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Enamel Thickness of Deciduous and Permanent Molars in Modern *Homo sapiens*

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KEY WORDS enamel thickness; variability; permanent; deciduous; molar

ABSTRACT This study presents data on the enamel thickness of deciduous (dm2) and permanent (M1–M3) molars for a geographically diverse sample of modern humans. Measurements were recorded from sections through the mesial cusps of unworn teeth. Enamel is significantly thinner on deciduous than on permanent molars, and there is a distinct trend for enamel to increase in relative thickness from M1 to M3. The relatively thicker enamel of M2s and especially M3s can be related to the overall reduction in size of more distal molar crowns, which has been attained through a differential loss of the dentine component. Enamel tends to be thicker on the protocone than on the paracone, and thicker on the protoconid than on the metaconid, but its distribution is not wholly concordant with models that predict increased thickness as a means by which to counter heavier attritional loss on these "functional" cusps. Indeed, the thickness of enamel tends to be more variable on cusp tips and occlusal surfaces than over the lateral aspects of cusps. The proportionately thicker enamel over the lateral aspects of the protocone and protoconid more likely serves as a means to prolong functional crown life by preventing cusp fracture, rather than being an adaptation to increase the attritional longevity of wear facets. The present data suggest that the human dentition is not predisposed to develop a helicoidal wear plane through the disposition of molar enamel thickness. Am J Phys Anthropol 126:14–31, 2005. © 2004 Wiley-Liss, Inc.

Tooth enamel thickness has long been considered to hold both functional and phylogenetic significance for the interpretation of hominoid evolution (Jolly, 1970; Simons and Pilbeam, 1972; Molnar and Gantt, 1977; Kay, 1981; Martin, 1985; Gantt, 1986; Beynon and Wood, 1986; Grine and Martin, 1988; Beynon et al., 1991; Macho and Thackeray, 1992; Molnar et al., 1993; Macho and Berner, 1994; Shellis et al., 1998; Schwartz, 2000b). For example, it has featured prominently in recent arguments over the relationships of the earliest (i.e., Late Miocene–Early Pliocene) putative hominins from eastern Africa. *Ardipithecus ramidus* is reported to possess thin molar enamel (White et al., 1994; Haile-Selassie, 2001), in common with extant African apes. On the other hand, *Orrorin tugenensis* is said to have relatively thick molar enamel (Senut et al., 2001), a feature that it shares with later undisputed hominins, including modern humans. Extremely thick molar enamel has been hypothesized as a synapomorphy of the three species of *Paranthropus* (Grine and Martin, 1988; Strait et al., 1997; Strait and Grine, 2001).

Until fairly recently, it was generally assumed that all teeth, and especially all molars of a given species, are endowed with similarly thick enamel caps. Grine and Martin (1988) reported some sparse data for living great apes and humans that indicated a tendency for enamel thickness to increase from M1 to M3, and Aiello et al. (1991) reported values obtained from very small samples (between 1–3 specimens each) for extant apes that suggested a tendency for it to increase distally from d_c to M_1. These indications were subsequently corroborated by Macho and Berner (1993) and Schwartz (2000a) for human permanent molars, and by Gantt et al. (2001) for human deciduous molars. To date, these three studies represent the only direct (i.e., nonradiographic) analyses of variation in human molar enamel thickness that employed statistically adequate samples. Macho and Berner (1993) examined maxillary molars (21 M^1, 12 M^2, and 11 M^3) of an Austrian population, and the data of Schwartz (2000a) were for mandibular molars (9 M_1, 13 M_2, and 7 M_3) obtained from the Dental School at Newcastle, UK. Gantt et al. (2001) measured deciduous molar crowns (15 dm^1, 17 dm^2, 17 dm_1, and 24 dm_2) of European-American and African-American children. As aptly noted by Schwartz (2000b, p. 228), "these measurements of enamel thickness may not be representative of the total range of variation

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present in contemporary or prehistoric human populations."

The tendency for deciduous and permanent molars to display a distalward increase in enamel thickness has been related to functional models of masticatory biomechanics (Macho and Berner, 1993, 1994; Spears and Macho, 1995, 1998; Macho and Spears, 1999; Schwartz, 2000a,b; Gantt et al., 2001). According to these scenarios, the thicker enamel of the more distal molars accords with the higher occlusal forces that some biomechanical models predict them to encounter (Molnar and Ward, 1977; Osborn and Baragar, 1985; Koolstra et al., 1988; Janis and Fortelius, 1988; Osborn, 1996). Thus, Macho and Berner (1993) observed that although the eruption pattern of human molars might imply that M1s should have the thickest enamel because they are in occlusion for the longest time, M2s and especially M3s have thicker enamel caps because they are believed to experience higher bite forces.

By the same token, differences in enamel thickness on the buccal and lingual cusps of human molars have been interpreted in a functional context by a number of workers (Shillingburg and Grace, 1973; Molnar and Gantt, 1977; Grine and Martin, 1988; Macho and Berner, 1993, 1994; Spears and Macho, 1995; Schwartz, 2000a,b; Gantt et al., 2001). It has been argued that enamel should be thicker over the tips and occlusal surfaces of the so-called "functional" cusps (Schwartz, 2000a) than the "guiding" cusps (Spears and Macho, 1995). That is, enamel should be thicker on cusps that are dominated by phase II (crushing/grinding) facets than on those dominated by phase I (shearing/guiding) facets, so as to effectively withstand the heavier abrasion on the former. Discrepancy in the thickness of enamel covering the buccal and lingual cusps also has been related to the development of a helicoidal occlusal wear plane in humans (Macho and Berner, 1994; Spears and Macho, 1995), although this has been questioned by Schwartz (2000a).

The purpose of this paper is to characterize and interpret variation in enamel thickness of the deciduous and permanent molars of a geographically diverse modern human sample. These data will add to the existing database for recent *Homo sapiens* that derives from physically sectioned crowns (Macho and Berner, 1993; Schwartz, 2000a; Gantt et al., 2001), and will be used to address hypotheses that posit a functional basis to the distribution of enamel along the molar row and across the different cusp surfaces.

MATERIALS AND METHODS

Sample

The present sample comprises 80 unworn deciduous and permanent modern human molars, with each maxillary and mandibular class from dm2 to M3 represented by 10 teeth (i.e., 10 dm^2, 10 dm_2, 10 M^1, 10 M_1, etc.). Each tooth was extracted from a cranium or mandible to ensure that its anatomical position was known with certainty. Only a single tooth from any one jaw was used, and each unworn crown was fully developed. All specimens were devoid of obvious pathology. Sex was known for only a small number of specimens.

The sample comprises individuals of European heritage (people from Western and Eastern Europe as well as Americans of European ancestry), Native North Americans, people from the Indian Subcontinent, and sub-Saharan Africans (San and South African Bantu-speaking populations). The entire sample is divided roughly evenly among these four geographic regions, although geographic representation is not equal for any given tooth.

On the basis of radiological analyses, Harris et al. (1999, 2001) reported significant differences in the thickness of deciduous molar enamel between individuals of African and European ancestry, but while these differences were clearly evident for dm1, they were "far more subtle" for dm2. However, because flat-plane radiographs are unlikely to accurately reflect the true thickness values determined by physical sections (Grine et al., 2001), the results reported by Harris et al. (1999, 2001) for dm1s should be viewed with circumspection.

Statistically significant levels of sexual dimorphism affect the overall crown dimensions of deciduous and permanent molars (e.g., Moorrees, 1957; Jacobson, 1982; Grine, 1986), but it is not evident that this is manifest in the thickness of the enamel cap. Although Gantt et al. (2001) reported a provisional test which suggested that females have thicker deciduous molar enamel, their results are questionable because several positively correlated variables were combined for all four molars in order to increase the effective sample size. Although data derived from flat-plane x-rays should be viewed with caution, it is perhaps noteworthy that several radiographic studies failed to identify significant sexual dimorphism in enamel thickness (Stroud et al., 1994; Harris and Hicks, 1998; Harris et al., 1999, 2001). Furthermore, a significant sexual difference in permanent molar enamel thickness was not evident in at least one study that employed physically sectioned crowns (Macho and Berner, 1993).

In light of the absence of substantive data pertaining to significant differences between the sexes or among modern human populations in enamel thickness, the molars examined here were treated as comprising a single sample. This is reasonable, as one reason for generating data on human tooth enamel thickness is to provide for interspecific comparisons, including those with fossils of unknown sex.

Specimen preparation and examination

The most accurate method by which enamel thickness can be measured is through the use of physical sections of the crown. Because this method is inherently destructive, noninvasive radiological methods, including the use of lateral flat-plane (bite wing) radiographs and computed tomography (CT), have been used extensively to document enamel thickness in living and fossil samples. However, measurements derived from flat-plane radiographs are unlikely to accurately reflect the true values as defined by physical sections (Grine et al., 2001). Grossly inaccurate measurements result with the use of standard CT methods (Grine, 1991), and accurate linear values of *thickly* enameled teeth can be obtained only by employing specific CT instrumentation and protocols (Spoor et al., 1993; Schwartz et al., 1998).

A recently developed method by which the thickness of the enamel cap can be analyzed in three dimensions holds considerable potential for enhancing our understanding of the distribution of enamel across the entire crown (Kono-Takeuchi et al., 1998; Kono et al., 2002). This technique, however, results in the complete destruction of the enamel cap, and because it is so complicated and time-consuming, it is impractical for the generation of statistically meaningful samples. Because of the myriad problems associated with radiographic determinations, and because of the practical limitations imposed by laser scanning methodology, the crowns examined here were physically sectioned through the mesial cusps to measure enamel thickness.

The tips of the two mesial cusps (protocone and paracone, or metaconid and protoconid) were examined under a binocular light microscope at up to 40× magnification to ensure that they were unworn. The cusp tips were then marked with a spot of permanent ink, and the crown was embedded in epoxy resin to prevent enamel from spalling during sectioning. The crown was cut from the roots, and then sectioned with a 0.15-mm diamond wafering blade (Buehler Isomet). The edge of the blade was positioned immediately distal to the ink marks to ensure that the mesial crown section included both dentine horns. The resultant block face was ground with 400 grade paper and polished with a sequence of diamond pastes to 0.25 μm (Buehler Microcloth) to obtain a topography-free buccolingual (BL) section that included the tips of both dentine horns. The polished surface was lightly etched with 0.5% H_3PO_4 for 15 sec to remove any smeared enamel, ultrasonicated in distilled H_2O, mounted on a stub, and coated with silver for examination by scanning electron microscopy (SEM; Amray 1810). Micrographs were recorded at variable magnifications between 7.5× and 11.0×, depending on the size of the specimen. Working distance was held under 25 mm to ensure accurate magnification. Micrographs were recorded using Polaroid Type 55 P/N film; positive enlargements were used for measurement.

