



Variation in hominoid molar enamel thickness

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Abstract

Enamel thickness has figured prominently in discussions of hominid origins for nearly a century, although little is known about its intra-taxon variation. It has been suggested that enamel thickness increases from first to third molars, perhaps due to varying functional demands or developmental constraints, but this has not been tested with appropriate statistical methods. We quantified enamel cap area (c), dentine area (b), and enamel-dentine junction length (e) in coronal planes of sections through the mesial and distal cusps in 57 permanent molars of *Pan* and 59 of *Pongo*, and calculated average (c/e) and relative enamel thickness ($((c/e)/\sqrt{b}) * 100$). Posteriorly increasing or decreasing trends in each variable and average (AET) and relative enamel thickness (RET) were tested among molars in the same row. Differences between maxillary and mandibular analogues and between mesial and distal sections of the same tooth were also examined. In mesial sections of both genera, enamel cap area significantly increased posteriorly, except in *Pan* maxillary sections. In distal sections of maxillary teeth, trends of decreasing dentine area were significant in both taxa, possibly due to hypocone reduction. Significant increases in AET and RET posteriorly were found in all comparisons, except for AET in *Pongo* distal maxillary sections. Several significant differences were found between maxillary and mandibular analogues in both taxa. Relative to their mesial counterparts, distal sections showed increased enamel cap area and/or decreased dentine area, and thus increased AET and RET. This study indicates that when AET and RET are calculated from samples of mixed molars, variability is exaggerated due to the lumping of tooth types. To maximize

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taxonomic discrimination using enamel thickness, tooth type and section plane should be taken into account. Nonetheless, previous findings that African apes have relatively thinner enamel than *Pongo* is supported for certain molar positions.

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Introduction

Anthropological analyses of dental material have traditionally focused on aspects of gross crown morphology and metrics, patterns of wear, and enamel thickness inferred from exposed areas of dentine. Enamel thickness has been commonly assessed as a linear measurement of enamel visible in worn or naturally fractured teeth, and is often characterized as “thick” or “thin” (e.g., Simons and Pilbeam, 1972: 58, figures 2-3). Martin (1983, 1985) demonstrated that it is difficult to assess enamel thickness accurately from exposed enamel. He measured thickness from buccolingual sections cut through the mesial cusp tips, which could be scaled in relation to a surrogate for body size to make comparisons across taxa, resulting in a measure of relative enamel thickness (RET).

Martin found that gorillas and chimpanzees both had thin enamel, orangutans possessed intermediate-thick enamel, and humans had thick enamel (which was similar to the findings of Gantt [1977] on linear enamel thickness measurements from a controlled plane of section). From these results, Martin proposed that the ancestral hominoid RET condition was thin, as seen in a hylobatid outgroup, and that the ancestral great ape and human condition was thick. Recently, Shellis et al. (1998) suggested that, as the total number of teeth sampled increased, extant hominoids showed slightly different average values than those reported by Martin (1983, 1985). Shellis et al.’s chimpanzee sample was reported to show a range of enamel thickness values that is more similar to that of orangutans (intermediate thickness) than to thin-enamelled gorilla teeth. However, Shellis et al.’s method of assessing enamel thickness was based on regression analysis, which may yield

different results depending on the composition of the sample (see below). Kono (2004) recently reported two-dimensional (2-D) and three-dimensional (3-D) enamel thickness and crown volume data measured from micro-computed tomographic images of a small sample of hominoid molars. Two-dimensional values of average enamel thickness demonstrate that there exists substantial overlap between *Pan* and *Gorilla*, providing additional support for Martin’s (1983, 1985) conclusion.

An obvious limitation of studies of enamel thickness is the partially destructive nature of direct sectioning techniques. Reported hominoid values from a controlled (physical) plane of section have necessarily been based on small sample sizes (Gantt, 1977; Martin, 1983, 1985; Grine and Martin, 1988; Andrews and Martin, 1991; Macho, 1994; Beynon et al., 1998; Shellis et al., 1998; Grine, 2002; Olejniczak and Martin, 2002; Schwartz et al., 2003; Smith et al., 2003b, 2004; Grine, 2005). Previous studies of extant ape molars have produced a maximum reported sample of 17 teeth from seven individuals of a single species (Martin, 1983). Shellis et al. (1998) provided enamel thickness data on a wide range of prosimian and anthropoid molars. However, samples of each species were very small and the majority of molar type values were determined from single teeth. In particular, the issue of increasing enamel thickness from first to third molars within non-human primates remains unresolved (Schwartz, 2000a). If a pattern of increase can be shown, then values derived from different molars serve to increase the variance of combined tooth samples. In this case, enamel thickness should be reported for individual molar positions to maximize the likelihood of detecting differences among taxa (Macho, 1994; Grine, 2002).

Aims

This study aimed to increase the number of reported values of enamel thickness from physical sections of *Pan* and *Pongo*, including a comparison between two subspecies of orangutans, and a re-evaluation of previously published data from Martin (1983, 1985). Within this larger sample, changes in enamel cap area (c), dentine area (b), enamel-dentine junction length (e), average enamel thickness (AET), and relative enamel thickness (RET) from M1 to M3 were examined. In addition, differences in the components of enamel thickness between maxillary and mandibular molars were tested, as well as differences between mesial and distal sections within a tooth. Individual variables were examined, as well as AET and RET, which may or may not change due to changes in the enamel and dentine components. Finally, data on relative enamel thickness in enlarged samples of *Pan* and *Pongo* were compared to data from a smaller sample of *Gorilla*. These results were considered in the context of recent studies of cross-sectional enamel thickness in modern human molars (Grine, 2002, 2005) and enamel volume in hominoid molars (Kono, 2004).

Background

Variation and patterning of enamel thickness

The best data for interpretation of enamel thickness variation are from studies of human molars (e.g., Macho, 1994). However, Schwartz (2000a) suggested that the majority of published data on enamel thickness in modern humans are derived from European populations, which may not be representative of the species mean and may underestimate variation. A more recent investigation of enamel thickness in disparate modern human regional populations found values similar to those reported for European populations, with low levels of variation within and among populations (Grine, 2002, 2005). Differences in enamel thickness between populations or subspecies of non-human primates have not previously been studied. It is not clear if the inclusion of multiple

populations or subspecies will increase the variance of this condition, an important consideration when studying fossil samples.

To date, no study has shown a statistically significant relationship between enamel thickness and position in the permanent molar row in non-human primates. Martin (1983) found a trend of posterior increases in average enamel thickness within extant ape dentitions, although third molars were variable in thickness (and trend analysis was not employed). Other studies have suggested a similar trend, but did not explicitly demonstrate significant changes in thickness between permanent molars (Aiello et al., 1991; Grine et al., in press). The strongest evidence for statistical differences in enamel thickness comes from studies of human dentitions that have explored functional implications of the patterning of enamel thickness. Macho's (1994) study of "relative" enamel thickness (partial cuspal enamel area divided by the mean M1 occlusal cross-sectional area) of human maxillary molars showed that human first molars have significantly thinner enamel than second and third molars, which was attributed to differences in the functional demands on anterior and posterior molars. Grine (2002, 2005) reported a similar, sometimes significant pattern in human permanent molars, but suggested that increases in "relative" enamel thickness (enamel cap area divided by dentine area) relate to decreases in the area of the underlying dentine due to tooth size reduction, rather than functional demands.

