern humans, this may result in tensile or compressive thresholds (depending on the location of the ameloblast sheet) being met earlier than in modern human molars, resulting in thinner enamel. As surface area alone measures size rather than complexity or steepness, the data presented here cannot directly address this issue. Future work focusing on EDJ topographic differences between Neandertals and modern humans will shed light on this hypothesis.

Although the causes of differences in enamel thickness and tissue proportions in Neandertals and modern humans await future studies of larger samples of fossil *Homo* molars, enamel thickness and tissue proportions do distinguish these groups. The data presented here show that categorical distinctions such as ‘‘thin enamel’’, ‘‘intermediate-thick enamel’’, and ‘‘thick enamel’’ have little paleobiological value at the subgeneric level, where dental tissue conformation (e.g., the percentage of the molar crown volume that is dentine) accounts for differences in enamel thickness, rather than differences in the absolute quantity of enamel on a tooth.

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Appendix A. Online supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhevol.2007.11.004.

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