Measurements

All measurements were recorded from photographic prints, using Bioquant System IV software interfaced with a SummaSketch II tablet. All values were recorded to the nearest 0.1 mm or 0.1 mm^2. Three area and 10 linear measurements were taken for each molar section (Fig. 1). Except where indicated, their designations and definitions accord with those of Martin (1983) so as to avoid confusion by the introduction of additional notations:

a: Total area of the tooth crown section delineated by the outer enamel perimeter and a straight line between the buccal and lingual cervical margins.

b: Area of dentine (and pulp) enclosed by the dentine-enamel junction (DEJ) and a straight line between the buccal and lingual cervical margins.

c: Area of the sectioned enamel cap.

d: Linear distance between the buccal and lingual cervical margins (bicervical diameter)

e: Perimeter length of the DEJ between the buccal and lingual cervical margins.

h: Maximum linear thickness of occlusal enamel on the buccal cusp (i.e., paracone or protoconid), measured perpendicular to the DEJ. This corresponds to measurement "5" of Macho and Thackeray (1992), "6" of Macho and Berner (1993), and "BOB" of Schwartz (2000a,b). It also corresponds to measurement "EA" of Gantt (1977; see also Molnar and Gantt, 1977), and "OT" of Beynon and Wood (1986) in that it was recorded at least 0.5 mm from the dentine horn tip.

i: Maximum linear thickness of occlusal enamel on the lingual cusp (i.e., protocone or metaconid), measured perpendicular to the DEJ. This corresponds to measurement "EB" of Gantt (1977; see also Molnar and Gantt, 1977), and "OT" of Beynon and Wood (1986) in that it was recorded at least 0.5 mm from the tip of the dentine horn. It also corresponds to measurement "4" of Macho and Thackeray (1992; see also Macho and Berner, 1993), and to "LOB" of Schwartz (2000a,b).

k: Linear enamel thickness on the buccal side of the buccal cusp measured perpendicular to the DEJ. This is recorded from the point where a line that is parallel to one between the tips of the dentine horns, and tangent to the lowest point on the DEJ between the cusps, intersects the DEJ at the side of the crown. It corresponds to measurement "JJ" of Gantt (1977), "6" of Macho and Thackeray (1992), and "8" of Macho and Berner (1993). Contrary to Schwartz (2000b), this measurement is not necessarily equivalent to "LT" of Beynon and Wood (1986), as the latter records maximum lateral enamel thickness at a point ca. 1 mm from the tip of the dentine horn.

l: Linear enamel thickness on the lingual side of the lingual cusp, measured perpendicular to the DEJ. This is recorded from a point determined as for measurement k. It corresponds to measurement "KK" of Gantt (1977), "3" of Macho and Thackeray (1992), and "1" of Macho and Berner (1993), but it is not necessarily equivalent to measurement "LT" of Beynon and Wood (1986), which records maximum lateral enamel thickness 1 mm from the tip of the dentine horn.

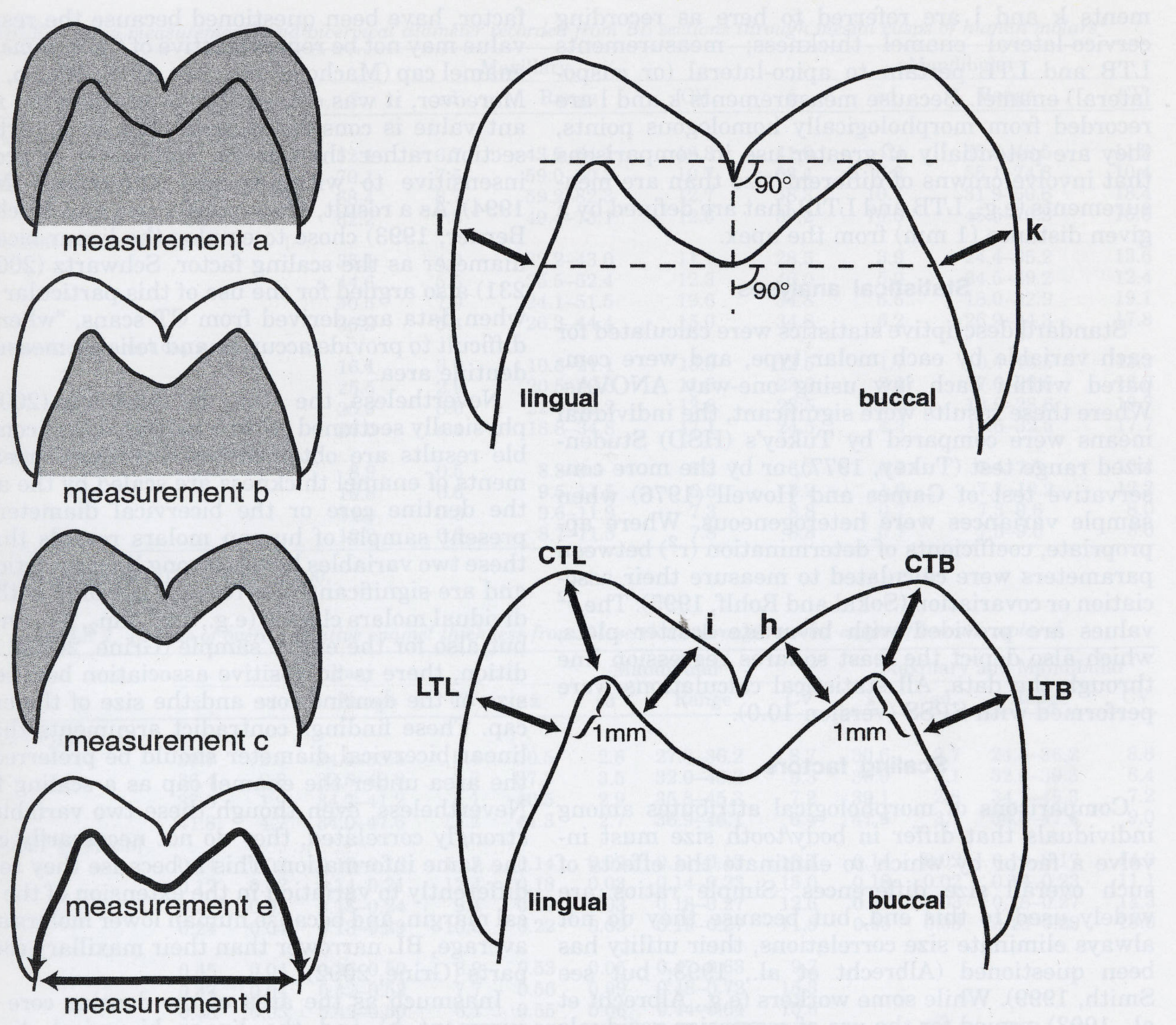

Fig. 1. Schematic cross-sections of molar crown, indicating measurements recorded in this study.

CTB: Linear enamel thickness on the apex of the buccal cusp. As defined by Beynon and Wood (1986), it is the distance between the tip of the dentine horn and the tip of the cusp. Because they did not differentiate buccal from lingual cusps, the designation used here is that of Grine and Martin (1988). It corresponds to measurement "A" of Gantt (1977; see also Molnar and Gantt, 1977), "2" of Macho and Thackeray (1992), "7" of Macho and Berner (1993), and "BCT" of Schwartz (2000a,b).

CTL: Linear enamel thickness on the apex of the lingual cusp. As defined by Beynon and Wood (1986), it is the distance between the apex of the dentine horn and the tip of the cusp. Because they did not differentiate between the lingual and buccal cusps, the designation used here follows that of Grine and Martin (1988). It corresponds to measurement "B" of Gantt (1977; see also Molnar and Gantt,1977), "1" of Macho and Thackeray (1992), "3" of Macho and Berner (1993), and "LCT" of Schwartz (2000a,b).

LTB: Maximum linear enamel thickness on the buccal side of the buccal cusp, measured perpendicular to the DEJ at a point approximately 1 mm cervical to the dentine horn. This measurement follows the definition of Beynon and Wood (1986), but because they did not differentiate the buccal from the lingual cusp, the designation used here is that of Grine and Martin (1988).

LTL: Maximum linear enamel thickness on the lingual side of the lingual cusp, measured perpendicular to the DEJ at a point approximately 1 mm cervical to the dentine horn. This measurement follows the definition of Beynon and Wood (1986), but because they did not differentiate between the lingual and buccal cusps, the designation used here follows that of Grine and Martin (1988).

Measurements k and l will likely differ from measurements LTB and LTL, depending on the size of the crown. In most cases, measurements k and l will be closer to the cervical margin, while LTB and LTL will be closer to the cusp tip. Therefore, measurements k and l are referred to here as recording cervico-lateral enamel thickness; measurements LTB and LTL pertain to apico-lateral (or cuspo-lateral) enamel. Because measurements k and l are recorded from morphologically homologous points, they are potentially of greater use in comparisons that involve crowns of different size than are measurements (e.g., LTB and LTL) that are defined by a given distance (1 mm) from the apex.

Statistical analyses

Standard descriptive statistics were calculated for each variable by each molar type, and were compared within each jaw using one-way ANOVAs. Where these results were significant, the individual means were compared by Tukey's (HSD) Studentized range test (Tukey, 1977), or by the more conservative test of Games and Howell (1976) when sample variances were heterogeneous. Where appropriate, coefficients of determination (r^2) between parameters were calculated to measure their association or covariation (Sokal and Rohlf, 1995). The r^2 values are provided with bivariate scatter plots, which also depict the least squares regression line through the data. All statistical calculations were performed with SPSS (version 10.0).

Scaling factors

Comparisons of morphological attributes among individuals that differ in body/tooth size must involve a factor by which to eliminate the effects of such overall size differences. Simple ratios are widely used to this end, but because they do not always eliminate size correlations, their utility has been questioned (Albrecht et al., 1993; but see Smith, 1999). While some workers (e.g., Albrecht et al., 1993) argued for the use of regression residuals that "control for size," residuals derived from regression analysis may result in erroneous conclusions, especially when the data under consideration are related allometrically (Jungers et al., 1995). As aptly noted by Schwartz (2000b), a surrogate that is derived from regression analysis is of questionable validity if it is not related isometrically to body size.

Various scaling measures have been used in the study of primate enamel thickness. While some workers used overall crown dimensions (e.g., crown base or cusp area; Beynon and Wood, 1986; Macho, 1994), these incorporate a component of enamel thickness, and are therefore not independent variables. Martin (1985), who examined BL sections through the cusp tips of molar teeth, used the area of the crown enclosed by the DEJ as the denominator. He also incorporated the length of the DEJ in the ratio (according to the formula $[(c/e)/\sqrt{b}]$) to derive a value for "relative average" enamel thickness. This scaling factor was used by Grine and Martin (1988), Dumont (1995), and Shellis et al. (1998).

The inclusion of DEJ length in the ratio, and the use of the area under the enamel cap as the scaling factor, have been questioned because the resultant value may not be representative of the *volume* of the enamel cap (Macho and Berner, 1993; Macho, 1994). Moreover, it was opined that even when the resultant value is considered in relation to a particular section rather than crown volume, it is probably insensitive to within-species differences (Macho, 1994). As a result, Macho (1994; see also Macho and Berner, 1993) chose to employ the linear bicervical diameter as the scaling factor. Schwartz (2000b, p. 231) also argued for the use of this particular factor when data are derived from CT scans, "where it is difficult to provide accurate and reliable measures of dentine area."

Nevertheless, the study by Schwartz (2000a) of physically sectioned crowns indicated that comparable results are obtained whether linear measurements of enamel thickness are scaled by the area of the dentine core or the bicervical diameter. The present sample of human molars reveals that the these two variables have a strong linear relationship and are significantly correlated, not only within individual molars classes (e.g., dm^2, dm_2, M^1, and M_1), but also for the entire sample (Grine, 2002). In addition, there is no positive association between the size of the dentine core and the size of the enamel cap. These findings contradict arguments that the linear bicervical diameter should be preferred over the area under the enamel cap as a scaling factor. Nevertheless, even though these two variables are strongly correlated, they do not necessarily convey the same information. This is because they respond differently to variation in the extension of the cervical margin, and because human lower molars are, on average, BL narrower than their maxillary counterparts (Grine, 2002).

Inasmuch as the area of the dentine core (measurement b) and the linear bicervical diameter (measurement d) have been employed in other studies, and because they do not always convey the same information, both were employed as scaling factors in the present study. In those instances in which the ratios derived from these two variables convey the same information, discussion will be limited to indices calculated from the dentine core area.