While a number of studies have examined differences in absolute or relative enamel thickness within and between buccal and lingual cusps of mesial sections (e.g., Martin, 1983; Macho and Berner, 1993, 1994; Macho, 1994; Schwartz, 2000a,b; Grine, 2005), few studies have compared enamel thickness between mesial and distal section planes within a tooth. Little is known about the distribution of enamel and dentine throughout a tooth, and it is not clear if cross-sectional planes of mesial and distal cusps are directly comparable. Martin (1983) suggested that it is more difficult to produce sections without obliquity from distal cusps than from mesial cusps, and did not present data from the distal cusps of his sample (however,

Grine and Martin [1988] presented data from five distal sections of Martin's [1983] human sample). Shellis et al. (1998) found general agreement between anthropoid regression lines derived from mesial and distal sections, yet their study did not directly compare planes of section. Kono et al. (2002) used a three-dimensional analysis to quantify enamel volume in a small sample of human first molars. They found that distal faces of mandibular M1s were thicker than mesial faces, but not in maxillary M1s, which was interpreted to be the result of cusp-specific patterning rather than directional trends. Kono (2004) provided cusp-specific linear thickness data for extant hominoids, and showed that distal cusps are equal in thickness or thicker than mesial cusps, particularly in mandibular molars. These results also appear to conform to functional demand, as thicker cusps were those from the "functional" side of the crown (sensu Khera et al., 1990; Schwartz, 2000a,b).

Scaling of enamel thickness

The RET index developed by Martin (1983, 1985) was specifically designed to allow comparison of enamel thickness among species of different body sizes. In particular, it was designed to be applicable when only isolated teeth were available for study, as was the case for the fossil teeth originally examined by him. Relative enamel thickness has often been used as a summary measure of enamel thickness for comparisons among individuals of a species and even for comparisons of enamel thickness among teeth from a single individual. It is not appropriate to use RET to compare enamel thickness among molar teeth from one individual, as the size adjustment makes no sense given that the animal has but one (adult) size, and this factor (either the square root of the dentine area or the bi-cervical diameter) differs for M1, M2, and M3. It seems likely that some measure of dentine for the three molars would better reflect the size of the animal, rather than the size of the individual tooth. Perhaps an average value of dentine area, i.e., $[b(M1) + b(M2) + b(M3)]/3$ (where b = dentine area), would be the better measure when a whole

molar series is available. If so, this might translate to using $b(M1)*f1$, $b(M2)*f2$, and $b(M3)*f3$, i.e., dentine multiplied by a factor for each tooth that would approximate this mean molar size value. Insufficient data are available at present to address this question more than speculatively, but it is important to recognize the limitations of RET for intra-individual and intra-taxon comparisons. Only if it were the case that enamel thickness should be scaled to the animal's size at the time of crown formation would a RET index be appropriate for intra-individual comparisons. Based on current data, we have no reason to think that teeth scale to anything other than adult body size. Comparisons of enamel thickness among teeth of an individual should therefore be based on average enamel thickness (AET), which is enamel cap area (c) divided by enamel-dentine junction length (e).

Materials and methods

Hominoid sample and measurements

The sample of *Pan*, *Pongo*, and *Gorilla* molars included material previously reported by Martin (1983, 1985) from the Natural History Museum (London) (BMNH), which are revised and re-reported here, and new *Pan* and *Pongo* material acquired on loan from the Peabody Museum (Harvard), Humboldt Museum (Berlin), State Anthropological Collection (Munich), University College London (UCL), University of Newcastle upon Tyne (Department of Oral Biology), and additional material from the BMNH (Table 1). The *Pan* sample included a total of 85 mesial and distal sections of 57 molars from ten *Pan troglodytes verus* individuals and 27 individuals of unknown subspecies (*P. troglodytes* subsp.). The *Pongo* sample included a total of 91 mesial and distal sections of 59 molars from eight Bornean individuals (*Pongo pygmaeus pygmaeus*), three Sumatran individuals (*P. p. abelii*), and a single individual of unknown subspecies (*P. pygmaeus* subsp.). The number of teeth in the enlarged sample of these two genera is more than

Table 1
The study sample

Taxon	M ¹	M ²	M ³	M ₁	M ₂	M ₃	Total
<i>Pan</i>							
P. t. v.	2	-	9	-	-	-	11
P. t. subsp.	4	3	2	21	10	6	46
Total	6	3	11	21	10	6	57
<i>Pongo</i>							
P. p. p.	7	6	3	6	7	5	34
P. p. a.	5	3	1	5	3	3	20
P. p. subsp.	1	-	1	1	1	1	5
Total	13	9	5	12	11	9	59
<i>Gorilla</i>							
G. g. subsp.	3	2	2	2	4	2	15

Note: Numbers given for molar positions are number of teeth sectioned. Multiple sections (mesial and distal) are available for the majority of teeth. P. t. v. = *Pan troglodytes verus*, P. t. subsp. = *Pan troglodytes* subspecies unknown, P. p. p. = *Pongo pygmaeus pygmaeus*, P. p. a. = *Pongo pygmaeus abelii*, P. p. subsp. = *Pongo pygmaeus* subspecies unknown, G. g. subsp. = *Gorilla gorilla* subspecies unknown. Several of the individuals were developing their permanent dentitions at the time of death, so not all molars were available, as only crown-complete molars were used in this analysis. Other individuals showed heavy wear on first and/or second molars, so only third molars were included.

three times greater than the sample reported by Martin (1983). The *Gorilla* sample included 29 mesial and distal sections of 15 molars from eight individuals of unknown subspecies (*Gorilla gorilla* subsp.). Only crown-complete molars were included in this analysis.

Several preparative techniques were employed to generate histological sections and block faces of the mesial and/or distal cusps, which have been previously described (Martin, 1983, 1985; Reid et al., 1998a,b; Smith et al., 2003b). Several aspects of each cross-section were measured: area of the enamel cap (c), length of the enamel-dentine junction (e), and dentine area (b) (Fig. 1). Average enamel thickness (AET) was calculated as c/e , and relative enamel thickness (RET) was calculated as $([c/e]/\sqrt{b}) * 100$ (Martin, 1983, 1985). 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 not included in statistical analyses. When multiple planes of section were available, the section with the lowest RET was used in the analysis, as obliquity necessarily causes an overestimate of this value (Martin, 1983; Smith et al., 2004).

Statistical analyses

In this study, we demonstrate a novel approach to testing for trends in enamel thickness throughout the molar row. Previous studies of enamel thickness employed analysis of variance (ANOVA) in order to test for differences between tooth types (e.g., Macho and Berner, 1993; Macho, 1994; Grine, 2002, 2005). However, ANOVA is insensitive to

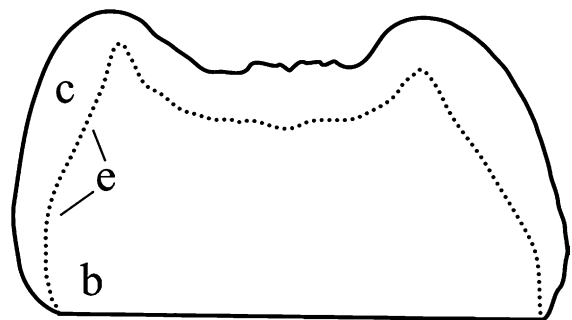


Fig. 1. A schematic of a *Pongo* molar showing the components of average and relative enamel thickness. The area of the enamel cap is represented as c, the area of the dentine under the enamel cap is represented as b, and the length of the enamel-dentine junction is represented as e. The average enamel thickness may be calculated as c/e , and relative enamel thickness may be calculated as $(c/e)/\sqrt{b} * 100$.

directional change, testing only whether the sample means are significantly different from one another. In addition, Jonckheere (1954) demonstrated empirically that ANOVA may fail to detect trends, since this is not the objective of the test. (This was confirmed in this study by a preliminary parametric analysis.) Because differences in the locations of the mean values do not directly address the current question of trends throughout the molar row, we have chosen to employ Conover's (1999) adaptation of the Jonckheere–Terpstra test for trends. In this test, Spearman's Rho is tested for significance (Spearman, 1904); the null hypothesis is that a particular variable, x , is equal in all molar positions ($H_0: M1(x) = M2(x) = M3(x)$), and the alternative hypothesis is that there is an ordered increase or an ordered decrease in x in posterior molars ($H_1: M1(x) \leq M2(x) \leq M3(x)$ or $M1(x) \geq M2(x) \geq M3(x)$). The test was performed individually for each component variable of RET (c, e, \sqrt{b}), as well as for AET and RET. Tests were performed separately on eight sets of data: maxillary molars of *Pan*, mandibular molars of *Pan*, maxillary molars of *Pongo*, and mandibular molars of *Pongo*, for both mesial and distal sections separately. In *Pongo*, averaged values were used for left and right antimeres within the maxillary or mandibular row of an individual to maintain independence of observations.

