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ENAMEL THICKNESS IN SOUTH AFRICAN AUSTRALOPITHECINES: NONINVASIVE EVALUATION BY COMPUTED TOMOGRAPHY

by

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ABSTRACT

Until recently, it has not been possible to systematically study enamel thickness in fossil hominids except by physically sectioning the teeth. Because sectioning studies destroy original specimens, sample sizes will always be low. For this reason, anthropologists have had to devise other methods for acquiring these data such as by measuring enamel in naturally fractured teeth or where it is exposed in worn teeth. It is clearly important to develop and apply non-invasive techniques to augment and expand the data base of early hominid enamel thickness. This is a first attempt to provide such data for a sample of South African australopithecines by utilizing high-resolution computed tomography (CT). This study is based on over 130 CT scans taken at 1 mm slice thickness on a sample of 22 original *Australopithecus africanus* and *A. robustus* lower molars from Sterkfontein, Kromdraai, Makapansgat, Swartkrans and Taung.

Mean values of absolute and relative enamel thickness between *A. africanus* and *A. robustus* are significantly different, confirming that robust australopithecines have thicker enamel than their gracile counterparts. CT sections were taken in the buccolingual plane through the mesial cusps (protoconid, metaconid). While the mean value of enamel thickness at the buccal cusp (protoconid) is greater in *A. robustus* than in *A. africanus*, the difference is not statistically significant. The difference in enamel thickness at the lingual cusp (metaconid) is statistically significant, however.

This study represents an important, albeit preliminary, first step in establishing a methodology for the non-invasive evaluation of enamel thickness in fossil hominids by computed tomography. It demonstrates the viability of the technique and the type of problem oriented approach that can be tackled using computed tomography in modern anthropological research. Measurements derived from CT cannot, of course, be expected to have the same degree of precision as those taken directly from sectioned teeth; nevertheless, important insights into the functional morphology of early hominid teeth are still easily decipherable from the CT data. Given that the alternative to CT is the physical destruction of original hominid fossils, the slight loss in mensurational accuracy seems well worth the price.

INTRODUCTION

"The most useful measurement of the amount of enamel on a tooth would be the volume of the tissue. This could be expressed as a thickness by dividing the volume of enamel by the surface area of the enamel/dentine junction over which the enamel formed; this area is proportional to the number of ameloblasts which formed the enamel"

(L. Martin, 1985:260).

Until recently, it has not been feasible to meet this goal in paleoanthropological studies. Determination of total enamel volume in fossil hominid teeth would require a complete set of sequential thin sections to be taken of original specimens, a procedure not enthusiastically endorsed by many museum curators. For this reason anthropologists have had to devise other methods for measuring enamel thickness, for example by utilizing naturally fractured teeth or by using teeth in which the enamel was exposed through wear (Beynon and Wood 1986; Gantt 1985; Kay 1981).

Due to its destructive nature, studies dependent upon sectioning techniques are only able to muster limited sample sizes for both extant and extinct primates (Molnar and Gantt 1977; Martin 1985; Grine and Martin 1988). For example, dental sections are available for only two *Australopithecus africanus* teeth (Stw 284, Stw 402), one *Paranthropus robustus*[1] tooth (KB 5223), and one *P. crassidens* tooth (SKX 21841) (Grine and Martin 1988). Thus it is important to develop and apply non-invasive, non-destructive imaging techniques to augment and expand the data base of early hominid enamel thickness. This contribution describes the feasability of providing such data through high-resolution computed tomography (CT).

Although Robinson (1956) was the first to specifically

[1] Grine and Martin (1988) place all species of "robust" australopithecines in the genus *Paranthropus*.

comment on enamel thickness in australopithecines, it was not until Jolly's (1970) classic paper on the "seed-eating hypothesis" that attention was focused on enamel thickness as an important functional adaptation of early hominid teeth. This theme was later reinforced by several other studies that related enamel thickness to occlusal wear patterns (Pilbeam 1972; Simons and Pilbeam 1972). By the end of the 1970's it had become anthropological dogma that australopithecine teeth were characterized by "hyper-thick" enamel even though actual measurements of enamel thickness remained few and far between. The limited number of direct enamel thickness measures available were based solely on naturally broken tooth fragments (Robinson 1956; Gantt 1983).

More recently, Beynon and Wood (1986) completed a study of enamel thickness in 47 East African australopithecine and early *Homo* teeth using naturally broken tooth fragments. They concluded that absolute enamel thicknesses at cusp tips and occlusal surfaces were significantly greater in robust australopithecines compared to early *Homo* even after correcting for overall tooth-size differences.