RESULTS

The three area measurements of the crown section are recorded in Table 1. Total section area (measurement a), which may be considered a surrogate for overall crown size, differs significantly among both maxillary and mandibular molars according to ranked and unranked ANOVAs. Tukey's (HSD) test revealed that this is due to the fact that the deciduous molars are significantly smaller than the permanent molars in both jaws. The differences among permanent molars are not statistically significant for either jaw. The same results pertain to the area of the enamel cap (measurement c) and the linear bicervical diameter (measurement d), where the permanent molars in either jaw are indistinguishable

TABLE 1. Area measurements and bicervical diameter recorded from BL sections through mesial cusps of human molars[1]

	Maxillary				Mandibular			
	x̄	sd	Range	CV	x̄	sd	Range	CV
Measurement a (total section area)								
dm2	52.1	6.7	43.9–64.1	12.8	41.0	4.9	35.6–48.5	11.9
M1	70.1	7.5	59.0–80.3	10.7	63.4	6.6	55.1–74.3	10.4
M2	68.4	8.7	59.2–82.3	12.7	58.3	10.7	31.9–69.6	18.4
M3	62.2	7.8	49.4–73.1	12.6	59.2	10.0	45.5–76.3	16.8
Measurement b (dentine area)								
dm2	36.1	4.0	32.2–43.0	11.1	28.5	3.9	24.4–35.2	13.6
M1	44.6	5.5	35.5–52.4	12.3	40.0	5.0	34.5–49.2	12.4
M2	40.5	7.9	24.1–51.5	19.6	34.8	6.6	18.0–42.9	19.1
M3	36.2	5.4	26.3–44.4	15.0	34.8	6.2	26.9–44.3	17.8
Measurement c (enamel cap area)								
dm2	16.1	3.0	10.8–21.1	18.9	12.5	1.7	10.4–16.5	13.3
M1	25.5	2.9	20.5–29.3	11.5	23.5	3.2	17.6–28.5	13.8
M2	25.9	3.6	22.6–33.2	13.8	23.5	4.6	13.9–28.6	19.7
M3	26.0	4.4	18.8–34.8	17.1	24.5	4.3	18.6–32.5	17.7
Measurement d (bicervical diameter)								
dm2	8.9	0.5	8.3–9.9	5.3	6.7	0.7	5.4–7.5	10.4
M1	10.8	0.6	9.5–11.5	5.6	8.2	1.0	7.1–10.2	12.2
M2	11.0	0.8	9.6–11.9	7.3	8.8	0.7	7.3–9.6	8.0
M3	10.2	0.8	8.7–11.5	7.8	8.8	0.7	7.5–9.0	8.0

[1] n = 10 for all samples; CV = (sd/x̄) · 100.

TABLE 2. Indices of overall relative enamel thickness from BL sections through mesial cusps of human molars[1]

	Maxillary				Mandibular				Maxillary and Mandibular			
	x̄	sd	Range	CV	x̄	sd	Range	CV	x̄	sd	Range	CV
Index c/a (×100)												
dm2	30.7	2.9	24.5–33.5	9.4	30.5	2.6	27.3–36.2	8.7	30.6	2.7	24.5–36.2	8.8
M1	36.4	2.8	32.5–40.9	7.7	37.3	3.5	32.0–43.3	9.3	36.9	3.1	32.0–39.3	8.4
M2	37.8	1.9	34.7–41.2	5.1	40.5	2.9	35.8–45.3	7.2	39.1	2.8	34.7–45.3	7.2
M3	41.8	4.7	34.0–47.6	11.2	41.3	2.7	36.9–46.1	6.4	41.6	3.7	34.0–47.6	9.0
Index RAET [(c/e)/√b]												
dm2	0.14	0.02	0.10–0.16	14.7	0.14	0.02	0.11–0.17	13.1	0.14	0.02	0.10–0.17	14.3
M1	0.17	0.02	0.14–0.21	12.4	0.18	0.03	0.14–0.23	15.0	0.18	0.02	0.14–0.23	11.1
M2	0.20	0.02	0.18–0.24	9.4	0.22	0.03	0.18–0.27	12.6	0.21	0.03	0.18–0.27	14.3
M3	0.24	0.04	0.18–0.29	16.6	0.22	0.03	0.19–0.27	11.8	0.23	0.03	0.18–0.29	13.0
Index √c/d												
dm2	0.45	0.04	0.36–0.50	8.9	0.53	0.05	0.47–0.63	9.7				
M1	0.47	0.04	0.42–0.53	7.7	0.56	0.09	0.48–0.72	15.3				
M2	0.46	0.03	0.42–0.50	6.1	0.55	0.06	0.44–0.64	10.6				
M3	0.50	0.06	0.42–0.63	11.6	0.57	0.07	0.49–0.67	11.5				

[1] n = 10 for separate maxillary and mandibular samples; n = 20 for combined maxillary and mandibular sample.

from one another, but significantly larger than the deciduous molars. Maxillary deciduous and permanent teeth do not differ significantly from one another with regard to the area of the dentine core (measurement b).

Relative size of the enamel cap

Because the shape of the enamel cap may vary at broadly homologous points, the area of the sectioned enamel cap is useful in the comparative assessment of its overall thickness (Martin, 1985). Index c/a reveals that a larger crown is not necessarily accompanied by a correspondingly thicker enamel cap, and that the more distal molars (M2 and M3) tend to possess relatively thicker enamel caps for their size (Table 2). ANOVAs reveal significant differences among both upper and lower molars. In both jaws, the means of dm2s are significantly smaller than those of the permanent molars, and M1 is significantly smaller than M3. In the maxilla, M^2 is also significantly smaller than M^3. As such, the enamel cap contributes relatively less to deciduous than to permanent molar crowns, and relatively more to the crowns of the more distal permanent molars.

The index by Martin (1985) of relative average enamel thickness (RAET) displays significant variance in both the maxilla (F = 25.7; $P < 0.0001$) and *mandible* (F = 26.1; $P < 0.0001$). There is a clear tendency for the enamel cap to become relatively thicker as one moves distally along either molar row (Fig. 2). In the maxilla, dm^2 and M^1 do not differ significantly from one another, but dm^2 is significantly thinner than either M^2 or M^3, and M^3 is significantly thicker than either M^1 or M^2. In the mandible, dm_2 is significantly thinner than any of the permanent molars, and M_1 is significantly thinner than either M_2 or M_3.

Maxillary and mandibular counterparts exhibit virtually the same values with regard to both the c/a and RAET indices (Table 2). In view of the negligible

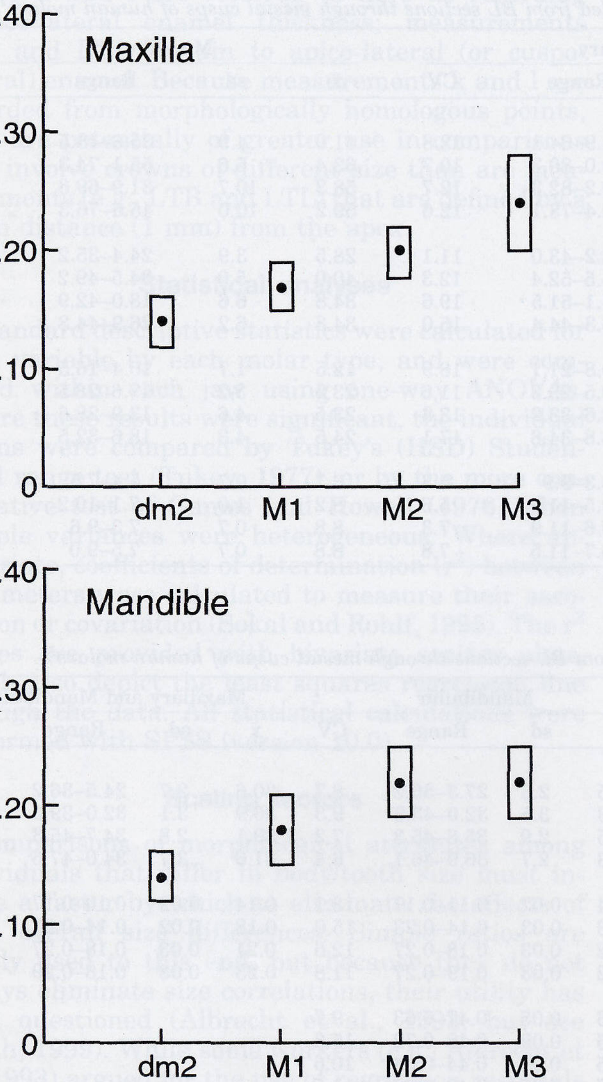

Fig. 2. Relative average enamel thickness of human maxillary and mandibular molars as expressed by RAET index [(c/e)/ $\sqrt{b} \times 100$]. N = 10 for all samples. Solid circles, sample means; vertical rectangles enclose mean ± 1 sd.

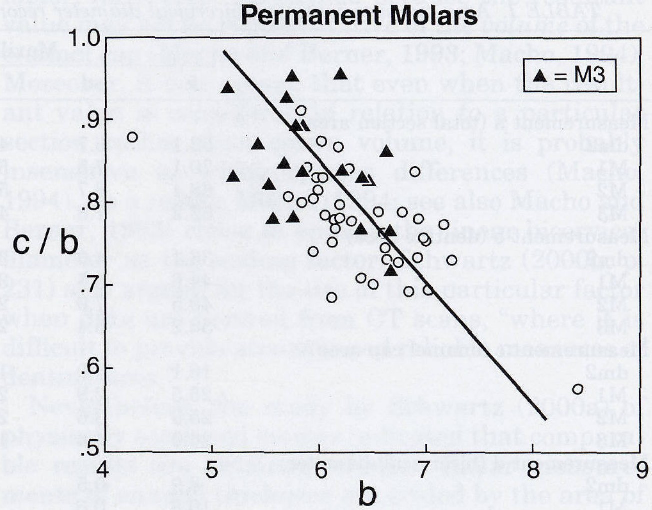

Fig. 3. Regression of relative enamel thickness (index c/b) against area of dentine core (measurement b) for maxillary and mandibular permanent molars. Note that M3s tend to combine *relatively thick enamel with small dentine cores.* LS regression coefficient = 0.423, and r = −0.527 (df = 59), resulting in RMA slope of −0.803 (sd = 0.09). Pearson product moment correlation is significant at $P < 0.01$. Third molars are represented by solid triangles; all other permanent molars are indicated by open circles. RMA slope is shown.

differences between upper and lower molars, their index values can be legitimately combined to summarize a distinct trend for relative enamel thickness to increase distally in modern humans (Fig. 2).

This trend, however, involves the deciduous and permanent molars in different ways. Among the permanent molars, the dentine core tends to decrease in size, whereas the enamel cap tends to increase in relative thickness from M1 to M3. This trend is statistically significant, as demonstrated by a least-squares regression analysis of relative enamel thickness against dentine core area (Fig. 3). In this instance, an index (c/b) is compared against the x axis (measurement b) in lieu of a $\log_e - \log_e$ slope. Allometry is indicated if a significant correlation exists between the index and variable x, because the index (= slope) changes in concert with the x variable (Mosimann and James, 1979). In this instance, the least-squares (LS) regression coefficient (slope) = 0.423, and r = −0.527 (df = 59). These values result in a reduced major axis (RMA) slope (−0.803, sd = 0.09) that is significantly below 1.0, indicating negative allometry in the traditional (i.e., $\log_e - \log_e$) sense. Moreover, the Pearson product moment correlation for these data (−0.527) is significant at $P < 0.01$, which indicates negative allometry in the sense of Mosimann and James (1979). Thus, the more distal permanent molars, and especially the M3s, gain relatively thicker enamel through a reduction in size of the dentine component of the crown. This negative allometric trend does not extend to the deciduous molars, as revealed by a least-squares regression analysis of the same two variables (c/b vs. b) for the total sample of deciduous and

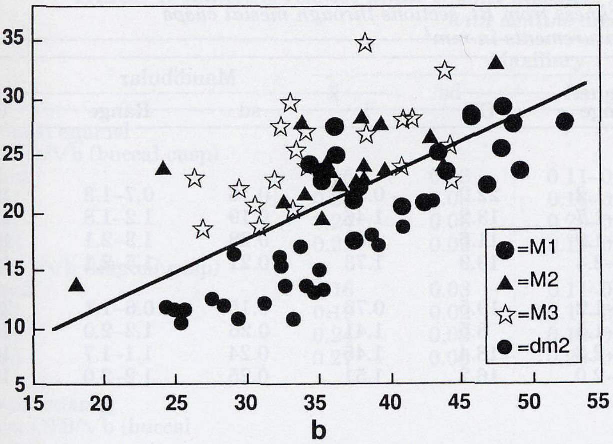

Fig. 4. Relationship between enamel area (measurement c) and dentine area (measurement b) for a sample of 80 human deciduous and permanent molars ($F = 17.88$; $p < 0.05$; $r = 0.65$; slope = 0.387). Corresponding values are given for upper and lower dm2s ($F = 32.2$; $p < 0.0001$; $r = 0.80$; slope = 0.443), M1s ($F = 5.63$; $p < 0.05$; $r = 0.49$; slope = 0.276), M2s ($F = 25.3$, $p < 0.0001$; $r = 0.76$; slope = 0.417) and M3s ($F = 7.39$; $p < 0.05$; $r = 0.54$; slope = 0.410). Note that dm2s and almost all M1s lie below the regression line, whereas M2s and M3s tend to lie above it.

permanent molars. In this instance, the regression coefficient = 0.895 and r = 0.632 (df = 79); these values result in an RMA slope (1.416, sd = 0.124) that is positively allometric. Thus, in contrast to the permanent molars, dm2s have a small dentine core coupled with relatively thin enamel.