Several statistical tests were employed to examine differences in c, e, \sqrt{b} , AET, and RET between subspecies of *Pongo*, between maxillary and mandibular analogues, and between mesial and distal sections from the same tooth. In order to test whether the two subspecies of *Pongo* differ in any of the variables measured, mean differences were tested for individual maxillary and mandibular molars with the Mann–Whitney U -test (Sokal and Rohlf, 1995), resulting in six sets of tests. This test was also used to examine differences between maxillary and mandibular analogues separately for mesial and distal samples of *Pan* and *Pongo*. Finally, differences were examined between the mesial and distal planes of section within a single tooth using Wilcoxon's signed-ranks test (Conover, 1999). Each tooth type of each taxon was tested separately for those positions that had four or more mesial–distal

pairs. Analyses were run with SPSS software (v. 11.5).

In order to examine whether RET is significantly different among multiple taxa (*Pongo*, *Pan*, *Gorilla*), Kruskal–Wallis tests for RET differences were performed using genus as the factor, testing all six tooth types separately in both mesial and distal sections (resulting in 12 sets of tests). When significance was achieved, the multiple comparisons technique described by Conover (1999) was implemented in order to determine which of the three genera differed from one another significantly. The following results are presented in four sections: 1) enamel thickness and position in the molar row, 2) enamel thickness and maxillary or mandibular position, 3) mesial–distal comparisons of enamel thickness, and 4) relative enamel thickness among hominoids.

Results

Enamel thickness and position in the molar row

Comparisons of the two subspecies of *Pongo* showed that none of the components of relative enamel thickness or the AET or RET indices differed for any tooth type. Thus, the subspecies were lumped in the subsequent tests. The results of the Jonckheere–Terpstra test for trends in enamel thickness variables from M1 to M3 are presented in Table 2 and Figs. 2 and 3. Among *Pan* molars, significant positive increasing trends were found in area of the enamel cap (c) in mandibular sections, as well as significant decreases in length of the enamel–dentine junction (e) and square root of the dentine area (\sqrt{b}) in maxillary distal sections. *Pongo* molars showed similar trends. Overall, AET and RET increased posteriorly in both taxa due to increased enamel area and/or decreased enamel–dentine junction length and/or dentine area.

Enamel thickness and maxillary or mandibular position

The average values for the components of RET in both taxa are shown in Table 3, where

Table 2

P-values of the Jonckheere–Terpstra test for trends in enamel thickness variables in the molar rows of *Pan* and *Pongo*

Taxon	n	Row	Sec	c	e	AET	rt. b	RET
<i>Pan</i>	12	max	mes	0.11	0.46	0.03+	0.36	0.04+
<i>Pan</i>	15	max	dis	0.22	0.00–	0.00+	0.01–	0.00+
<i>Pan</i>	28/30	mand	mes	0.00+	0.09	0.00+	0.10	0.04+
<i>Pan</i>	27/28	mand	dis	0.01+	0.37	0.00+	0.46	0.01+
<i>Pongo</i>	19	max	mes	0.00+	0.07	0.00+	0.34	0.00+
<i>Pongo</i>	13	max	dis	0.09	0.01–	0.23	0.02–	0.04+
<i>Pongo</i>	22	mand	mes	0.02+	0.06	0.00+	0.07	0.00+
<i>Pongo</i>	20	mand	dis	0.01+	0.04–	0.00+	0.35	0.00+

Row = maxillary (max) or mandibular (mand), Sec = mesial (mes) or distal (dis) sections, c = area of enamel cap, e = length of enamel-dentine junction, AET is calculated as c/e, rt. b = square root of dentine area under the enamel cap, RET is calculated as $([c/e]/\sqrt{b}) * 100$. Significant results are in **bold**; + following the reported p-value indicates that the variable increases from M1 to M3, – indicates a decrease from M1 to M3.

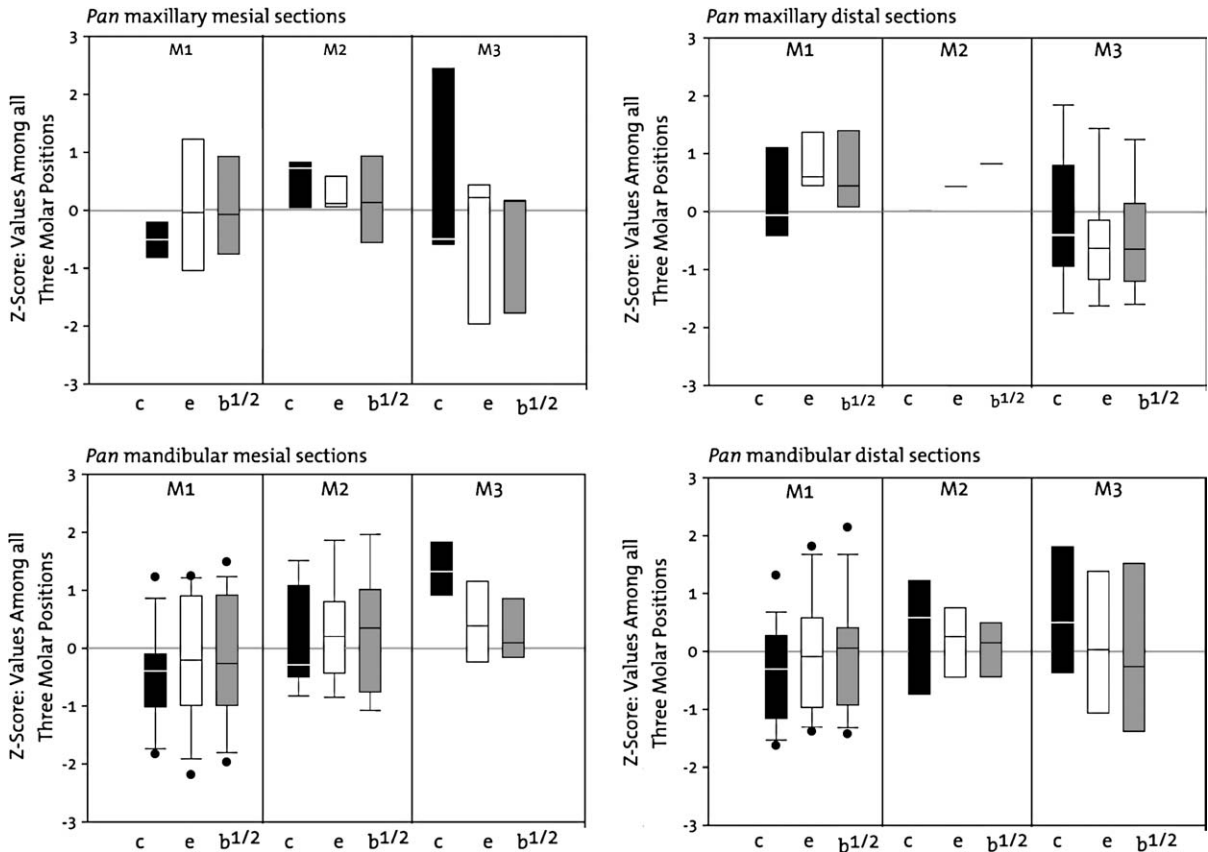


Fig. 2. Anterior-to-posterior trends in enamel thickness variables in *Pan* molars. Variable c = area of enamel cap, e = length of enamel-dentine junction, and rt. b = square root of dentine area under the enamel cap. Z-scores were calculated for each variable for each tooth and section type. The range of z-scores was plotted from left (M1) to right (M3) to show directional trends. Ends of boxes represent 25% and 75% ranges of the data; ends of whiskers represent 10% and 90% ranges of the data; dots represent outliers; the line in each box is the mean.