In a more controlled study using finely polished sections, Grine and Martin (1988) were able to measure enamel thickness on four South African australopithecine molars by carefully sectioning each tooth buccolingually through the mesial two cusps (protoconid and metaconid). They also sectioned two australopithecine specimens from Omo, one buccolingually through the entoconid and hypoconid and the other mesiodistally through the protoconid and hypoconid. Although sample sizes were necessarily small given the destructive nature of such procedures, they concluded that relative enamel thickness values in *A. africanus* fell within the 99% confidence limits for the means of their combined upper and lower molar sample of modern *Homo sapiens*, whereas the *Paranthropus robustus*, *P. crassidens*, and *P. boisei* values fell well above those same limits.

Conventional radiographic techniques have also been used to assess enamel thickness in australopithecines but their limitations are well recognized because of relatively low contrast and geometric errors due to inherent magnification errors and/or X-ray beam angulation variations (Sperber 1985). Computed tomography does not have such inherent geometric distortions because of the fixed geometry thinly collimated X-ray beam (typically 1-2mm) and has great potential for non-invasive studies of dental structures (Zonneveld and Wind 1985; Conroy 1987; Conroy and Vannier 1987, 199la,b; but see Grine 1991).

METHODS

This study of enamel thickness is based upon approximately 130 high-resolution CT scans of specimens listed in Table 1. All scans were taken at slice thicknesses of 1 mm. Pixel edge length in the plane of section varied between 0,1 – 0,3 mm. CT sections were taken in the buccolingual plane through the mesial cusps (protoconid and metaconid) in order to be as comparable as possible to the data reported by Martin (1985) and Grine and Martin (1988).

Each specimen was properly aligned in the CT scanner by first producing a topogram (digital radiograph) of the specimen from which the desired CT slice could be automatically selected by using the built-in light-pen integrated into the CT console. In selected cases, contiguous sequences of 1 mm thin CT sections were taken through the entire tooth in order to determine: 1) total enamel volume; and 2) total dentine/enamel surface area over which the enamel formed (see below).

All scans were taken on a Siemens Somatom DR3 CT Scanner in the Radiology Department, Hillbrow Hospital, Johannesburg (operating at 125 KVP and 160 to 520 mAs; with a scan file diameter of 552 mm). The Somatom DR3 can scan objects with density values from air (-1000 Hounsfield Units or H.U.) to cortical bone (+1000 H.U. typically). By definition, water is 0 H.U. The maximum range of X-ray attenuation measured by the DR3 is ordinarily +3072 H.U., and under softward control, we can extend this to approximately +7000 H.U. Extended bone range window settings were used since the density of the fossils was well beyond +1000 Hounsfield units, the upper limit of cortical bone in normal CT viewing. The CT scans (512^2 or 256^2 matrices) and digital scan projection radiographs used for localization of CT sections (topograms) were stored on 8" floppy disks (DEC RX01 format, 0,5 byte/disk) and carried back to the Mallinckrodt Institute of Radiology, Washington University Medical School, St. Louis. There they were copied from the floppy disks onto magnetic tape using a Siemens Evaluscope-DR reviewing console and transferred from the tape to a DEC MicroVax 3600. The images were sent from the Vax to a Macintosh IIfx workstation via a thin-wire Ethernet network with a DECNET/PACER protocol. There they were automatically converted into an image (PICT format) which could be stored, scaled, and displayed in an image analysis program (IMAGE) developed by Wayne Rasband at the National Institutes of Health (NIH).

Original australopithecine specimens from Sterkfontein (N=10), Swartkrans (n=9), Kromdraai (n=1), Makapansgat (n=1), and Taung (n=1) were examined utilizing the methods described above (Table 1). These specimens represent both gracile (n=12) and robust (n=10) australopithecines and are currently housed in the Department of Anatomy, University of the Witwatersrand, Johannesburg, and the Transvaal Museum, Pretoria. The specimens from Swartkrans and Kromdraai are referred to *A. robustus* and those from Sterkfontein, Makapansgat and Taung to *A. africanus*. Only lower molars exhibiting little, if any, occlusal wear were used in this study.