Regression lines that compare the raw areas of the enamel cap and dentine core have a slope that is significantly lower than 1.0 for all molar types together, and for individual molar groups (Fig. 4). Moreover, these two variables are only weakly correlated. Thus, within any molar class, crowns that have a large dentine core do not necessarily have a large enamel cap. Finally, the dm2s and approximately half of the M1s fall below the regression line, whereas nearly all of the M2s and M3s fall above it (Fig. 4). This reveals that the more distal molars tend to possess a larger enamel cap for the size of their dentine core.

By contrast, the $\sqrt{c}/d$ index, which relates enamel cap area to linear bicervical diameter, results in a different pattern from that established by the RAET index (Table 2). In the first instance, mandibular molars do not differ significantly from one another, and the difference among maxillary molars just borders on significance according to one-tailed ANOVAs ($F = 2.69$; $P = 0.06$), where only dm^2 and M^3 differ significantly for this index. In the second instance, mandibular molar values are significantly larger than the corresponding maxillary values for all three molar classes (dm2: $F = 17.0$, $P < 0.001$; M1: $F = 8.9$, $P < 0.01$; M2: $F = 18.7$, $P < 0.001$; M3: $F = 5.89$, $P < 0.03$). This rather dramatic departure from the comparability of maxillary and mandibular values established by the RAET index is related to the fact that lower molars are generally narrower BL than their maxillary counterparts (Jacobson, 1982; Grine, 1986; Kieser, 1990). For example, in the present sample, upper molars exceed their mandibular counterparts by an average of some 12% with regard to the area of the dentine core, but by approximately 20% in bicervical diameter (Table 1).

The CVs indicate that M^3 displays consistently, albeit only slightly greater variation than the other maxillary molars in relative thickness, and that in no instance is M_3 the most variable mandibular molar (Table 1). In view of the well-known overall *morphometric variability that characterizes third* molars (Nelson, 1938; Thomsen, 1955; Moorrees, 1957; Jacobson, 1982; Kieser, 1990), they might have been expected to be the most variable in enamel thickness. However, the variation that is manifest in the morphology of the enamel cap does not appear to affect its thickness to the same extent.

Linear enamel thickness

Absolute linear thickness values are recorded in Table 3. The ratios derived from these values, scaled against the dentine core area ($\sqrt{b}$) and the linear bicervical diameter (measurement d), are recorded in Tables 4 and 5, respectively. Inasmuch as the two index values correspond very closely in most instances, discussion will be restricted to the former ($x/\sqrt{b}$), except where the data differ.

Intracuspal distribution of enamel

In almost all instances, enamel tends to be thicker on the lateral side of the cusp than at the tip or over the occlusal surface. This holds for the buccal as well as the lingual cusps of the maxillary and mandibular dm2s, M1s, and M2s. Only in the third molars does cusp tip (cuspal) and/or occlusal enamel exceed lateral enamel in thickness, and even in these crowns, cuspo-lateral enamel is thickest on the M_3 protoconid, and the lateral and cuspal values are but exiguously different on the protocone of M^3 and the metaconid of M_3. As expected, enamel tends to be thicker cuspo-laterally than cervico-laterally on both cusps of all molars.

Comparisons between cusps

There are significant differences between the buccal and lingual cusps of all molars. In general, enamel tends to be thicker on the protocone than on the paracone, and thicker on the protoconid than on the metaconid (Table 6; Fig. 5). Exceptions to this relate to the occlusal basin of maxillary permanent molars, where the paracone and protocone values are nearly identical, and the tips of M_1 cusps, where enamel is thicker on the metaconid than the protoconid. The buccal and lingual cusps differ significantly from one another in all four maxillary molars with regard to thickness over the cusp tip, and in all three mandibular permanent molars with regard to cervico-lateral thickness. In addition, cuspo-lateral enamel is significantly thicker on the protocone than

TABLE 3. Linear measurements of enamel thickness from BL sections through mesial cusps of human molars. Measurements in mm[1]

	Maxillary				Mandibular			
	x̄	sd	Range	CV	x̄	sd	Range	CV
Occlusal enamel								
Measurement h (buccal cusp)								
dm2	0.86	0.19	0.6–1.2	22.0	0.84	0.16	0.7–1.3	19.5
M1	1.41	0.19	1.0–1.7	13.2	1.46	0.19	1.2–1.8	12.7
M2	1.56	0.18	1.4–1.9	11.6	1.69	0.28	1.3–2.1	16.3
M3	1.73	0.34	1.2–2.4	19.9	1.73	0.21	1.5–2.1	12.0
Measurement i (lingual cusp)								
dm2	0.98	0.19	0.7–1.2	19.5	0.73	0.15	0.6–1.1	20.7
M1	1.33	0.11	1.1–1.5	8.5	1.41	0.26	1.2–2.0	18.6
M2	1.54	0.28	1.3–2.2	18.4	1.45	0.24	1.1–1.7	16.6
M3	1.62	0.26	1.3–2.0	16.2	1.51	0.25	1.2–2.0	16.5
Cuspal enamel								
Measurement CTB (buccal cusp)								
dm2	0.61	0.27	0.3–1.2	44.7	0.71	0.15	0.5–1.0	20.6
M1	1.15	0.35	0.6–1.8	30.6	1.04	0.28	0.5–1.4	26.5
M2	1.44	0.32	1.0–2.1	22.4	1.65	0.48	0.8–2.4	29.0
M3	1.75	0.20	1.4–2.1	11.5	1.73	0.23	1.4–2.1	13.5
Measurement CTL (lingual cusp)								
dm2	1.02	0.39	0.5–1.5	37.6	0.70	0.16	0.4–1.0	22.8
M1	1.15	0.35	0.6–1.8	30.6	1.30	0.21	1.1–1.7	16.2
M2	1.91	0.37	1.4–2.7	19.2	1.46	0.29	1.0–2.0	20.1
M3	2.01	0.28	1.6–2.4	13.8	1.47	0.15	1.3–1.8	10.3
Cuspo-lateral enamel								
Measurement LTB (buccal cusp)								
dm2	1.11	0.16	0.8–1.3	14.8	1.13	0.08	1.0–1.3	6.6
M1	1.53	0.18	1.3–1.9	11.9	1.69	0.15	1.3–1.8	9.1
M2	1.63	0.14	1.5–2.0	8.7	1.88	0.19	1.6–2.2	10.0
M3	1.59	0.16	1.3–1.9	10.1	1.94	0.22	1.6–2.3	11.5
Measurement LTL (lingual cusp)								
dm2	1.36	0.26	0.8–1.7	19.2	0.99	0.07	0.9–1.1	7.1
M1	1.76	0.24	1.0–2.2	13.4	1.54	0.16	1.3–1.7	10.4
M2	2.01	0.27	1.8–2.5	13.5	1.52	0.10	1.4–1.6	6.4
M3	2.00	0.23	1.7–2.6	11.5	1.48	0.17	1.2–1.8	11.6
Cervico-lateral enamel								
Measurement k (buccal cusp)								
dm2	0.93	0.16	0.7–1.1	17.6	0.98	0.15	0.8–1.2	15.8
M1	1.32	0.30	0.8–2.0	23.0	1.69	0.19	1.3–1.9	11.5
M2	1.52	0.23	1.1–1.9	15.0	1.69	0.29	1.0–2.0	16.9
M3	1.41	0.21	1.1–1.7	14.8	1.54	0.45	1.0–2.2	28.9
Measurement l (lingual cusp)								
dm2	1.32	0.22	0.9–1.7	24.1	0.87	0.10	0.8–1.0	11.8
M1	1.60	0.36	1.0–2.2	22.7	1.32	0.21	1.0–1.6	16.1
M2	1.39	0.33	0.9–1.8	24.0	1.19	0.18	1.0–1.5	15.2
M3	1.67	0.38	0.8–2.0	22.5	1.14	0.18	0.8–1.4	15.8

[1] n = 10 for all samples.

on the paracone in M^2 and M^3, and significantly thicker on the protoconid than on the metaconid in M_2 and M_3.

The discrepancy in enamel thickness between cusps also may be considered in relation to gradients along the molar row. With reference to cuspal thickness, there is an arguable trend of decreasing discrepancy between the buccal and lingual cusps from dm^2 to M^3 (Fig. 5). The disparity between buccal and lingual cusps in cuspo-lateral thickness increases distally among the permanent molars in both jaws, although the discrepancy in M2s and/or M3s is no greater than in dm2s.

Comparisons between molars

There is a nearly universal increase in relative linear enamel thickness among maxillary molars from dm2 to M3 (Fig. 6). The only notable exception pertains to the cervico-lateral enamel of the protocone, which tends to be thinnest in M^2. The trend for a distalward increase in relative enamel thickness is less notable among mandibular molars, except that it is universally thicker on M_1s than on dm_2s. Occlusal and cuspal enamel tends to increase in thickness from M_1 to M_3, but this trend is less evident with regard to the lateral aspects of the cusps. Specific intermolar comparisons for each of the four cusps are described below (Table 4).

