

Brief Communication: Enamel Thickness Trends in the Dental Arcade of Humans and Chimpanzees

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ABSTRACT In addition to evidence for bipedality in some fossil taxa, molar enamel thickness is among the few characters distinguishing (thick-enameled) hominins from the (thin-enameled) African apes. Despite the importance of enamel thickness in taxonomic discussions and a long history of scholarship, measurements of enamel thickness are performed almost exclusively on molars, with relatively few studies examining premolars and anterior teeth. This focus on molars has limited the scope of enamel thickness studies (i.e., there exist many fossil hominin incisors, canines, and premolars). Increasing the available sample of teeth from which to compare enamel thickness measurements from the fossil record could substantially increase our understanding of this aspect of dental biology, and perhaps facilitate greater taxonomic resolution of early hominin fossils. In this

study, we report absolute and relative (size-scaled) enamel thickness measurements for the complete dentition of modern humans and chimpanzees. In accord with previous studies of molars, chimpanzees show lower relative enamel thickness at each tooth position, with little overlap between the two taxa. A significant trend of increasing enamel thickness from anterior to posterior teeth is apparent in both humans and chimpanzees, indicating that inter-taxon comparisons should be limited to the same tooth position in order to compare homologous structures. As nondestructive imaging techniques become commonplace (facilitating the examination of increasing numbers of fossil specimens), studies may maximize available samples by expanding beyond molars. *Am J Phys Anthropol* 136:237–241, 2008. © 2008 Wiley-Liss, Inc.

Morphological characters distinguishing African apes from modern humans are identifiable in nearly all aspects of the postcranial skeleton, as well as their cranial and dental anatomy, soft tissues, and genetic material (e.g., Andrews and Martin, 1987; Ruvolo, 1997; Gibbs et al., 2002). Interpretation of the affinities of fossils is more difficult; the fossil record of the latest Miocene and earliest Pliocene of Africa has yielded fossils with few characters by which to assess their taxonomic placement relative to African apes and later hominins (e.g., White et al., 1994). Perhaps the most widely cited character complex diagnostic of hominins is the locomotor skeleton, assessed via indirect evidence of bipedality [e.g., a relatively anterior placement of the foramen magnum in *Sahelanthropus tchadensis* (Brunet et al., 2002)] or by more direct inferences of the locomotor repertoire [e.g., femoral architecture in *Orrorin tugenensis* (Senut et al., 2001)].

Postcranial and cranial remains are often fragmentary, however, and occur with less frequency in the fossil record than dental elements. Relying on these more numerous dental remains, the relative thickness of molar enamel is another source of taxonomic information frequently employed in studies of early hominin fossils. Molar enamel thickness has been described in the seminal diagnosis of nearly every hominin taxon in recent years (White et al., 1994; Brunet et al., 1995; Asfaw et al., 1999; Haile-Selassie, 2001; Leakey et al., 2001; Senut et al., 2001; Brunet et al., 2002), due in large part to the well-documented distinction of thin-enameled African apes from thick-enameled hominins (e.g., Martin, 1983; Grine and Martin, 1988; Kono, 2004). Moreover, enamel thickness has a long his-

tory of scholarship among those concentrating on whether particular fossils are attributable to Homininae (e.g., “*Eoanthropus*,” Miller, 1918; “*Ramapithecus*,” Kay, 1981). Despite this long history and active study, nearly all investigations of enamel thickness have concentrated on molars, with substantially less attention paid to premolars and the anterior dentition. The utility of enamel thickness as a taxonomic indicator in hominin paleontology may be expanded if teeth other than molars are also found to distinguish African apes from hominins. Towards this end, the goal of the present study is to assess whether anterior teeth and/or premolars are as effective as molars at distinguishing chimpanzees from modern humans.

MATERIALS AND METHODS

A sample of recent human and chimpanzee teeth was chosen from material previously prepared for studies of

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TABLE 1. Mean values of chimpanzee and human enamel thickness measurements