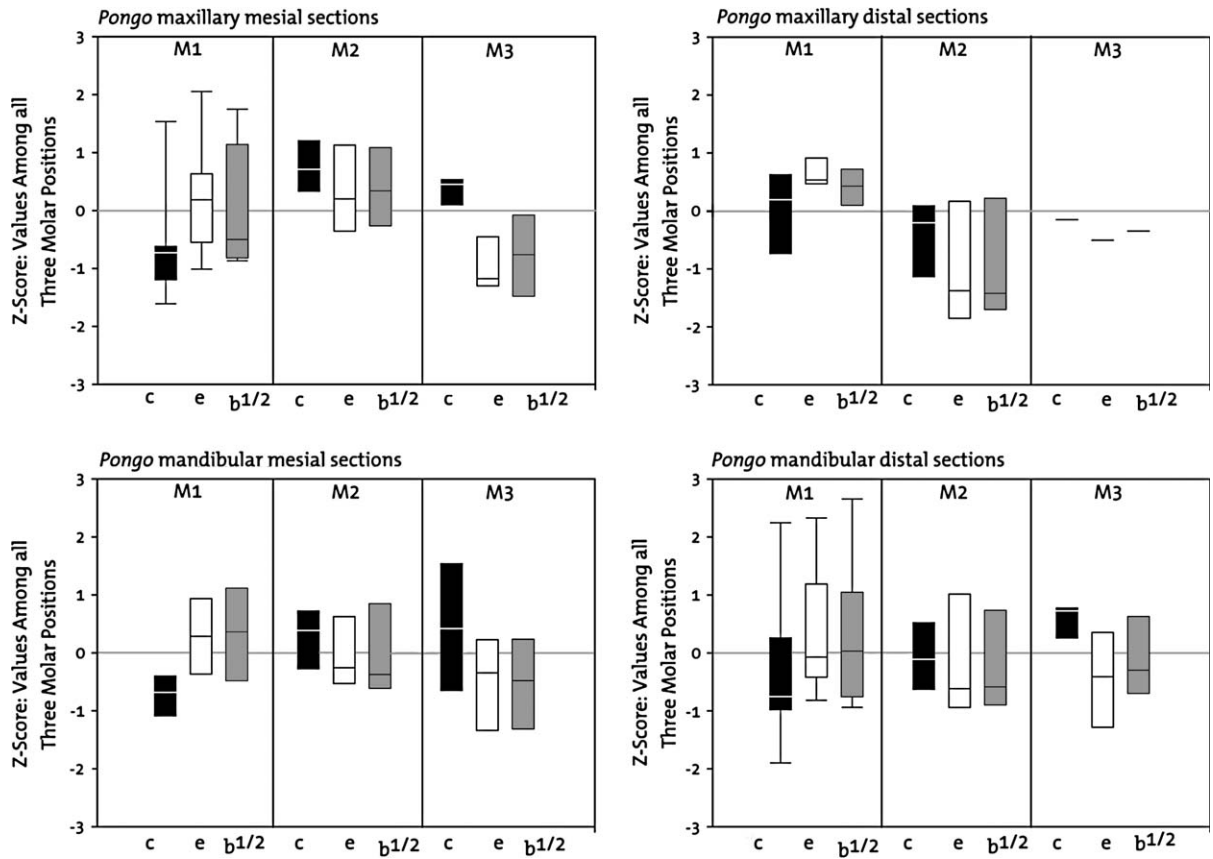


Fig. 3. Anterior-to-posterior trends in enamel thickness variables in *Pongo* molars. Variable c = area of enamel cap, e = length of enamel-dentine junction, and $rt. b$ = square root of dentine area under the enamel cap. Z-scores were calculated for each variable for each tooth and section type. The range of z-scores was plotted from left (M1) to right (M3) to show directional trends. Ends of boxes represent 25% and 75% ranges of the data; ends of whiskers represent 10% and 90% ranges of the data; dots represent outliers; the line in each box is the mean.

significant results of the Mann–Whitney *U*-test are indicated (individual values of the 205 sections are available upon request from the first author). *Pan* mesial sections of maxillary M1s showed a significantly greater square root of dentine area than their mandibular counterparts, as well as a significantly smaller AET (and RET). This trend was evident in all comparisons of mesial sections of *Pan* maxillary and mandibular molars, although these differences were not significant in second and third molars. *Pan* distal sections showed only a significant difference in enamel-dentine junction length in M1s, which was greater in maxillary than in mandibular M1s. In general, distal sections of maxillary molars also showed a greater square

root of dentine area than their mandibular counterparts, as well as a smaller AET (and RET), although these differences were not significant.

Mesial sections of *Pongo* maxillary molars generally showed greater values of the components of RET (as well as AET and RET) than mandibular molars, but these differences were non-significant, except for M2. Distal sections of maxillary molars generally showed greater values of the components of RET (as well as AET and RET) than mandibular analogues, although these differences were significant only in the M1s. Thus, *Pan* maxillary molars generally showed a greater dentine area than mandibular analogues, which

Table 3

Averages for the components of average enamel thickness (AET) and relative enamel thickness (RET) in molars of *Pan* and *Pongo*