A number of measures of enamel thickness have been defined over the past several years and from these a number of indices of relative enamel thickness have been calculated (see Fig. 1.8 in Grine and Martin 1988). I have followed Martin (1985) and Grine and Martin (1988) in

TABLE 1 (all measurements are in millimeters)

Specimen	tooth	taxon	enamel area (c)	EDJ length (e)	c/e	buc. cusp ht	ling.cusp ht
Taung 1	LM1	*A. africanus*	23,25	17,17	1,35	2,17	2.17
MLD 2	LM2	*A. africanus*	45,52	20,06	2,27	3,10	2.91
TM 1536	RM1	*A. africanus*	14,63	14,40	1,02	1,90	1.67
STW 14	RM3	*A. africanus*	35,11	20,64	1,70	2,39	1.74
STW 269	RM3	*A. africanus*	33,61	17,89	1,88	2,20	2.20
STW 278	RM3	*A. africanus*	38,94	20,35	1,91	2,56	3.02
STW 308	RM2	*A. africanus*	33,84	17,95	1,89	2,62	2.62
STW 309	RM1	*A. africanus*	32,18	19,13	1,68	2,22	2.50
STW 364	RM1	*A. africanus*	25,48	14,62	1,74	2,67	2.22
STW 412	RM2	*A. africanus*	19,52	16,28	1,20	1.96	1.74
STW 419	LM2	*A. africanus*	25,43	15,34	1,66	2.17	1.96
SK 6	RM2	*A. robustus*	52,22	21,47	2,43	3.48	3.26
SK 6	RM3	*A. robustus*	48,20	23,55	2,05	3,04	3.26
SK 19	RM2	*A. robustus*	23,32	13,86	1,68	2,86	2.71
SK 25	RM1	*A. robustus*	34,59	16,24	2,13	2,54	3.05
SK 25	RM2	*A. robustus*	44,70	21,42	2,09	3,45	3.17
SK 37	LM2	*A. robustus*	46,88	19,75	2,37	3,33	3.33
SK 61	RM1	*A. robustus*	45,89	22,17	2,07	2,56	2.82
SK 63	LM1	*A. robustus*	36,59	17,64	2,07	2,59	3.10
SK 1587	LM2	*A. robustus*	30,86	16,50	1,87	2,50	2.50
KB 5223	LM1	*A. robustus*	31,24	30,07	1,56	1,52	1.74

defining relative (or average) enamel thickness as the ratio of enamel cap area in the plane of section (c) divided by the length of the enamel/dentine junction (EDJ) of the same section (e). The vertical thickness of enamel of the buccal and lingual cusps are measured from the cuspal tips perpendicular to a line drawn tangent to the apices of the dentine horns (measurements f and g in Fig. 1 of Grine and Martin 1988) (Figure 1).

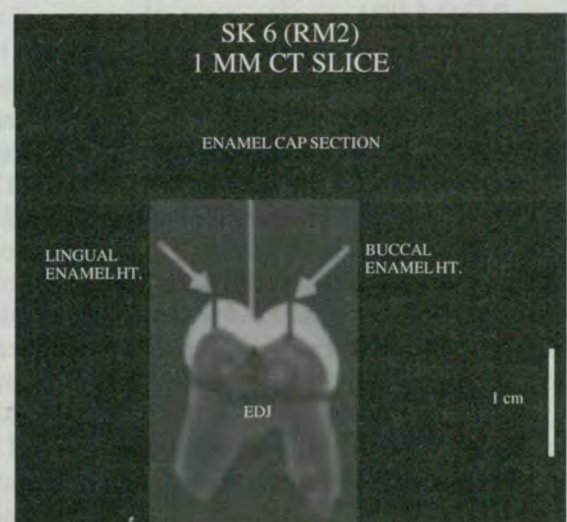

Figure 1 1mm thin CT slice of SK 6 (RM_2) showing measurements used in this study: CT sectioned enamel cap area (in white), enamel height at buccal and lingual mesial cusps (protoconid and metaconid) (white arrows), length of enamel/dentine junction (EDJ) (black arrow).

As each scaled CT section was brought up into the IMAGE program on the workstation, the area of the sectioned enamel cap was determined by thresholding (level slicing) the image so that the gray scale levels of all pixels comprising the enamel were highlighted. The area of the highlighted pixels could then be automatically calculated by the IMAGE program. The length of the EDJ could also be calculated by manually tracing its contour on the computer screen with a built-in cursor. Determination of enamel thickness of buccal and lingual cusps was a straightforward procedure using the built-in ruler command of the IMAGE program. The CT scan data are associated with a header record that contains calibration information, most importantly the field of view, matrix size (256 or 512), magnification factor, and number of pixels per 10 cm. All measurements were recorded (in millimeters) and entered into a statistical program (Statview II) for analysis.