	<i>n</i>	Total area of the crown section (mm ²)	Area of coronal dentine (mm ²)	Area of the enamel cap (mm ²)	Length of the enamel-dentine junction (mm)	AET (mm)	RET
Maxillary teeth							
Chimpanzee I1	2	77.24	62.80	14.44	29.55	0.49	6.17
Human I1	32	46.19	32.73	13.46	21.55	0.62	10.91
Chimpanzee I2	1	63.39	51.09	12.30	25.06	0.49	6.87
Human I2	31	38.94	26.78	12.16	19.04	0.64	12.51
Chimpanzee C	0	—	—	—	—	—	—
Human C	22	59.29	40.28	19.02	20.96	0.91	14.43
Chimpanzee P3	1	52.24	40.22	12.01	20.46	0.59	9.26
Human P3	19	61.30	39.18	22.12	19.99	1.10	17.69
Chimpanzee P4	1	51.53	38.99	12.54	19.59	0.64	10.25
Human P4	26	60.91	38.01	22.90	20.01	1.14	18.55
Chimpanzee M1	6	54.65	41.44	13.22	20.21	0.66	10.33
Human M1	40	67.77	42.67	25.11	20.66	1.22	18.72
Chimpanzee M2	3	56.25	41.32	14.93	20.52	0.73	11.37
Human M2	29	72.60	43.70	28.89	20.61	1.40	21.40
Chimpanzee M3	3	51.88	37.08	14.80	19.25	0.77	12.82
Human M3	52	68.08	40.96	27.13	19.70	1.38	21.76
Mandibular teeth							
Chimpanzee I1	7	62.78	50.88	11.90	25.62	0.46	6.53
Human I1	16	34.02	23.97	10.05	18.21	0.55	11.23
Chimpanzee I2	6	66.54	54.10	12.44	25.74	0.48	6.59
Human I2	12	38.89	27.49	11.40	19.23	0.59	11.28
Chimpanzee C	2	107.59	90.32	17.27	31.82	0.54	5.71
Human C	20	56.96	40.12	16.84	20.89	0.81	12.91
Chimpanzee P3	6	56.46	44.54	11.93	19.84	0.60	9.03
Human P3	17	51.25	33.16	18.08	17.85	1.01	17.78
Chimpanzee P4	7	49.07	36.20	12.87	18.79	0.68	11.40
Human P4	17	54.67	32.88	21.79	18.12	1.20	21.19
Chimpanzee M1	17	45.82	32.84	12.98	18.23	0.71	12.64
Human M1	58	62.47	40.51	21.95	20.37	1.08	17.02
Chimpanzee M2	9	49.90	35.30	14.61	19.14	0.76	12.91
Human M2	47	56.58	34.44	22.15	18.54	1.20	20.54
Chimpanzee M3	4	52.52	35.24	17.28	19.47	0.89	15.01
Human M3	45	56.23	33.36	22.86	18.32	1.25	21.72

AET, average enamel thickness; RET, relative enamel thickness.

incremental development (Dean et al., 1993; Reid et al., 1998; Reid and Dean, 2006; Smith et al., 2007; Reid et al., in press) and molar enamel thickness (Smith et al., 2005, 2006a). Additional teeth were added from African, Asian, and European human populations, as well as a small number of chimpanzee anterior teeth from populations detailed by Smith et al. (2007). A total of 483 human teeth and 75 chimpanzee teeth were measured (see Table 1 for tooth-specific sample sizes). Smith et al., (2006a) did not find consistent differences in molar enamel thickness among human populations; thus populations in this study were combined for each tooth position, as the primary aim was to assess inter-taxon differences.

Multiple preparative techniques were employed to generate labial-lingual sections of anterior teeth, and buccal-lingual sections of premolars and molar mesial cusps; these techniques are described in detail elsewhere (e.g., Reid et al., 1998; Smith et al., 2007). Differences in preparation derived primarily from the type of saw used or the embedding regime prior to sectioning; these differences do not impact the resultant plane of section used for enamel thickness measurements. Sections of anterior teeth and premolars were consistently prepared to capture the tips of the cusps and the maximum extension of the cervical enamel. In some cases it is difficult to capture a true buccal-lingual section across both lower premolar cusps due to tooth asymmetry, which may contrib-

ute to greater variance within and between taxa at these particular tooth positions.

Slight reconstructions of the outer enamel surface were made prior to measurement in those sections showing light to moderate wear (based on the profiles of unworn teeth), or if a small amount of cervical enamel was missing (based on the curvature and orientation of the outer enamel surface relative to the enamel-dentine junction). Sections with heavy wear, or with both cervices missing, were not included in the analysis. Sections that showed an oblique orientation (relative to a plane passing through the respective dentine horn tips) were also excluded. When multiple planes of section were available for a single tooth, the one with the lowest relative enamel thickness (RET) [following Martin (1983); see below] was chosen for this analysis.

Several variables were quantified on micrographs of each section using a digitizing tablet interfaced with SigmaScan software (SPSS Science, Inc.). Following terminology introduced by Martin (1983), these variables include the total area of the tooth crown section (a), the area of the enamel cap (c), the length of the enamel-dentine junction (e), and the area of the coronal dentine enclosed by the enamel cap (b) (e.g., see Smith et al., 2005: Fig. 1, p. 579). Following Martin (1983, 1985), average enamel thickness (AET) is calculated as $[c/e]$, yielding the average straight-line distance (mm units), or thickness, from the enamel-dentine junction to the