Tooth	n	Row	Sec	c	e	AET	rt. b	bi-cd	RET	CV
<i>Pan</i>										
M1	6	max	mes	13.22 ± 0.97	20.21 ± 2.10	0.66* ± 0.04	6.41* ± 0.61	9.68** ± 1.23	10.33** ± 1.39	13.46
M2	3	max	mes	14.93 ± 0.71	20.52 ± 0.53	0.73 ± 0.03	6.42 ± 0.40	11.22** ± 1.67	11.37 ± 0.97	8.53
M3	3	max	mes	14.80 ± 2.88	19.25 ± 2.45	0.77 ± 0.12	6.07 ± 0.60	10.07 ± 2.05	12.82 ± 2.58	20.12
M1	15 ^a	mand	mes	12.98 ± 1.83	18.22 ± 1.98	0.71 ± 0.05	5.71 ± 0.49	7.78 ± 0.86	12.64 ± 1.11	8.78
M2	9	mand	mes	14.61 ± 2.06	19.14 ± 1.50	0.76 ± 0.08	5.92 ± 0.47	8.49 ± 0.97	12.91 ± 1.46	11.31
M3	4	mand	mes	17.28 ± 1.19	19.47 ± 1.29	0.89 ± 0.05	5.93 ± 0.26	8.02 ± 0.41	15.00 ± 1.35	9.00
M1	5	max	dis	14.09 ± 1.57	20.75* ± 2.01	0.68 ± 0.06	6.37 ± 0.82	8.99 ± 1.24	10.86 ± 1.98	18.23
M2	1	max	dis	13.61	19.36	0.70	6.51	11.14	10.79	—
M3	9	max	dis	13.31 ± 2.18	16.13 ± 3.00	0.83 ± 0.08	5.22 ± 0.89	7.52 ± 1.31	16.36 ± 3.16	19.32
M1	16	mand	dis	14.12 ± 1.68	18.68 ± 1.46	0.76 ± 0.07	5.77 ± 0.42	8.07 ± 0.62	13.18 ± 1.56	11.84
M2	6 ^b	mand	dis	15.60 ± 2.04	18.89 ± 1.47	0.82 ± 0.07	5.80 ± 0.32	8.53 ± 1.04	14.39 ± 1.27	8.83
M3	5	mand	dis	16.20 ± 2.37	18.98 ± 1.91	0.85 ± 0.08	5.78 ± 0.67	7.79 ± 1.05	14.92 ± 2.09	14.01
<i>Pongo</i>										
M1	9	max	mes	21.76 ± 3.33	22.16 ± 1.37	0.98 ± 0.15	7.32 ± 0.49	11.78 ± 0.75	13.51 ± 2.14	15.84
M2	6	max	mes	27.33** ± 2.54	22.61 ± 1.52	1.21 ± 0.14	7.54 ± 0.43	12.12* ± 0.60	16.18 ± 2.31	14.28
M3	4	max	mes	25.68 ± 0.95	20.51 ± 0.74	1.25 ± 0.09	6.94 ± 0.34	11.89 ± 0.93	18.15 ± 1.99	10.96
M1	8	mand	mes	20.23 ± 2.50	21.93 ± 1.86	0.93 ± 0.13	7.29 ± 0.61	10.87 ± 1.15	12.85 ± 2.29	17.82
M2	8	mand	mes	22.54 ± 2.41	20.89 ± 1.26	1.08 ± 0.11	7.04 ± 0.50	10.78 ± 1.48	15.44 ± 2.19	14.18
M3	6	mand	mes	22.99 ± 3.11	19.97 ± 2.16	1.16 ± 0.17	6.70 ± 0.66	9.97 ± 1.44	17.62 ± 3.78	21.45
M1	8	max	dis	24.13* ± 4.20	22.41* ± 0.81	1.08 ± 0.18	7.50* ± 0.37	11.66 ± 0.99	14.36 ± 2.20	15.32
M2	4	max	dis	21.80 ± 2.54	19.17 ± 2.30	1.14 ± 0.13	6.48 ± 0.77	10.52 ± 0.79	17.91 ± 3.29	18.37
M3	1	max	dis	22.76	20.22	1.13	6.90	10.99	16.30	—
M1	9	mand	dis	20.13 ± 4.23	20.83 ± 1.33	0.96 ± 0.15	6.75 ± 0.57	10.72 ± 0.84	14.24 ± 1.71	12.01
M2	7	mand	dis	21.78 ± 3.15	20.00 ± 1.22	1.09 ± 0.17	6.48 ± 0.44	10.96 ± 0.75	17.02 ± 3.27	19.21
M3	4	mand	dis	23.45 ± 1.13	19.75 ± 1.11	1.19 ± 0.05	6.56 ± 0.36	10.57 ± 0.92	18.18 ± 1.37	7.54

Note: n = the number of teeth, Row = maxillary (max) or mandibular (mand), Sec = mesial (mes) or distal (dis) sections. Means presented with the standard error indicated: c = area of enamel cap; e = length of enamel-dentine junction; AET is calculated as c/e; rt. b = square root of dentine area under the enamel cap; bi-cd = bi-cervical diameter, defined as the distance between buccal and lingual cervices; RET is calculated as $([c/e]/\sqrt{b}) * 100$; CV is calculated as the standard deviation of RET divided by the mean. Values of c are in mm²; e, AET, rt. b, and bi-cd are in mm; and RET is dimensionless.

Significant results of the Mann–Whitney *U*-test for differences between maxillary and mandibular teeth are indicated as: * = $p \leq 0.05$, ** = $p \leq 0.01$.

^a Sample size for LM1 mesial RET is 17.

^b Sample size for LM2 distal RET is 7.

resulted in a lower AET (and RET), while *Pongo* maxillary molars showed more enamel and/or dentine area than mandibular analogues, which led to variable patterning of AET (and RET).

Mesial-distal comparisons of enamel thickness

The average values for the components of RET in mesial and distal sections of both taxa are shown in Table 3. The Wilcoxon's signed-ranks test showed several significant differences between mesial and distal sections within individual molars (Table 4). In general, increased enamel cap area and/or decreased dentine area from mesial to distal sections in both taxa led to increased AET (and RET) values distally. Decreases in dentine area were related to decreased enamel-dentine junction length in distal sections (which also increased AET and RET).

Relative enamel thickness among hominoids

The results of the Kruskal–Wallis tests for RET differences among hominoids are shown in Table 5. Trends in RET values are shown for mesial and distal sections of each molar position in Fig. 4. *Pan* and *Gorilla* did not show significant differences in RET in any comparison. Both *Pan* and *Gorilla* showed significantly thinner enamel than *Pongo* in mesial sections of maxillary M1,

maxillary M3, and mandibular M2, as well as in distal sections of maxillary M1. In the majority of mandibular molar comparisons of both mesial and distal sections, overlapping values of RET did not permit taxonomic distinction.

Discussion

Enamel thickness and position in the molar row

This study provides evidence for a statistically significant trend of increasing enamel thickness from M1 to M3 in hominoids, which supports the previous suggestion by Martin (1983). Shellis et al.'s (1998) report did not find this trend, which we interpret to be due to small sample sizes for each species and variation within tooth types. Increases in AET (and RET) from M1 to M3 in mesial sections were generally the result of significant increases in the area of the enamel cap, while significant increases in AET (and RET) in distal sections were often the result of significant decreases in the length of the enamel-dentine junction (and/or the area of the dentine), and sometimes also significant increases in the area of the enamel cap. *Pan* and *Pongo* showed few differences in these trends. These results are in contrast to the results of Grine (2002, 2005) on mesial sections of human molars, which suggest that a posterior increase in “relative” enamel thickness (c/b) is the result of

Table 4

P-values for Wilcoxon's signed-ranks test of components of AET and RET between mesial and distal sections of *Pan* and *Pongo*

Taxon	n	Tooth	Row	c	e	AET	rt. b	RET
<i>Pan</i>	5	M1	max	0.14	0.89	0.10	0.34	0.04+
	10 ^a	M1	mand	0.01+	0.14	0.04+	0.15	0.39
	5 ^b	M2	mand	0.89	0.14	0.04+	0.04–	0.03+
<i>Pongo</i>	8	M1	max	0.02+	0.89	0.02+	0.21	0.05+
	8	M1	mand	0.48	0.12	0.03+	0.09	0.04+
	7	M2	mand	0.09	0.02–	0.75	0.02–	0.09

Codes for row, c, e, AET, rt. b, and RET are as in Tables 2 and 3.

Significant results are in **bold**; + following the reported p-value indicates that the variable increases from mesial to distal sections, – indicates a decrease from mesial to distal sections. Tests were not performed for tooth types where less than 4 pairs were available.

^a Sample size for M1 RET is 12.

^b Sample size for M2 RET is 6.