With reference to the relative thickness of enamel on the protocone, occlusal enamel is significantly thinner on dm^2 than on M^2 or M^3, and significantly thinner on M^1 than on M^3. Cuspal and cuspo-lateral enamel is significantly thinner on dm^2 and M^1 than

TABLE 4. Indices of relative linear enamel thickness from BL sections through mesial cusps of human molars, with dentine area as scaling factor[1]

	Maxillary				Mandibular			
	x̄	sd	Range	CV	x̄	sd	Range	CV
Occlusal enamel								
Index $h/\sqrt{b}$ (buccal cusp)								
dm2	0.15	0.03	0.11–0.21	21.6	0.16	0.03	0.14–0.24	19.3
M1	0.20	0.03	0.16–0.25	12.7	0.23	0.03	0.18–0.27	13.7
M2	0.24	0.03	0.20–0.28	12.0	0.29	0.04	0.23–0.35	13.4
M3	0.29	0.06	0.19–0.41	21.7	0.29	0.03	0.25–0.33	9.8
Index $i/\sqrt{b}$ (lingual cusp)								
dm2	0.16	0.03	0.11–0.21	19.5	0.14	0.03	0.11–0.21	19.9
M1	0.19	0.02	0.17–0.23	11.2	0.23	0.05	0.17–0.34	20.7
M2	0.24	0.03	0.19–0.30	13.9	0.25	0.04	0.19–0.30	17.1
M3	0.27	0.05	0.20–0.34	18.2	0.26	0.05	0.18–0.33	18.8
Cuspal enamel								
Index $CTB/\sqrt{b}$ (buccal cusp)								
dm2	0.10	0.04	0.05–0.18	41.9	0.13	0.04	0.03–0.18	35.6
M1	0.17	0.04	0.10–0.23	26.1	0.17	0.04	0.08–0.21	25.6
M2	0.22	0.05	0.17–0.31	20.8	0.28	0.07	0.13–0.40	25.3
M3	0.29	0.04	0.25–0.34	12.9	0.30	0.05	0.25–0.37	15.2
Index $CTL/\sqrt{b}$ (lingual cusp)								
dm2	0.17	0.06	0.08–0.25	35.1	0.13	0.03	0.07–0.18	25.7
M1	0.21	0.04	0.15–0.26	10.3	0.21	0.03	0.16–0.25	15.2
M2	0.29	0.05	0.21–0.40	18.1	0.25	0.04	0.17–0.33	16.9
M3	0.34	0.05	0.26–0.39	15.6	0.25	0.02	0.22–0.28	8.9
Cuspo-lateral enamel								
Index $LTB/\sqrt{b}$ (buccal cusp)								
dm2	0.19	0.02	0.14–0.22	10.5	0.21	0.02	0.19–0.25	9.5
M1	0.22	0.03	0.18–0.27	13.6	0.27	0.03	0.22–0.30	11.1
M2	0.25	0.02	0.22–0.29	8.0	0.33	0.05	0.27–0.44	15.2
M3	0.27	0.03	0.23–0.31	11.1	0.33	0.03	0.30–0.40	9.0
Index $LTL/\sqrt{b}$ (lingual cusp)								
dm2	0.23	0.04	0.15–0.30	17.4	0.19	0.02	0.17–0.22	10.5
M1	0.26	0.05	0.20–0.36	19.2	0.25	0.03	0.20–0.30	12.0
M2	0.31	0.04	0.26–0.38	12.9	0.26	0.04	0.23–0.37	15.4
M3	0.33	0.04	0.28–0.42	12.1	0.25	0.02	0.23–0.29	8.0
Cervico-lateral enamel								
Index $k/\sqrt{b}$ (buccal cusp)								
dm2	0.16	0.02	0.12–0.20	15.3	0.19	0.03	0.14–0.23	17.3
M1	0.19	0.05	0.10–0.29	25.2	0.27	0.04	0.21–0.32	13.4
M2	0.23	0.03	0.17–0.27	14.1	0.29	0.03	0.24–0.32	8.9
M3	0.24	0.03	0.19–0.28	13.4	0.26	0.07	0.18–0.38	25.3
Index $l/\sqrt{b}$ (lingual cusp)								
dm2	0.22	0.03	0.15–0.26	14.4	0.16	0.03	0.13–0.21	17.3
M1	0.23	0.06	0.12–0.32	25.0	0.21	0.04	0.15–0.26	18.0
M2	0.21	0.05	0.14–0.29	22.3	0.21	0.03	0.16–0.25	14.2
M3	0.28	0.06	0.14–0.35	19.8	0.19	0.03	0.14–0.24	14.5

[1] n = 10 for all samples.

on M^2 or M^3, and cervico-lateral enamel is significantly thicker on M^3 than on dm^2 or M^2.

With reference to the paracone, occlusal enamel is significantly thinner on dm^2 than on the three permanent molars, and significantly thicker on M^3 than on M^1 or M^2. Cuspal enamel differs significantly among all four maxillary molars, and both cuspo- and cervico-lateral enamel are significantly thicker on M^2 and M^3 than on either dm^2 or M^1.

With reference to the protoconid, occlusal enamel is significantly thinner on dm_2 than on the permanent molars, and significantly thinner on M_1 than on either M_2 or M_3. Cuspal enamel is significantly thinner on both dm_2 and M_1 than on M_2 or M_3. Both cuspo- and cervico-lateral enamel is significantly thinner on dm_2 than on any of the permanent molars, and cuspo-lateral enamel is significantly thinner on M_1 than on M_2 or M_3.

With reference to the metaconid, occlusal enamel is significantly thinner on dm_2 than in any of the permanent molars, but the latter do not differ from one another in this measurement. However, the corresponding index scaled against the linear bicervical diameter (Table 5) results in values where dm_2 and M_1 are equivalent to one another, and significantly thinner than either M_2 or M_3. Cuspal enamel is

TABLE 5. Indices of relative linear enamel thickness from BL sections through mesial cusps of human molars, with linear bicervical diameter as scaling factor[1]

	Maxillary				Mandibular			
	$\bar{x}$	sd	Range	CV	$\bar{x}$	sd	Range	CV
Occlusal enamel								
Index h/d (buccal cusp)								
dm2	0.10	0.02	0.07–0.14	22.7	0.13	0.02	0.11–0.17	15.9
M1	0.13	0.02	0.10–0.16	15.3	0.17	0.03	0.13–0.22	17.9
M2	0.14	0.02	0.12–0.16	11.3	0.19	0.03	0.15–0.24	13.1
M3	0.17	0.04	0.11–0.27	25.7	0.20	0.03	0.17–0.25	14.1
Index i/d (lingual cusp)								
dm2	0.11	0.02	0.07–0.15	20.0	0.11	0.02	0.09–0.15	17.3
M1	0.12	0.01	0.10–0.14	10.6	0.11	0.05	0.12–0.28	44.0
M2	0.14	0.02	0.11–0.19	16.6	0.17	0.03	0.13–0.22	18.2
M3	0.16	0.03	0.12–0.22	19.5	0.18	0.04	0.12–0.24	20.6
Cuspal enamel								
Index CTB/d (buccal cusp)								
dm2	0.07	0.03	0.03–0.12	43.5	0.11	0.03	0.07–0.14	24.8
M1	0.11	0.04	0.06–0.17	33.6	0.12	0.03	0.53–0.16	28.3
M2	0.13	0.02	0.10–0.18	18.6	0.18	0.05	0.10–0.23	25.0
M3	0.17	0.03	0.14–0.22	14.5	0.20	0.02	0.15–0.24	11.6
Index CTL/d (lingual cusp)								
dm2	0.11	0.04	0.05–0.16	36.0	0.11	0.03	0.06–0.15	26.2
M1	0.14	0.03	0.09–0.19	25.2	0.15	0.03	0.11–0.20	18.8
M2	0.16	0.04	0.09–0.23	24.4	0.17	0.03	0.13–0.21	18.2
M3	0.20	0.04	0.16–0.26	17.7	0.17	0.02	0.15–0.21	10.7
Cuspo-lateral enamel								
Index LTB/d (buccal cusp)								
dm2	0.12	0.02	0.09–0.15	15.3	0.17	0.02	0.15–0.20	9.9
M1	0.14	0.02	0.11–0.18	14.7	0.20	0.03	0.15–0.24	16.4
M2	0.15	0.02	0.13–0.17	10.1	0.21	0.02	0.19–0.24	8.9
M3	0.16	0.02	0.13–0.19	12.2	0.22	0.30	0.19–0.28	13.5
Index LTL/d (lingual cusp)								
dm2	0.15	0.03	0.10–0.20	19.6	0.15	0.02	0.13–0.20	15.2
M1	0.17	0.03	0.12–0.23	18.2	0.18	0.04	0.14–0.26	21.2
M2	0.18	0.02	0.16–0.22	12.1	0.18	0.02	0.15–0.22	10.2
M3	0.20	0.02	0.17–0.24	11.2	0.17	0.23	0.14–0.21	13.5
Cervico-lateral enamel								
Index k/d (buccal cusp)								
dm2	0.10	0.02	0.07–0.14	19.2	0.15	0.03	0.11–0.21	22.1
M1	0.12	0.03	0.08–0.19	23.6	0.20	0.04	0.15–0.26	21.0
M2	0.14	0.02	0.10–0.16	13.8	0.19	0.03	0.12–0.24	17.7
M3	0.14	0.02	0.11–0.19	16.6	0.18	0.06	0.11–0.27	31.6
Index l/d (lingual cusp)								
dm2	0.15	0.02	0.10–0.17	15.5	0.13	0.03	0.10–0.19	20.5
M1	0.15	0.04	0.10–0.22	24.8	0.15	0.04	0.11–0.22	24.8
M2	0.13	0.03	0.08–0.18	26.8	0.14	0.03	0.10–0.20	20.4
M3	0.17	0.04	0.08–0.23	24.8	0.13	0.02	0.09–0.17	18.5

[1] n = 10 for all samples.

TABLE 6. Mean absolute percentage difference (MAPD) between buccal and lingual cusp means in linear enamel thickness

	Occlusal	Cuspal	Cuspo-lateral	Cervico-lateral
Maxillary				
dm2	11.7	40.3	20.4	29.9
M1	−6.0	21.0	13.1	17.2
M2	1.5	24.7	18.9	−8.3
M3	−6.4	13.1	20.4	15.5
Mandibular				
dm2	−12.7	−1.4	−16.6	−11.0
M1	−3.2	19.7	−9.0	−21.9
M2	−14.0	−11.5	−19.3	−29.5
M3	−12.6	−15.0	−23.6	−26.3

MAPD = (lingual − buccal)/buccal × 100. Positive values, lingual > buccal. Negative values, buccal > lingual.

significantly thinner on dm_2 than on any of the permanent molars, and it is significantly thinner on M_1 than on M_2 or M_3. Here, too, the corresponding index scaled against the linear bicervical diameter (Table 5) results in equivalent means for dm_2 and M_1, and these are significantly smaller than those for M_2 and M_3. Lateral enamel is significantly thinner on dm_2 than in any of the permanent molars, but the latter do not differ from one another in these measurements.

Variability in enamel thickness

Among maxillary molars, dm^2 has the highest CVs for 7 of 8 measurements, and the second highest for the eighth (Table 4). In the mandibular arcade, dm_2 has the highest CVs for 3 of 4 measurements that relate to occlusal and apical thickness. The only