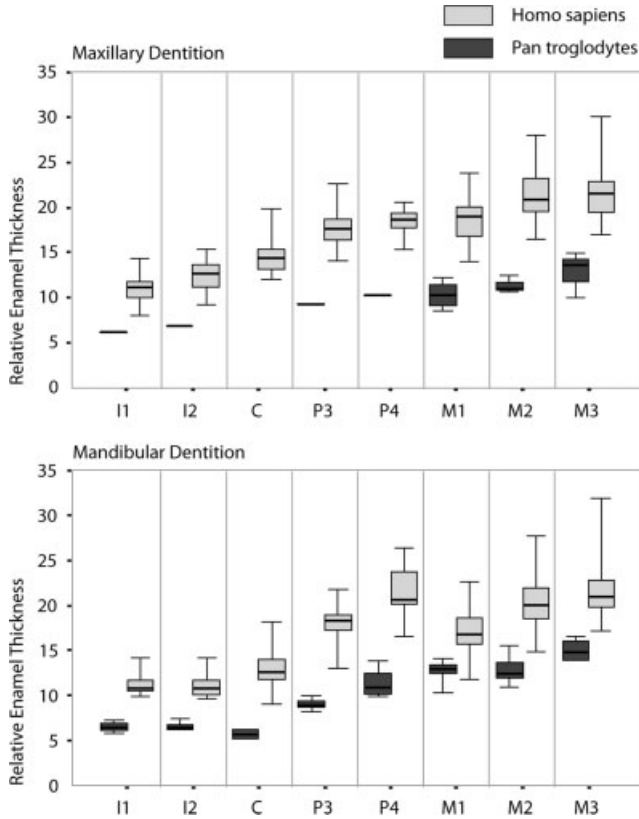


Fig. 1. Box-and-whisker plots depicting RET in human and chimpanzee dental arcades. Whiskers represent data ranges, ends of boxes represent 75th and 25th percentiles, and solid lines within boxes represent mean values. With the exception of first and second mandibular molars, ranges of modern humans and chimpanzees do not overlap.

outer enamel surface. RET is calculated as $[100 \times [c/e]/\sqrt{b}]$; RET is a unitless measure in which AET is scaled for size, yielding a measurement suitable for inter-taxon comparisons. The Mann–Whitney *U*-test was employed to test for inter-taxon differences in RET between equivalent tooth positions in cases where sample sizes of that tooth position were four or greater in each taxon. Despite marked differences in the shape of certain tooth positions between humans and chimpanzees (e.g., canines, lower P3), comparisons were intentionally made between spatially and developmental homologous elements. The Jonckheere–Terpstra test was employed to test the significance of intra-taxon trends in AET throughout the dental row; maxillary and mandibular rows were tested separately for each taxon.

RESULTS

Mean values of each variable, as well as the AET and RET indices for each tooth position in both taxa are presented in Table 1 and Figures 1 and 2. Humans show greater mean RET (and AET) at every tooth position; this result is significant for each comparison where sample sizes for both taxa are greater than four (Table 2). Moreover, with the exception of first and second mandibular molars, there is no overlap between chimpanzee and human RET values at any tooth position (see Fig. 1). A significant increasing trend in AET from anterior to posterior teeth (central incisors to third molars) was

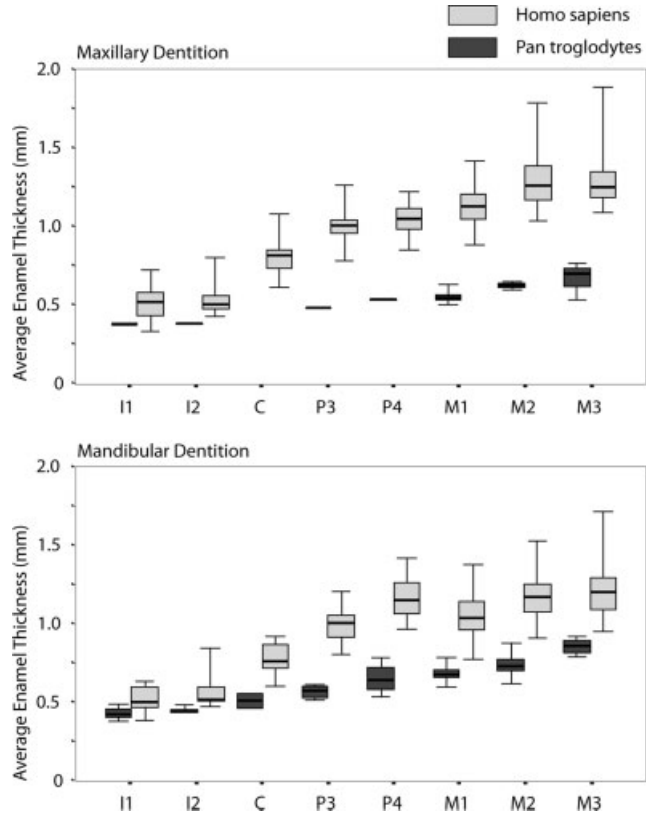


Fig. 2. Box-and-whisker plots depicting AET in human and chimpanzee dental arcades. Whiskers represent data ranges, ends of boxes represent 75th and 25th percentiles, and solid lines within boxes represent mean values. There is a significant increasing trend in enamel thickness from anterior to posterior teeth in maxillary and mandibular rows of both taxa, although the mean value for the human mandibular fourth premolar is greater than the lower first molar mean.