Table 5
Results of the Kruskal–Wallis tests of RET among *Pan*, *Pongo*, and *Gorilla* mesial and distal sections

Tooth	Row	Section	H	Pan-Gorilla	Pan-Pongo	Gorilla-Pongo
M1	max	mes	7.90*	=	<	<
M2	max	mes	5.42	=	=	=
M3	max	mes	6.44*	=	<	<
M1	mand	mes	1.52	=	=	=
M2	mand	mes	6.52*	=	<	<
M3	mand	mes	3.42	=	=	=
M1	max	dis	8.08*	=	<	<
M2	max	dis	3.70	=	=	=
M3	max	dis	0.91	=	=	=
M1	mand	dis	5.26	=	=	=
M2	mand	dis	5.43	=	=	=
M3	mand	dis	3.31	=	=	=

H = Kruskal–Wallis test statistic, significance indicated as: * = $p \leq 0.05$. Comparisons between taxa are the results of Conover's (1999) post-hoc test with significance at alpha = 0.05; significant differences are indicated by the direction; non-significant values are shown as equivalent.

a decrease in dentine area rather than an increase in enamel cap area. It appears that the distribution of these tissues within the molar row differs between apes and humans, which is perhaps related to the trend of posterior molar reduction in *Homo* (reviewed in Grine, 2002, 2005).

Several studies have reported that occlusal cross-sectional area generally increases in both *Pan* and *Pongo* from M1 to M2 and decreases from M2 to M3, with a common order of $M2 > M1 > M3$ (Ashton and Zuckerman, 1950; Schuman and Brace, 1954; Pilbeam, 1969; Mahler, 1973; Smith, 1999; Swindler, 2002). Although several of these studies reported that sequences showed a large amount of variation within species, the consensus is that M2 is generally the largest tooth within a molar row, and M3 is often the smallest tooth. This study demonstrates that this is due to a maximal dentine area in second molars of *Pan*, but not maximal enamel cap area. In *Pongo*, M2s show the greatest enamel cap and dentine area only among mesial sections of maxillary molars. In other molar row comparisons, enamel cap and/or dentine areas in second molars are less than in first and/or third molars. This suggests that there are differences in the distribution of enamel and dentine between the two genera. Kono (2004) also reported differences in tissue distribution between these taxa, which were suggested as the basis for the discrepancies between

the 2-D and 3-D assessments of enamel thickness and volume in *Pan* and *Pongo*. Differences in cross-sectional crown shape are emphasized by 2-D analyses (such as in the present study), which may not be evident when the volume of the entire crown is considered (as in Kono, 2004).

Martin (1983) noted that the most common exception to this trend of increasing enamel thickness was in third molars, which occasionally showed thinner enamel than would be expected given a pattern of increase posteriorly. The expanded sample in the current study also showed that third molars are frequently the most variable for RET, as revealed by the coefficient of variation (Table 3). Studies of metric variation in crown dimensions of extant great apes have shown that the coefficient of variation of crown dimensions and/or occlusal cross-sectional area (M-D*B-L) typically increases from M1 to M3 in maxillary and mandibular rows (e.g., Schuman and Brace, 1954; Pilbeam, 1969; Mahler, 1973). It is possible that previous studies of enamel thickness had not detected significant differences in molars due to small sample sizes, high variance in M3, and lack of appropriate statistical tests for trends. Martin (1983) also noted the difficulty of sectioning low-crowned, highly crenulated teeth with precision. Mesial and distal sections from third molars are the most difficult to prepare, as the cusps are often

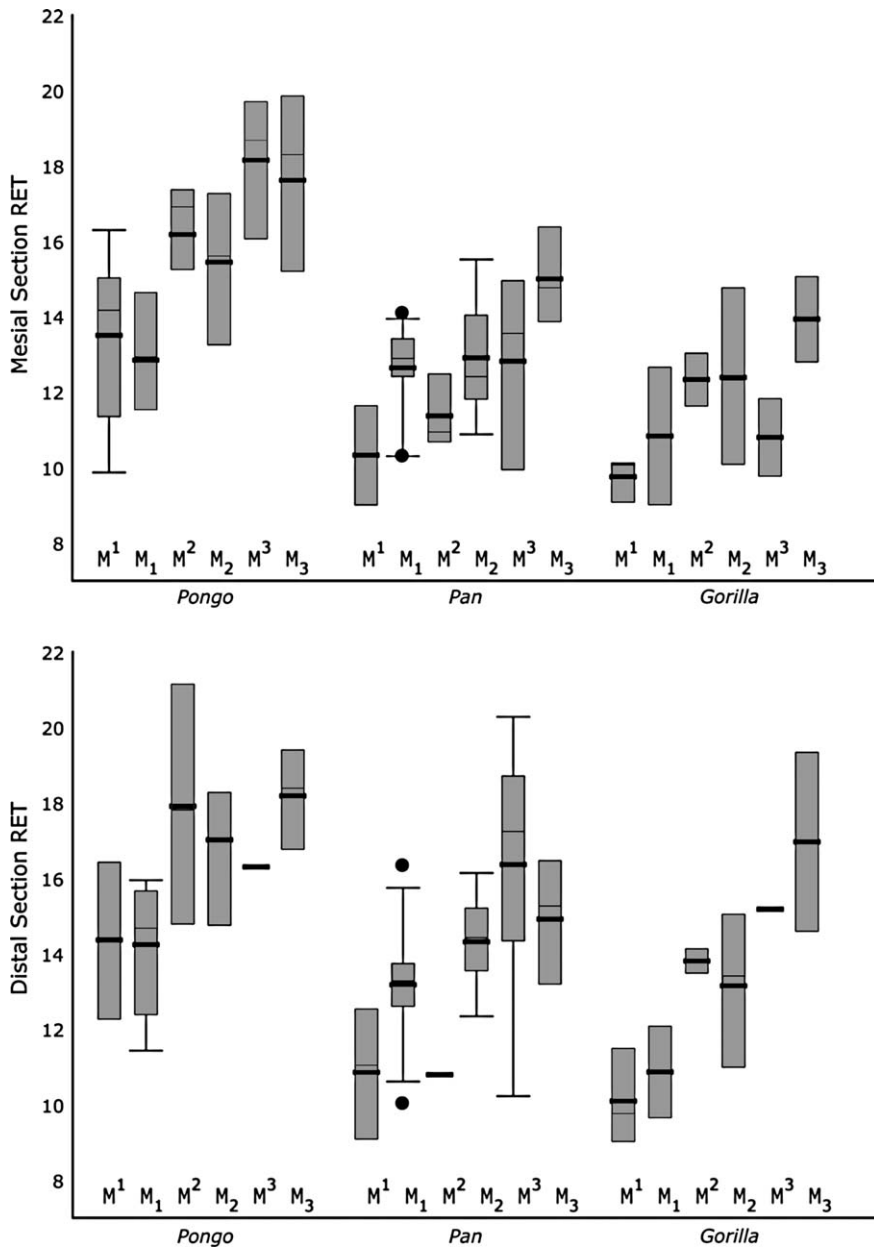


Fig. 4. Relative enamel thickness (RET) in mesial and distal planes of section for each molar type in *Pongo*, *Pan*, and *Gorilla*. Ends of boxes represent 25% and 75% ranges of the data; ends of whiskers represent 10% and 90% ranges of the data; dots represent outliers; the thick line in a box is the mean, the thin line is the median.

poorly defined, particularly in taxa that have crenulated molars such as *Pan* and *Pongo* (Fig. 5), which may affect the variability of these section planes.