The precision of any measurement calculated from a CT scan is of course, limited by the size of the pixels that make up the image (i.e. pixel edge length). The overall reliability of the measurements derived from the australopithecine CT's was cross-checked in two independent ways. Two specimens, Sts 14 and Sts 96, were CT scanned at right angles to their naturally fractured enamel caps. Enamel thicknesses calculated by the IMAGE program were consistently within 0,2 – 0,3 mm of the true values measured directly on the original specimens (i.e., within the pixel edge length values of the CT images). It is worth emphasizing that since this small mensurational imprecision is essentially random with respect to membership in either *A. africanus* or *A. robustus*, it does not significantly influence the results of comparative differences in absolute or relative enamel thicknesses observed between these two fossil species. Indeed, random measurement error would actually make it **more difficult** to obtain the statistically significant results reported below.

The second cross-check on the reliability of the CT methods was quite fortuitous. One of the South African specimens actually sectioned through the mesial cusps by Grine and Martin (1988) was KB 5223, a slightly damaged unworn RM_1 from Member 3, Kromdraai (Grine 1982). Direct measurements of enamel cap area (c) and EDJ length (e) gave values of 31,71 and 19,56 respectively for a c/e ratio 1,62 (corrected values for the slightly damaged enamel cap were 36,39, 18,00

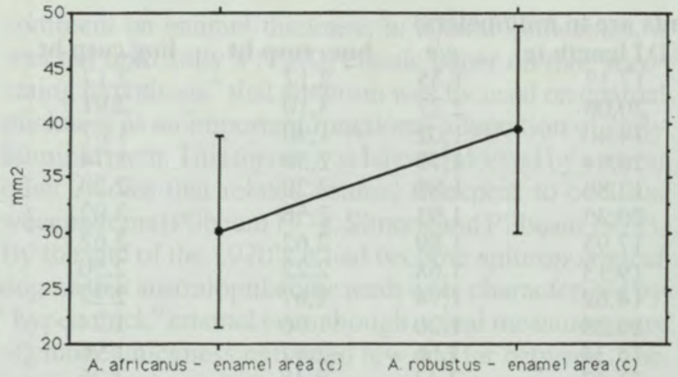

Figure 2. Mean and one standard deviation bar for enamel area

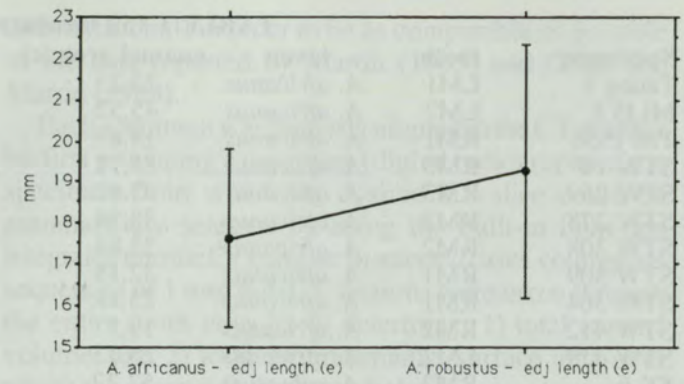

Figure 3. Mean and one standard deviation bar for EDJ Length

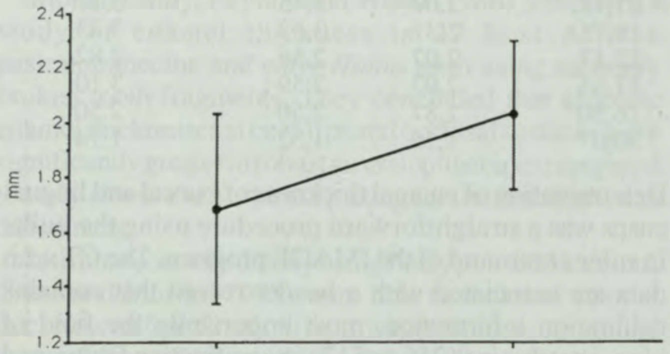

Figure 4. Mean and one standard deviation bar for relative enamel thickness (C/E)

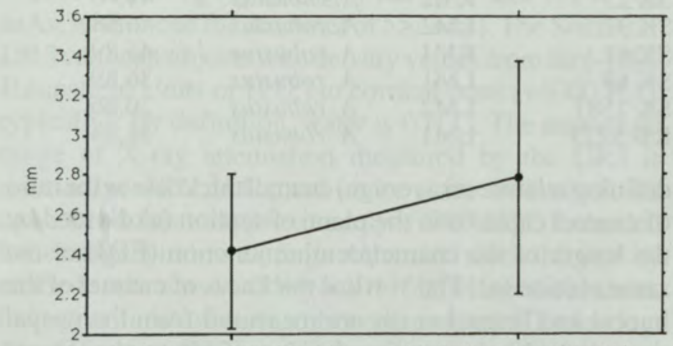

Figure 5. Mean and one standard deviation bar for enamel thickness at Buccal cusp