TABLE 2. Results of Mann–Whitney U tests for differences in relative enamel thickness between chimpanzees and humans

	Maxillary teeth		Mandibular teeth	
	Z-Statistic	P-value	Z-Statistic	P-value
I1	–	–	–3.74	0.001
I2	–	–	–3.37	0.001
C	–	–	–	–
P3	–	–	–3.57	0.001
P4	–	–	–3.78	0.001
M1	–3.91	0.001	–5.78	0.001
M2	–	–	–4.67	0.001
M3	–	–	–3.29	0.001

Tested for sample sizes of four or greater for each tooth type.

detected in the maxillary and mandibular dentitions of both humans and chimpanzees ($P < 0.001$) (see Fig. 2). An exception to this trend was found in human mandibular P4 and M1; a post hoc Mann–Whitney *U* test revealed that the P4 mean value is significantly greater than the M1 mean value ($Z = -3.101, P < 0.01$).

DISCUSSION

The data presented here confirm that the difference in human and chimpanzee RET previously identified in molars (e.g., Martin, 1983; Kono, 2004; Smith et al.,

2005, 2006a) is also apparent in the anterior dentition and premolars. Despite a wide range of intra-taxon variation in enamel thickness (e.g., Schwartz and Dean, 2005; Smith et al., 2005, 2006a; Olejniczak et al., 2008), humans and chimpanzees show markedly different degrees of enamel thickness (see Fig. 1). Sample sizes of chimpanzee teeth in our study are smaller than those of homologous human teeth, and enamel thickness ranges of humans and chimpanzees may show some overlap with expanded samples. Nonetheless, highly significant differences are apparent for all tooth positions tested, and expanded samples are not likely to mitigate significant differences in the location of the mean values for each group (despite the introduction of some interspecies overlap). It is likely that these inter-taxon differences in enamel thickness reflect disparate dietary adaptations. Thinner enamel in chimpanzees may be advantageous for a diet rich in soft fruits, while thicker enamel in humans facilitates omnivory or hard-object feeding (e.g., Andrews and Martin, 1991) and greater resistance to abrasion (e.g., Kono, 2004). Thick enamel in recent humans also likely reflects the retention of thick enamel found in fossil hominins (Grine and Martin, 1988; Andrews and Martin, 1991).

Recent studies of molar enamel thickness have demonstrated that many taxa, including modern humans and chimpanzees, show an anterior-to-posterior trend of increasing enamel thickness at different tooth positions (e.g., Macho and Berner, 1993; Grine, 2005; Smith et al., 2005, 2006a). The data presented here demonstrate that increasing enamel thickness distally along the molar row is part of a greater, overall trend of increasing AET from the central incisor to the third molar in both chimpanzees and modern humans (see Fig. 2). Experimental data are lacking for nonhuman primates, but some researchers have hypothesized that an anterior-to-posterior increase in enamel thickness may be related to differential bite forces along the tooth row (e.g., Macho and Berner, 1993, 1994), while others have suggested that enamel thickness is greater in posterior human molars because of a reduction of the size of the dentine component of the molar crown distally (Grine, 2005). Although further consideration of the biomechanics of enamel thickness distribution within the dental arcade is outside the scope of this report, it is notable that the trends found here support previous studies showing that the position of teeth within the jaw should be taken into consideration when making intra- and inter-taxon enamel thickness comparisons (e.g., Macho and Berner, 1993; Smith et al., 2005).

The data reported in this study expand the utility of enamel thickness in studies of early hominin diagnoses by demonstrating that each tooth position provides differentiation between African apes and humans. Given that the number of unworn or lightly worn molars in the human fossil record is small, the data presented here increase the scope of enamel thickness studies by providing comparative data for additional tooth positions. Recent advances in medical imaging techniques have demonstrated that enamel thickness may also be measured accurately via microtomography (Tafforeau, 2004; Olejniczak and Grine, 2006); these nondestructive techniques are expanding the number of molars available for studies of hominin enamel thickness (e.g., Brunet et al., 2005; Smith et al., 2006b; Olejniczak et al., in press). The data presented above demonstrate that dental specimens other than molars may also be included in these

studies, potentially expanding available samples and providing additional insight into the dental biology of hominin taxa.

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