Functional and developmental implications

It is not clear how the patterning of enamel and dentine relates to functional demands or to

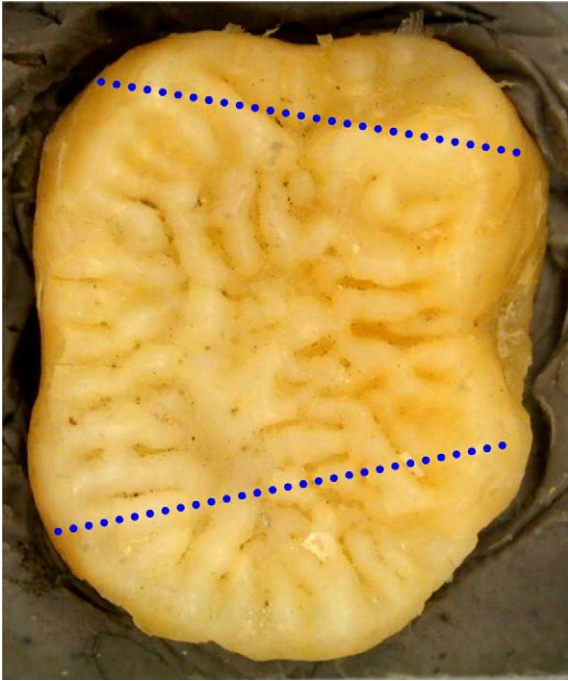


Fig. 5. Occlusal view of a *Pongo* third molar, showing the approximate section planes for the mesial and distal cusps. Note the highly crenulated occlusal surface and the poorly defined cusps.

developmental constraints, such as the room available for teeth to develop (Spencer, 1998, 1999; Kono et al., 2002; Boughner and Dean, 2004; Grine et al., in press). Spencer (1998) demonstrated that, in humans, the highest muscle force magnitudes of the anterior temporalis and the superficial masseter during biting activity occurred while biting on the first molar, and decreased posteriorly. Comparative EMG data on other primates are lacking. The results of Grine (2002, 2005) lend some support to Spencer's EMG data; Grine showed that cross-sectional dentine area in human molars decreases from anterior to posterior molars, while the area of enamel remains relatively constant, such that the size of the tooth (rather than the thickness of enamel) may be correlated with the magnitude of potential bite forces. In light of a lack of data regarding bite force magnitude in extant hominoids, it is unclear whether the enamel thickness trends reported here

are related to force dissipation; if they are related, then the posteriorly increasing pattern of enamel cap area is different from the pattern seen in human molars. (See Kono [2004] and Grine [2005] for detailed reviews of functional models proposed to account for trends in enamel thickness and its distribution.)

Martin (1983) suggested that the trend of increasing enamel thickness in posterior molars may relate to developmental differences among molars. At that time, there were no published data to support this. Grine (2002, 2005) and Smith et al. (2003b) reviewed published data on histological estimates of crown formation time and noted that, within a species, an increasing posterior molar gradient may exist for both crown formation time and enamel thickness. Increasing crown formation time in posterior molars is particularly evident in *Pan* and *Homo* (Reid et al., 1998a,b; summarized in Smith et al., 2003b: table 7). A recent histological investigation of the *Pan* material used in this study showed that specific cusps of first molars formed in a shorter period than the same cusps in second and third molars, and that cusps in second molars generally showed the longest molar crown formation times (Smith, 2004). Data on crown formation time in *Pongo* are limited to a single juvenile, which appears to show a longer formation time in M2 than in M1 (Beynon et al., 1991).

It is unlikely that differences in secretion rates account for differences in enamel cap area within a species (contra Grine, 2005), as no significant differences were found for cuspal enamel secretion rates (within analogous regions) among *Pan* molars (Smith, 2004). Thus, posterior increases in enamel cap area (and AET) are the product of an increased period of crown formation time in this taxon. This appears to be partially related to differences in molar size; cusp-specific crown formation time was positively correlated with cusp-specific enamel-dentine junction length and bi-cervical diameter. *Pan* may show a relationship of increasing crown formation time with molar size, but this remains to be tested within *Homo*, which appears to show increasing crown formation time and decreasing molar size.

Smith et al. (2003a) did not find a significant relationship between RET and crown formation

time among 19 species of fossil and extant hominoids. Thin enamel was found in species that formed their crowns over both short and long periods of time, implying that extant hominoids with thin enamel are not all limited by the amount of time allocated to crown formation. When the relationship between RET and *cuspal* enamel formation time was considered, a significant positive association was found. It is not surprising that hominoids with thick enamel required more time to form cuspal enamel, but it was unexpected that several of these taxa completed the rest of their crowns in a relatively short period of time. A relationship may exist between enamel thickness and crown formation time within the molar row of a species, but this is not apparent in comparisons among hominoid species. Hominoid enamel thickness is not necessarily limited by the amount of time required to form the crown, and the degree of enamel thickness may be related to several developmental factors that differ among species.

As shown above, enamel and dentine components of a tooth crown vary along the molar row, and changes in the area of dentine may occur independently of changes in the area of enamel. The changing relationships of molar crown components reported in this study are not unprecedented, as Grine (2002, 2005) also noted this in humans. Given their separate embryological origins, this is not surprising, as variation may be due to differences in the number of secretory cells, the rate of secretion, or the duration of ameloblast and odontoblast secretion. This also holds for differences within molars, as distal sections may show more enamel cap area and/or less dentine area than mesial sections. Cuspal initiation, formation, and completion times differ among cusps; mesial cusps may begin initiation sooner and complete crown formation sooner than distal cusps (Reid et al., 1998a,b). Developmental differences also exist between buccal and lingual cusps within mesial or distal planes (Reid et al., 1998a,b; Smith et al., 2004). Differences in mesial and distal dentine growth have not been reported to date, but it is likely that developmental differences will be found that relate to known morphological differences (e.g., distal crown “waisting,” hypocone reduction from M1 to M3, distal cusp height reduction).

Enamel thickness and maxillary or mandibular position

Kono et al. (2002) found that, in humans, enamel volume was similar between maxillary and mandibular first molars. Martin (1983) and Grine (2002, 2005) found this when examining enamel cap area in ape and human molars. However, Kono (2004) found that *Pan* maxillary M1s showed greater enamel cap area, dentine area, and enamel-dentine junction length than mandibular M1s. In this study, area of the enamel cap was approximately equal in maxillary and mandibular molars of *Pan*, yet *Pongo* maxillary molars generally showed greater enamel cap area than their mandibular counterparts. It is not clear if these differences are due to differences in functional demands between positions or between taxa. There was also a trend in both taxa for maxillary molars to show greater dentine area, although these differences were not significantly different between most maxillary and mandibular analogues.

Metric studies show that maxillary and mandibular analogues in *Pan* and *Pongo* differ in their M-D and B-L dimensions; maxillary teeth tend to be shorter in M-D dimensions, and broader in B-L dimensions, which may explain larger cross-sectional enamel and dentine areas in maxillary sections. Results on the patterning of AET (and RET) between maxillary and mandibular teeth are different in *Pan* and *Pongo*. *Pan* maxillary molars tend to have thinner enamel than mandibular molars, while there is a non-significant trend in *Pongo* for mandibular molars to have relatively thinner enamel than maxillary molars. This is due to different relationships of the components of AET (and RET) in molar rows of both taxa.

Mesial-distal comparisons of enamel thickness

When mesial and distal sections are compared within the same tooth, distal sections often showed greater enamel cap area, smaller enamel-dentine junction length, and/or smaller dentine area, resulting in greater AET (and RET). These trends are similar in *Pan* and *Pongo*. This parallels the finding of changes in enamel cap area, dentine

area, AET, and RET from M1 to M3 (although the latter trend in RET was driven more by changes in enamel cap area than in dentine area). Differences between mesial and distal sections may reflect an overall decrease in dentine horn height and bi-cervical diameter from the front to the back of the tooth. Average buccolingual crown width tends to decrease from mesial to distal cusps in *Pan* and *Pongo* molars (Ashton and Zuckerman, 1950; Swindler, 2002). Differences in crown width across mesial and distal cusps appear to be the result of decreasing root area distally (which must be relatively greater than the corresponding increase in enamel cap area shown in this study).