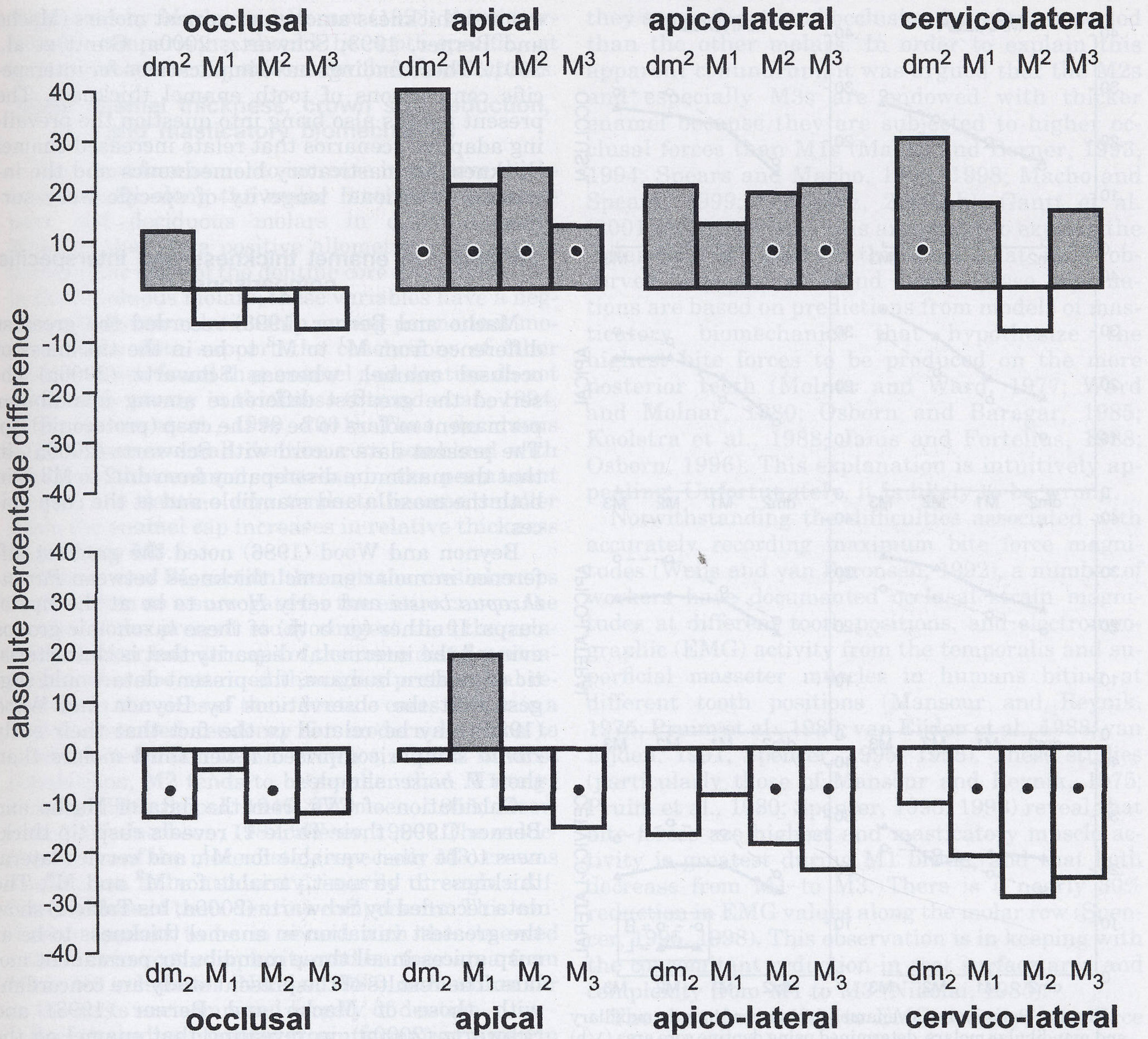

Fig. 5. Mean absolute percentage difference (MAPD) between buccal and lingual cusp values for linear enamel thickness. MAPD is calculated as: (lingual mean − buccal mean)/buccal mean × 100. Positive values (shaded boxes), lingual > buccal. Negative values (open boxes), buccal > lingual. Solid circles denote instances in which there is a statistically significant difference between corresponding index means. Values are recorded in Table 6.

instances in which the third molars exhibit the greatest variability pertain to lateral thickness measurements among the mandibular molars.

Enamel on the cusp tip tends to be more variable in thickness than elsewhere. This is especially notable for both cusps of dm^2 and M^1, and for the protoconids of dm_2, M_1, and M_2. On the other hand, cuspolateral enamel tends to be the least variable on either cusp among the maxillary and mandibular molars.

Variability tends to be greater on the paracone than on the protocone with regard to occlusal and cuspal enamel, but lateral enamel variation is greater on the protocone, which may be related to the variable presence and expression of the Carabelli trait. There is no clear pattern of distinction between the buccal and lingual cusps of the mandibular molars in terms of variability in linear enamel thickness.

The trends in variability for the relative (scaled) linear dimensions generally accord with those noted above for the absolute measurements, although there are a few notable differences (cf. Tables 3 and 4). In particular, with regard to the maxillary molars, the CVs recorded for dm^2 are highest in 4 of 8 measurements, while the CVs for M^1 are the highest in the remaining 4. In keeping with the pattern established by the absolute di-

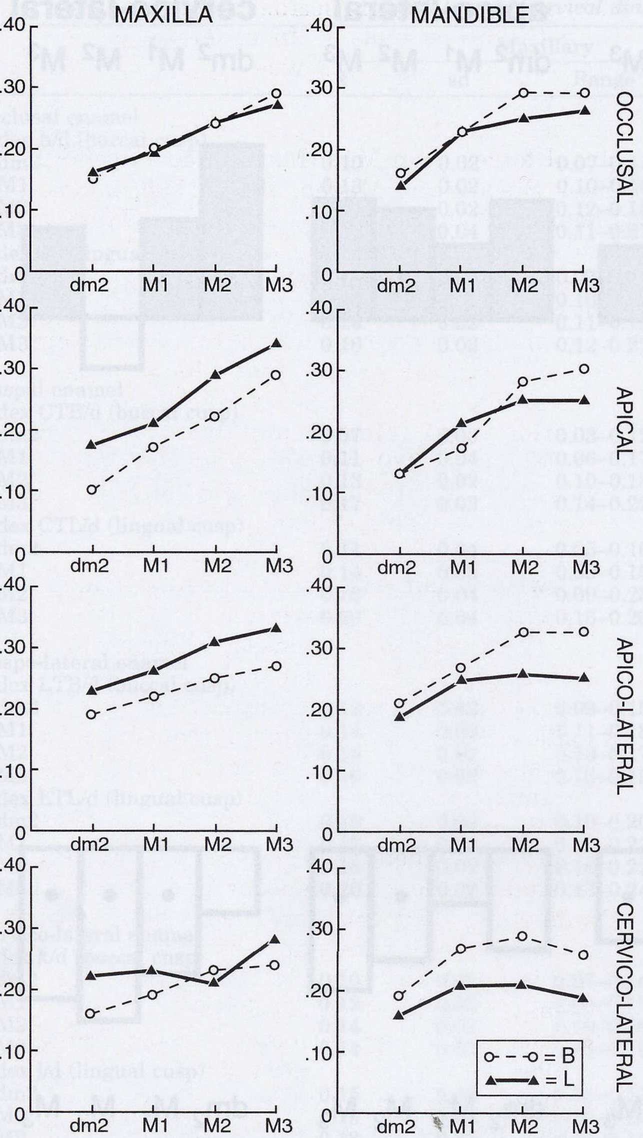

Fig. 6. Relative linear enamel thickness of human maxillary and mandibular molars, determined using dentine core area ($\sqrt{b}$) as scaling factor. Circles, sample means for buccal cusps; triangles, sample means for lingual cusps. Note that protocone and protoconid means tend to exceed paracone and metaconid means, respectively, and that there is a general trend for relative thickness to increase from dm2 to M3.

mensions, relative linear thickness tends to be more variable both cuspally and occlusally on the paracone than on the protocone, while cuspo-lateral enamel tends to be more variable on the protocone. In contrast to the absolute values, the protoconid tends to be less variable than the metaconid with regard to all relative dimensions except cuspal thickness.

DISCUSSION

The results reported here accord with those of other studies that have documented significant differences between deciduous and permanent teeth, and a distalward gradient of increased relative enamel thickness among permanent molars (Macho and Berner, 1993; Schwartz, 2000a; Gantt et al., 2001). These findings have implications for interspecific comparisons of tooth enamel thickness. The present results also bring into question the prevailing adaptive scenarios that relate increased enamel thickness to masticatory biomechanics and the increased attritional longevity of specific wear surfaces.

Variability in enamel thickness and interspecific comparisons

Macho and Berner (1993) recorded the greatest difference from M^1 to M^3 to be in the thickness of occlusal enamel, whereas Schwartz (2000a) observed the greatest difference among mandibular permanent molars to be at the cusp (protoconid) tip. The present data accord with Schwartz (2000a), in that the maximum discrepancy from dm2 to M3 is in both the maxilla and mandible and at the cusp apices.

Beynon and Wood (1986) noted the greatest difference in molar enamel thickness between *Paranthropus boisei* and early *Homo* to be at the tips of cusps. If either (or both) of these taxonomic groups evinced the intermolar disparity that is characteristic of modern humans, the present data would suggest that the observations by Beynon and Wood (1986) may be related to the fact that their early *Homo* sample comprised fewer third molars than their *P. boisei* sample.

Calculation of CVs from the data of Macho and Berner (1993, their Table 1) reveals cusp tip thickness to be most variable for M^1, and cervico-lateral thickness to be most variable for M^2 and M^3. The data recorded by Schwartz (2000a, his Table 1) show the greatest variation in enamel thickness to be at cusp apices in all three mandibular permanent molars. The results of the present study are concordant with those of Macho and Berner (1993) and Schwartz (2000a), in revealing that enamel on the cusp tips of human deciduous and permanent molars is particularly variable in thickness. If this observation extends to other species, it could have implications for the finding by Beynon and Wood (1986) about the differences in cuspal enamel thickness between *P. boisei* and early *Homo*. In light of the potential variability of this measurement, the distinction that they reported may be an artifact of the small samples available to them.

The present study also accords with others (Macho and Berner, 1993; Schwartz, 2000a) that documented a distinct tendency for the relative thickness of the enamel cap (overall and at specific locations) to increase from M1 to M3 in both jaws, but particularly in the maxilla. That deciduous molars have significantly thinner enamel than the permanent molars accords with the findings of Gantt et al. (2001).

The differences in relative enamel thickness from dm2 to M3 documented here further strengthen the suggestion by Macho and Berner (1993) that inter-specific comparisons should be tooth-specific, at least where such comparisons involve *Homo sapiens*.

Molar enamel thickness, crown size reduction, and masticatory biomechanics

The trend for enamel to increase in relative thickness distally along the molar involves the permanent and deciduous molars in different ways. Whereas there is a positive allometric relationship between the sizes of the dentine core and enamel cap in the deciduous molars, these variables have a negative allometric relationship among permanent molars. These data support the conclusions of other studies which found that enamel and dentine do not necessarily covary in thickness (Stroud et al., 1994, 1998; Harris et al., 1999, 2001). Thus, deciduous molars have a small dentine core combined with relatively thin enamel, whereas in the permanent molars, the dentine core tends to become smaller while the enamel cap increases in relative thickness from M1 to M3.

Insofar as a BL section through the mesial cusps can be taken as a surrogate for the entire crown, the results of the present study suggest that the relatively thicker enamel caps of the more distal permanent molars are attained through a preferential reduction in the sizes of their dentine cores. There is a well-documented tendency for modern humans to exhibit a reduction in M3 crown size, and in most populations, M2 tends to be smaller than M1 (e.g., Nelson, 1938; Seipel, 1946; Thomsen, 1955; Moorrees, 1957; Jacobson, 1982; Kieser, 1990). The reduction in size of the more distal (especially M3) crowns would seem to be attained primarily through a differential loss of their dentine components. This conclusion appears to be in accord with the observed reduction in root complexity and surface area from M1 to M3 in humans (Nikolai, 1985), at least insofar as the roots are composed largely of dentine.

Recent studies of molar crown formation times in humans and chimpanzees indicate that this increases distally from M1 to M3 in both species (Reid et al., 1998a,b). It might be tempting to speculate that crown formation time should correlate with enamel thickness, but this is not a necessary relationship, because prolonged crown formation may be coupled with a reduced secretory rate of ameloblasts. Indeed, Reid et al. (1998a,b) showed that the thinly enameled M3s of chimpanzees take longer to form (ca. 3.5–4.0 years) than thickly enameled modern human homologues (ca. 3.1–3.4 years). Thus, amelogenesis and odontogenesis may be uncoupled to the extent that in chimpanzees, prolonged M3 formation time is associated with a reduced rate of ameloblast secretion, whereas in humans, prolonged M3 formation time is associated with a reduced rate of odontoblast secretion.

Macho and Berner (1993) observed that the eruption pattern of human molars might imply that M1s should have the thickest enamel because they are in functional occlusion for a longer period than the other molars. In order to explain this apparent conundrum, it was argued that the M2s and especially M3s are endowed with thicker enamel because they are subjected to higher occlusal forces than M1s (Macho and Berner, 1993, 1994; Spears and Macho, 1995, 1998; Macho and Spears, 1999; Schwartz, 2000a,b). Gantt et al. (2001) even extended this argument to explain the differences in enamel thickness that they observed between dm1s and dm2s. These explanations are based on predictions from models of masticatory biomechanics that hypothesize the highest bite forces to be produced on the more posterior teeth (Molnar and Ward, 1977; Ward and Molnar, 1980; Osborn and Baragar, 1985; Koolstra et al., 1988; Janis and Fortelius, 1988; Osborn, 1996). This explanation is intuitively appealing. Unfortunately, it is likely to be wrong.