Relative enamel thickness among hominoids

This study partially supports the results for RET in hominoids reported by Martin (1983, 1985), who found that enamel thickness was similar within *Pan* and *Gorilla*, but distinguished African from Asian large-bodied hominoids. The current study shows that RET distinguishes *Pan* and *Gorilla* from *Pongo* most often when mesial sections of maxillary molars were compared. In contrast, Shellis et al. (1998) reported that *Pan* and *Pongo* both possessed a similar condition of enamel thickness, which distinguished them from *Gorilla*. The disagreement between our results and those of the latter study may be explained by the comparatively small hominoid sample measured by Shellis et al. (1998). In addition, their technique for assessing enamel thickness—which is based on whether regression residuals fall above or below the best-fit line in a regression of average enamel thickness versus dentine area—is also different than the technique used here (the RET index). The slopes of the best-fit regression lines reported by Shellis et al. (1998) are subject to change depending on sample constitution. For example, a regression of average enamel thickness versus dentine area showed *Pan* to have average enamel thickness (Shellis et al., 1998: 515, figure 2). If the comparative sample was changed to include more ceboids (many of which have thinner enamel per dentine area than *Pan*), then the slope of the regression line is likely to change in such a way as to show *Pan* above the line, and therefore having

thick enamel. The opposite effect would be apparent if more thick-enamelled taxa were included in the regression. Because sample constitution varies from study to study, and total sampled taxa are limited, we advocate the use of RET as the measure of whether enamel is relatively thicker in one taxon than another. The RET index provides a summary of enamel thickness that is independent of the comparative sample, and also provides a context in which any sample can be compared to previously published measurements (e.g., Martin et al., 2003: 364–365, Appendix B; Smith et al., 2003b: 291, table 2).

It is notable in this study that differences were not found between subspecies of *Pongo*. Little is known about differences in enamel thickness between subspecies. Smith et al. (2003b) reported a RET value of 13.6 for a *Pan paniscus* lower third molar that falls within the reported range of third molars for the mixed sample of *P. troglodytes* reported here. However, Dumont (1995) demonstrated that congeneric ceboid and chiropteran species have notably different RET values. A large degree of variation in RET has also been reported in small samples of different species of *Proconsul* and *Lufengpithecus* (Beynon et al., 1998; Schwartz et al., 2003; Smith et al., 2003b), which appears similar to or greater than the variation within *Pongo* reported here.

Implication for scaling of enamel thickness in future studies

The appropriate index of enamel thickness for intra-taxon comparisons is AET. Values of RET within *Pan* and *Pongo* are presented in this work for comparative purposes only. These two indices often yield similar results when compared among molars or planes of section, save for rare instances where enamel cap area remains unchanged, but dentine area changes (e.g., *Pongo* maxillary distal sections from M1 to M3). In addition, because enamel-dentine junction length and dentine area are related (as enamel-dentine junction length is the partial perimeter of dentine area), parallel changes in AET and RET may occur when enamel cap area is held constant and dentine area changes (e.g., between *Pan* mandibular second molar

mesial and distal sections). Regardless, the AET index yields a linear dimension of enamel thickness, and should be used to assess trends among molars and between both molar analogues and planes of section within species when volumetric data are not available.

The results of this study, as well as those of Grine (2002, 2005), suggest that in some instances, dentine area does not remain constant along the molar row, between molar analogues, or within a tooth. Measures of relative enamel thickness that employ tooth-specific dentine area as a surrogate for body size may thus be flawed. It is difficult to discern a priori if dentine area measurements from a specific molar may be a more appropriate scalar. Another measure that has been employed as a scalar in enamel thickness studies, the bi-cervical diameter (measured between buccal and lingual cervices in cross-sections), may be better suited for standardizing size differences among taxa. Schwartz (2000a) and Grine (2002) recently employed bi-cervical diameter as a scalar for body size (although scalars are probably not necessary for intra-specific comparisons). While bi-cervical diameter has not been directly examined in individuals of known body size, Grine (2002) demonstrated a strong positive association between dentine area and bi-cervical diameter, and Shellis et al. (1998) suggested that the former scales isometrically with body size among primates.

We measured bi-cervical diameter in the specimens examined in this study, tested them with the methods described above, and found that both dentine area and bi-cervical diameter show similar patterns along the molar row and between molar analogues (Table 3), indicating that both may have the same effect on the scaling of enamel thickness. This is similar to the results of Grine (2002). However, Kono (2004) reported that dentine volume decreased from first to second molars in *Pan* and *Homo*, but a transverse 2-D plane at the lowest point of cervical enamel did not appear to show such a marked decrease, supporting the use of bi-cervical area over dentine volume as a surrogate for body size. As expected, comparisons of maxillary and mandibular analogues in the present study showed that maxillary molars have greater bi-cervical diameters than mandibular molars.

Thus, within either maxillary or mandibular molars, dentine area or bi-cervical diameter may be an equivalent scalar of average enamel thickness. Future work on individuals of known body mass may shed additional light on this issue.

Summary and conclusions

Analysis of enamel cap area, enamel-dentine junction length, dentine area, average enamel thickness (AET), and relative enamel thickness (RET) in mesial and distal sections of *Pan* and *Pongo* molars showed several significant trends from M1 to M3. In general, enamel cap area increased, enamel-dentine junction length and dentine area decreased, and AET (and RET) increased posteriorly. This study represents the first known demonstration of significant increases in AET (and RET) throughout the molar row in non-human primates. In contrast to the results of Grine (2002, 2005) for humans, changes in enamel thickness from first to third molars in mesial sections of *Pan* and *Pongo* were mainly driven by increases in enamel cap area rather than decreases in dentine area. The functional implications of increased enamel area are unknown. When compared to histological data on crown formation time, it appears that the increased enamel cap area (and AET and RET) is related to an increase in crown formation time, although this has yet to be tested in the *Pongo* sample.

Comparisons of maxillary and mandibular analogues showed differences within and between *Pan* and *Pongo*. In general, maxillary molars showed greater dentine area (and sometimes enamel cap area), which we interpret to be due to relatively greater buccolingual crown width. Comparisons of sections within molars showed that enamel cap area often increased from mesial to distal sections, and dentine area (and sometimes enamel-dentine junction length) decreased. This parallels the finding of significant decreases in dentine area in distal sections of maxillary molars from M1 to M3, also possibly related to crown reduction. Changes in these components often led to increased AET (and sometimes RET) in distal sections. Given the known pattern of reduction in

buccolingual crown width from mesial to distal cusps, it appears that the dentine component has reduced more than the enamel component has increased.

The present study has demonstrated that changes in enamel cap area, enamel-dentine junction length, and dentine area may lead to differences in AET (and RET) from anterior to posterior molars, between maxillary and mandibular analogues, and between mesial and distal sections. This suggests that AET and RET should not be lumped for molar positions (or planes of section), which agrees with the findings of Macho (1994) and Grine (2002) for human molars. The results of comparisons of relative enamel thickness between *Pan*, *Gorilla*, and *Pongo* showed that the African apes are statistically indistinguishable when each molar position is compared. However, *Pan* and *Gorilla* showed significantly thinner enamel than *Pongo* when certain sections were compared. These results differ from those of Shellis et al. (1998), but are in agreement with the 2-D data from Kono (2004). Additional work on larger samples of extant and fossil hominoids is necessary to clarify the functional and phylogenetic aspects of enamel thickness, which may be accomplished with the use of non-destructive high resolution micro-computed tomography (e.g., Kono, 2004).

Finally, this study suggested that scaling factors based on dentine area or bi-cervical diameter may be flawed; neither scalar is constant among molars or between molar analogues or planes of section. Future work on individuals of known body mass may further clarify this issue.

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