Notwithstanding the difficulties associated with accurately recording maximum bite force magnitudes (Weijs and van Spronsen, 1992), a number of workers have documented occlusal strain magnitudes at different tooth positions, and electromyographic (EMG) activity from the temporalis and superficial masseter muscles in humans biting at different tooth positions (Mansour and Reynik, 1975; Pruim et al., 1980; van Eijden et al., 1988; van Eijden, 1991; Spencer, 1995, 1998). These studies (particularly those of Mansour and Reynik, 1975; Pruim et al., 1980; Spencer, 1995, 1998) reveal that bite forces are highest and masticatory muscle activity is greatest during M1 biting, and that both decrease from M1 to M3. There is a nearly 30% reduction in EMG values along the molar row (Spencer, 1995, 1998). This observation is in keeping with the concomitant reduction in root surface area and complexity from M1 to M3 (Nikolai, 1985).

The data pertaining to EMG activity, bite force magnitude, and molar root configuration indicate a central role for M1 as a point for the production of high-magnitude bite forces in humans. This is in contradiction to the predictions from basic biomechanical models that the highest bite forces will be witnessed by the third molars.

The relatively thicker enamel of human distal molars is explicable as a result of odontogenic processes related to tooth size reduction, where overall crown size reduction has resulted from the preferential loss of the dentine component of the crown. As such, it is not necessary to invoke functional/adaptive scenarios derived from questionable models of masticatory biomechanics to explain the relatively thicker enamel of human M2s and M3s. In order to test this hypothesis, it will be necessary to obtain data on enamel thickness at different molar positions in primate taxa (e.g., *Papio hamadryas*) that do not exhibit distal molar crown size reduction.

Functional significance of enamel thickness differences between cusps

The data recorded here corroborate earlier observations on human molars that enamel tends to be thicker on the protocone than on the paracone, and thicker on the protoconid than on the metaconid (Molnar and Gantt, 1977; Grine and Martin, 1988; Macho and Berner, 1993; Schwartz, 2000a; Gantt et al., 2001). This same general discrepancy was also documented for a small sample of sectioned *Australopithecus* and *Paranthropus* molars (Grine and Martin, 1988), and by CT for a larger sample of South African australopith upper molars (Macho and Thackeray, 1992). By contrast, the CT study by Conroy (1991) of South African australopith lower molars recorded that enamel thickness on the protoconid exceeded that on the metaconid in only 43% (9 of 21) of specimens. Schwartz (2000b) observed a discrepancy between buccal and lingual cusp thickness in a sample of orangutan upper molars (n = 8), but failed to find it in the chimpanzee (n = 6) and gorilla (n = 9) upper molars he examined.

Differences in enamel thickness on the buccal and lingual cusps of human molars have been interpreted in a functional context by a number of workers (e.g., Shillingburg and Grace, 1973; Molnar and Gantt, 1977; Grine and Martin, 1988; Macho and Spears, 1999; Schwartz, 2000a,b; Gantt et al., 2001), and have been related to the development of a helicoidal occlusal wear plane (Macho and Berner, 1994; Spears and Macho, 1995). In particular, it was argued that enamel should be thicker over the tips and occlusal surfaces of the so-called "functional" (Schwartz, 2000a) or "supporting" (Macho and Spears, 1999) cusps than over the "guiding" cusps (Spears and Macho, 1995; Macho and Spears, 1999). The tips and occlusal surfaces of the protocone and protoconid comprise phase II (crushing/grinding) surfaces, whereas the paracone and metaconid are dominated by phase I (shearing) surfaces (Kay, 1977). It was posited that enamel should be expected to be thicker in relation to phase II surfaces in order to provide additional material by which to better withstand the heavier loss through abrasion on these facets (Macho and Berner, 1993, 1994; Spears and Macho, 1995; Macho and Spears, 1999). Thus, occlusal and apical enamel should be notably thicker on the protocone than on the paracone, and thicker on the protoconid than on the metaconid.

With regard to occlusal enamel, this expectation is borne out by dm^2 and all mandibular molars, but the difference between the buccal and lingual cusps is statistically significant only for dm_2 and M_2 (Fig. 5). Macho and Berner (1993) also documented occlusal enamel to be thicker on the paracone than on the protocone in the M^2s and M^3s comprising their sample, and while their data suggest that it is also thicker on the protocone of M^1, the discrepancy is very slight.

With regard to enamel over the tip of the cusp, the expectation is met by all four maxillary molars, but is satisfied only by M_2 and M_3 among the mandibular molars. In this instance, the difference between buccal and lingual cusps is statistically significant for all upper molars, and for M_3 among mandibular molars. The data of Schwartz (2000a) indicate apical enamel to be thicker on the protoconid of M_1, which contradicts the present results. Because our M_1 samples are the same size, this disparity in our data is likely due to the variability in enamel thickness at this location. Indeed, the comparatively high degree of variability that characterizes enamel thickness at the cusp tip would seem to be contrary to prevailing functional design expectations for the apices of either "functional" or "supporting" cusps. Moreover, Kono et al. (2002) also recorded that enamel is "distinctly thin" at and near the tips of the paracone and protoconid in all five maxillary and five mandibular molars examined by them.

It is evident that models which predict an increase in enamel thickness to counter heavier attritional loss on phase II occlusal surfaces and on the tips of the either "functional" cusps (i.e., protocone and protoconid) are not uniformly supported by the data on human molars. Thus, while cuspal enamel in maxillary molars, and occlusal enamel in mandibular molars is distributed in general accord with these expectations, the distribution of occlusal enamel in maxillary molars and cuspal enamel in mandibular molars is certainly contradictory. The relative high degree of variability displayed by the thickness of cuspal enamel is also inconsistent with these prevailing models.

On the other hand, the present data reveal that even in those instances where expectations are met by the distribution of occlusal enamel, the discrepancies in its thickness are lower than those for either cuspo- or cervico-lateral enamel (Figs. 5, 6). Also, the expected discrepancies in cuspal thickness exceed those in lateral enamel only with reference to dm^2, M^1, and M^2. Indeed, it is only in its cuspo-lateral distribution that the expectation for thicker protocone and protoconid enamel is convincingly met by all maxillary and mandibular molars. In addition, in almost all teeth, enamel tends to be relatively thicker over the lateral side of the cusp than at its tip or over its occlusal aspect. This observation is in accordance with Kono et al. (2002), who recorded that the buccal faces of the lower molars and lingual faces of the upper molars have thicker enamel than do other crown surfaces.

Theses observations are of interest, because the cuspo-lateral aspects of the protocone and protoconid are related to phase I shearing/guiding activity during mastication. Even though these surfaces are not directly involved in crushing and grinding, they may be differentially thickened so as to effectively withstand and/or dissipate the pressures generated at the tips and on the occlusal surfaces of these cusps. In this regard, the proportionately thicker cuspo-lateral enamel of the protocone and protoconid would be serve as a means to prolong functional crown life by preventing cusp fracture, rather than as a mechanism by which to increase the attritional longevity of a wear facet.

The discrepancy in linear enamel thickness between buccal and lingual cusps was also argued to predispose humans to develop a helicoidal occlusal wear plane (Macho and Berner, 1993, 1994). In this regard, it was posited that the changes from M^1 to M^3 serve to increase the symmetry of the more distal molars, thereby resulting in a more equitable distribution of occlusal forces (Macho and Berner, 1994; Spears and Macho, 1995). The data by Schwartz (2000a) on mandibular permanent molars, however, led him to question the validity of this model.

The present data for maxillary molars correspond with those recorded by Macho and Berner (1993) with regard to cuspal enamel, in that there is a trend for the discrepancy between the protocone and paracone to decrease distally. However, the current sample shows no difference in occlusal discrepancy from M^1 to M^3. The current data also correspond to those reported by Schwartz (2000a), in that there is a trend for the disparity in cuspal thickness between the protoconid and metaconid to increase from M_1 to M_3. Finally, the discrepancy in thickness of the cuspo-lateral between the buccal and lingual cusps increases distally from M1 to M3 in both jaws, which also runs counter to the model proposed by Macho and Berner (1994). Thus, the results of the present study accord with those of Schwartz (2000a) in suggesting that the human dentition is not predisposed to develop a helicoidal wear plane by the disposition of molar enamel thickness.

CONCLUSIONS

The results of the present study have implications for several hypotheses that have been proposed pertaining to the functional significance of enamel thickness as it varies along the molar row and across the molar crown. These results also have implications for comparisons of enamel thickness between humans and other primate species.

The data recorded here for a sexually and geographically mixed sample of recent *Homo sapiens* accord with those presented by others who documented a distinct tendency for the relative thickness of the enamel cap to increase overall, and at specific locations from dm2 to M3 in both jaws, but particularly in the maxilla (Macho and Berner, 1993; Schwartz, 2000a; Gantt et al., 2001). In the first instance, this has clear implications for interspecific comparisons of enamel thickness, and further strengthens the suggestion by Macho and Berner (1993) that such comparisons should be tooth-specific, at least where they involve modern humans.

In terms of the distalward increase in relative enamel thickness along the molar row, the present data reveal that enamel thickness does not covary with the size of the dentine/pulp core of the crown. Deciduous molars (dm2s) have a small dentine core combined with relatively thin enamel. In the permanent molars, on the other hand, the dentine core tends to become smaller, while the enamel cap increases in relative thickness from M1 to M3. This suggests that the more distal molars attain relatively thicker enamel through a preferential reduction in the size of their dentine core. This has two potential implications. In the first instance, modern humans exhibit a well-documented, general tendency for molar crown size to decrease from M1 to M3. The implication from the present study is that this reduction in crown size was attained primarily through a differential loss of the dentine component over the enamel component. This proposition would appear to be in accord with the concomitant reduction in root complexity and surface area from M1 to M3 (Nikolai, 1985), insofar as the roots are composed largely of dentine. In the second instance, because the relatively thicker enamel of human distal molars is explicable as a result of odontogenetic processes related to tooth size reduction, it is not necessary to invoke functional/adaptive scenarios derived from questionable models of masticatory biomechanics to explain the relatively thick enamel of human M2s and M3s. In order to test this proposal, it will be necessary to obtain data on enamel thickness at different molar positions in primate taxa that do not exhibit distalward molar crown size reduction.

With regard to the distribution of enamel across the crown, the data recorded here corroborate earlier observations that it tends to be thicker on the protocone than on the paracone, and thicker on the protoconid than on the metaconid (Macho and Berner, 1993; Schwartz, 2000a; Gantt et al., 2001). However, while there is a general correlation between enamel thickness and the cusp's overall role in a "functional" (Schwartz, 2000a) or "guiding" (Macho and Spears, 1999) capacity, enamel is not necessarily thicker on those surfaces where it would be required to better withstand heavier attritional loss through wear. Thus, although enamel at the cusp tip is significantly thicker on the protocone than on the paracone for all upper molars, an equivalent discrepancy is found only in the M3 among mandibular molars. Indeed, the comparatively high degree of variability that characterizes enamel thickness at the cusp apex seems to be contrary to prevailing functional design expectations. While occlusal enamel is generally thicker on the protococnid than on the metaconid in mandibular molars (and significantly so in dm_2 and M_2), its distribution in the maxillary permanent molars is contradictory to functional design expectations related to enhanced attritional life. Finally, in almost all teeth, enamel tends to be thicker over the lateral side of the cusp than over its tip or occlusal aspect, and it is only in its cuspo-lateral placement that the expectation for increased thickness on the protocone and protoconid is met by all molars. The cuspo-lateral aspects of these cusps are related to phase I shearing/guiding activity during mastication, but the differentially thickened enamel here may serve to better withstand and/or dissipate the pressures generated at the tips and opposing phase II occlusal surfaces of these cusps. The proportionately thicker enamel on the cuspo-lateral surfaces of the "functional" cusps would serve as a means to prolong functional crown life by preventing cusp fracture, rather than as a mechanism by which to increase the attritional longevity of a wear facet. In this regard, it would be of considerable interest to establish whether structural aspects of enamel that are of mechanical relevance (e.g., prism decussation) display concomitant variability in distribution across the molar crown. The results of this study accord with the conclusion reached by Kono et al. (2002), that the pattern of enamel thickness across the molar crown is only partly explained as an adaptation to the functional demands of mastication.

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LITERATURE CITED

Aiello LC, Montgomery C, Dean C. 1991. The natural history of deciduous tooth attrition in hominoids. J Hum Evol 21:397–412.

Albrecht GH, Gelvin BR, Hartman SE. 1993. Ratios as a size adjustment in morphometrics. Am J Phys Anthropol 91:441–468.

Beynon AD, Wood BA. 1986. Variation in enamel thickness and structure in East African hominids. Am J Phys Anthropol 70: 177–193.

Beynon AD, Dean MC, Reid DJ. 1991. On thick and thin enamel in hominoids. Am J Phys Anthropol 86:295–309.

Conroy GC. 1991. Enamel thickness in South African australopithecines: noninvasive determination by computed tomography. Palaeontol Afr 28:53–59.

Dumont ER. 1995. Enamel thickness and dietary adaptations among extant primates and chiropterans. J Mammal 76:1127–1136.

Games PA, Howell JF. 1976. Pairwise multiple comparison procedures with unequal N's and/or variances: a Monte Carlo sudy. J Educ Stat 1:113–125.

Gantt DG. 1977. Enamel of primate teeth: its thickness and structure with reference to functional and phyletic implications. Ph.D. thesis, Washington University, St. Louis.

Gantt DG. 1986. Enamel thickness and ultrastructure in hominoids with reference to form, function and phylogeny. In: Swindler DR, Erwin J, editors. Comparative primate biology, volume 1, systematics, evolution and anatomy. New York: Alan R. Liss. p 453–475.

Gantt DG, Harris EF, Rafter JA, Rahn JK. 2001. Distribution of enamel thickness on human deciduous molars. In: Brook A, editor. Dental morphology 2001. Sheffield: Sheffield Academic Press. p 167–190.

Grine FE. 1986. Anthropological aspects of the deciduous teeth of South African blacks. In: Singer R, Lundy JK, editors. Variation, culture and evolution in African populations. Johannesburg: Witwatersrand University Press. p 47–83.

Grine FE. 1991. Computed tomography and the measurement of enamel thickness in extant hominoids: implications for its palaeontological application. Palaeontol Afr 28:61–69.

Grine FE. 2002. Scaling of tooth enamel thickness, and molar crown size reduction in modern humans. S Afr J Sci 98:503–509.

Grine FE, Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, editor. Evolutionary history of the "robust" australopithecines. New York: Aldine de Gruyter. p 3–42.

Grine FE, Stevens NJ, Jungers WL. 2001. Evaluation of dental radiograph accuracy in the measurement of enamel thickness. Arch Oral Biol 46:1117–1125.

Haile-Selassie Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412:178–181.

Harris EF, Hicks JD. 1988. Enamel thickness in maxillary human incisors: a radiographic assessment. Arch Oral Biol 43: 825–831.

Harris EF, Hicks JD, Barcroft BD. 1999. Absence of sexual dimorphism in enamel thickness of human deciduous molars. In: Mayhall JT, Heikkinen T, editors. Dental morphology 1998. Oulu, Finland: Oulu University Press. p 338–349.

Harris EF, Hicks JD, Barcroft BD. 2001. Tissue contributions to sex and race: differences in tooth crown size of deciduous molars. Am J Phys Anthropol 115:223–237.

Jacobson A. 1982. The dentition of the South African Negro. Anniston, AL: Higginbotham.

Janis CM, Fortelius M. 1988. On the means by whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biol Rev 63:197–230.

Jolly CJ. 1970. The seed-eaters: a new model of hominid differentiaton based on a baboon analogy. Man 5:5–26.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. Yrbk Phys Anthropol 38:137–161.

Kay RF. 1977. The evolution of molar occlusal in the cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327–352.

Kay RF. 1981. The nut-crackers: a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141–152.

Kieser JA. 1990. Human adult odontometrics: the study of variation in adult tooth size. Cambridge: Cambridge University Press.

Kono RT, Suwa G, Tanijiri T. 2002. A three-dimensional analysis of enamel distribution patterns in human permanent first molars. Arch Oral Biol 47:867–875.

Kono-Takeuchi R, Suwa G, Kanazawa E, Tanijiri T. 1998. A new method of evaluating enamel thickness based on a three-dimensional measuring system. Anthropol Sci 105:217–229.

Koolstra JH, van Eijden TMJG, Weijs WA, Naeije M. 1988. A three-dimensional mathematical model of the human masticatory system predicting maximum bite forces. J Biomech 21: 563–576.

Macho GA. 1994. Variation in enamel thickness and cusp area within human maxillary molars and its bearing on scaling techniques used for studies of enamel thickness between species. Arch Oral Biol 39:783–792.

Macho GA, Berner ME. 1993. Enamel thickness of human maxillary molars reconsidered. Am J Phys Anthropol 92:189–200.

Macho GA, Berner ME. 1994. Enamel thickness and the helicoidal occlusal plane. Am J Phys Anthropol 94:327–337.

Macho GA, Spears IR. 1999. Effects of loading on the biomechanical behavior of molars of *Homo*, *Pan*, and *Pongo*. Am J Phys Anthropol 109:211–227.

Macho GA, Thackeray JF. 1992. Computed tomography and enamel thickness of maxillary molars of Plio-Pleistocene hominids from Sterkfontein, Swartkrans, and Kromdraai (South

Africa): an exploratory study. Am J Phys Anthropol 89:133–143.
Mansour RM, Reynick RJ. 1975. In vivo occlusal forces and moments: I. Forces measured in terminal hinge position and associated moments. J Dent Res 54:114–120.
Martin LB. 1983. The relationship of the later Miocene Hominoidea. Ph.D. thesis, University College London.
Martin LB. 1985. Significance of enamel thickness in hominoid evolution. Nature 314:260–263.
Molnar S, Gantt DG. 1977. Functional implications of primate enamel thickness. Am J Phys Anthropol 46:447–454.
Molnar S, Ward SC. 1977. On the hominid masticatory complex: biomechanical and evolutionary perspectives. J Hum Evol 6:551–568.
Molnar S, Hildebolt C, Molnar IM, Radovcic J, Gravier M. 1993. Hominid enamel thickness: I. The Krapina Neandertals. Am J Phys Anthropol 92:131–138.
Moorrees CFA. 1957. The Aleut dentition. A correlative study of dental characteristics in an Eskimoid people. Cambridge, MA: Harvard University Press.
Mosimann JE, James FC. 1979. New statistical methods for allometry with applications to Florida red-winged blackbirds. Evolution 23:444–459.
Nelson CT. 1938. The teeth of the Indians of Pecos Pueblo. Am J Phys Anthropol 23:261–293.
Nikolai RJ. 1985. Bioengineering analysis of orthodontic mechanics. Philadelphia: Lea & Febiger.
Osborn JW. 1996. Features of human jaw design which maximize the bite force. J Biomech 29:589–595.
Osborn JW, Baragar FA. 1985. Predicted pattern of human muscle activity during clenching derived from a computer assisted model: symmetric vertical bite forces. J Biomech 18:599–612.
Pruim GJ, De Jongh HJ, Ten Bosch JJ. 1980. Forces acting on the mandible during bilateral static bite at different bite force levels. J Biomech 13:755–673.
Reid DJ, Beynon AD, Ramirez-Rozzi FV. 1998a. Histological reconstruction of dental development in four individuals from a medieval site in Picardie, France. J Hum Evol 35:463–477.
Reid DJ, Schwartz GT, Dean C, Chandrasekera MS. 1998b. A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. J Hum Evol 35:427–448.
Schwartz GT. 2000a. Enamel thickness and the helicoidal wear plane in modern human mandibular molars. Arch Oral Biol 45:401–409.
Schwartz GT. 2000b. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. Am J Phys Anthropol 111:221–244.
Schwartz GT, Thackeray JF, Reid C, van Reenen JF. 1998. Enamel thickness and the topography of the enamel-dentine junction in South African Plio-Pleistocene hominids with special reference to the Carabelli trait. J Hum Evol 35:523–542.
Seipel CM. 1946. Variation in tooth position: a metric study of variation and adaptation in the deciduous and permanent dentitions. Svensk Tandlakare-Tidskrift [Suppl] 39. Upsala: State Inst. Human Genet. Race Biol.
Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). C R Acad Sci [IIa] 332:137–144.
Shellis RP, Beynon AD, Reid DJ, Hiiemae KM. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:507–522.
Shillingburg H Jr, Grace C. 1973. Thickness of enamel and dentin. S Calif Dent Assoc 41:33–52.
Simons EL, Pilbeam DR. 1972. *Hominoid paleoprimatology*. In: Tuttle R, editor. The functional and evolutionary biology of primates. Chicago: Aldine. p 36–62.
Smith RJ. 1999. Statistics of sexual size dimorphism. J Hum Evol 36:423–459.
Sokal RR, Rohlf FJ. 1995. Biometry. The principles and practice of statistics in biological research. 3rd ed. New York: W.H. Freeman.
Spears IR, Macho GA. 1995. The helicoidal occlusal plane—a functional and biomechanical appraisal of molars. In: Radlenski RJ, Renz H, editors. Proceedings of the 10th International Symposium on Dental Morphology. Berlin: "M" Marketing Services. p 391–397.
Spears IR, Macho GA. 1998. Biomechanical behavior of modern human molars: implications for interpreting the fossil record. Am J Phys Anthropl 106:467–482.
Spencer M. 1995. Masticatory system configuration in anthropoid primates. Ph.D. thesis, State University of New York, Stony Brook.
Spencer M. 1998. Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. J Hum Evol 34:25–54.
Spoor CF, Zonneveld FW, Macho GA. 1993. Linear measurements of cortical bone and dental enamel by computed tomography: applications and problems. Am J Phys Anthropol 91:469–484.
Strait DS, Grine FE. 2001. The systematics of *Australopithecus garhi*. Ludus Vitalis 9:109–135.
Strait DS, Grine FE, Moniz MA. 1997. A reappraisal of early hominid phylogeny. J Hum Evol 32:17–82.
Stroud JL, Buschang PH, Goaz PW. 1994. Sexual dimorphism in mesiodistal dentine and enamel thickness. Dentomaxillofac Radiol 23:169–171.
Stroud JL, English J, Buschanf PH. 1998. Enamel thickness of the posterior dentition: its implications for nonextraction treatment. Angle Orthod 68:141–146.
Thomsen S. 1955. Dental morphology and occlusion in the people of Tristan da Cunha. Results of the Norwegian Scientific Expedition to Tristan da Cunha, 1937–1938. No. 25. Oslo: Det Norske Videnkaps-Akademi.
Tukey JW. 1977. Exploratory data analysis. Reading, MA: Addison-Wesley.
van Eijden TMGJ. 1991. Three-dimensional analyses of human bite-force magnitude and moment. Arch Oral Biol 36:535–539.
van Eijden TMGJ, Klok EM, Weijs WA, Koolstra JH. 1988. Mechanical capabilities of the human jaw muscles studied with a mathematical model. Arch Oral Biol 33:819–826.
Ward SC, Molnar S. 1980. Experimental stress analysis of topographic diversity in early hominid gnathic morphology. Am J Phys Anthropol 53:383–395.
Weijs WA, van Spronsen P. 1992. Variation in adult human jaw muscle size: computer models predicting the biomechanical consequences of the variation. In: Davidovitch Z, editor. The biological mechanisms of tooth movement and craniofacial adaptation. Columbus, OH: Ohio State University College of Dentistry. p 549–557.
White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of hominid from Aramis, Ethiopia. Nature 371:306–312.