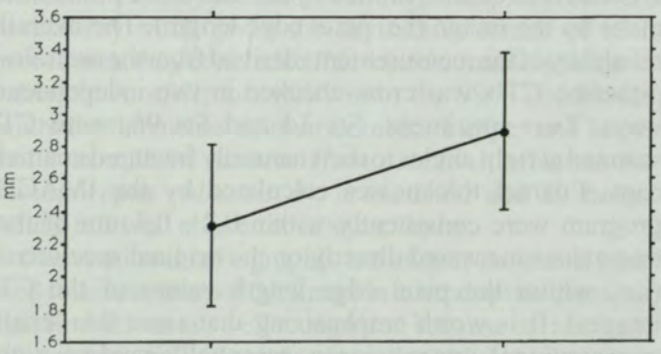

Figure6. Mean and one standard deviation bar for enamel thickness at Lingual Cusp

and 1,02 respectively) (Grine and Martin 1988). Evaluation of a CT section through the mesial cusps of the unworn LM_1 from the same individual gave reasonably similar results (31,24 and 20,07 for a c/e ratio of 1,56; Table 1).

RESULTS AND DISCUSSION

The raw data for enamel thickness measurements are presented in Table 1 and basic statistical data in Tables 2 – 6. Sample means and one standard deviation bars for each of the measurements are illustrated in Figures 2 - 6.

The mean value of enamel cap area in CT sections taken through the mesial cusps of the lower molars is 30.15 mm^2 in *A. africanus* and 39.45 mm^2 in *A. robustus*, a statistically significant difference at the 5% level (Table 2; p=,026). However, the mean EDJ lengths of 17,63 mm in *A. africanus* and 19.27 mm in *A. robustus* are not significantly different (Table 3; p=,160).

As discussed above, relative enamel thickness (or average enamel thickness) is measured as the ratio of the sectioned enamel cap area to the EDJ length from the buccal to the lingual cervix of the same section. Mean values for this ratio of 1,69 mm in *A. africanus* and 2,03 mm in *A. robustus* are significantly different at the 5% level (Table 4; p=,019), confirming that robust australopithecines have relatively thicker enamel than their gracile counterparts.

While the mean value of enamel thickness at the buccal cusp is greater in *A. robustus* (2,79 mm) than in *A. africanus* (2,42 mm), this difference approaches, but is not, statistically significant at the 5% level (Table 5; p=,092). However, the difference in enamel thickness at the lingual cusp between *A. robustus* (2,89 mm) and *A. africanus* (2,32 mm) is statistically significant (Table 6; p=,013). (Undoubtedly, differences between the two species would be even greater if the extremely small, rather thin enamelled specimen KB 5223 were not included in the *A. robustus* sample).

TABLE 2: Enamel area (mm^2) in South African australopithecines

	Mean	SD	95% lower	95% upper	Prob. (2-tail)
A. africanus	30,15	8,69	24,63	35,67	,258*
A, robustus	39,45	9,41	32,72	46,19	
combined sample	34,38	10,00	29,95	38,81	

TABLE 3: EDJ length (mm) in South African australopithecines

	Mean	SD	95% lower	95% upper	Prob. (2-tail)
A. africanus	17,63	2,17	16,25	19,01	,160
A. robustus	19,27	3,09	17,06	21,48	
combined sample	18,37	2,69	17,18	19,57	

TABLE 4: Relative enamel thickness (c/e) in South African australopithecines

	Mean	SD	95% lower	95% upper	Prob. (2-tail)
A. africanus	1,69	,35	1,47	1,91	,0188*
A. robustus	2,03	,27	1,84	2, 23	
combined sample	1,84	,36	1,69	2,00	

TABLE 5: Enamel thickness at buccal cusp (mm) in South African australopithecines

	Mean	SD	95% lower	95% upper	Prob. (2-tail)
A. africanus	2,42	,39	2,17	2,66	,0924
A. robustus	2,79	,59	2,37	3,21	
combined sample	2,59	,51	2,36	2,81	

TABLE 6: Enamel thickness at lingual cusp (mm) in South African australopithecines

	Mean	SD	95% lower	95% upper	Prob. (2-tail)
A. africanus	2,32	,50	2,00	2,63	,0129*
A. robustus	2,89	,49	2,55	3,24	
combined sample	2,59	,513	2,36	2,81	

* indicates significane at P<0.05 level

The results reported here can be compared and contrasted to similar data for small samples of australopithecines and larger samples of extant hominoids provided by Grine and Martin (1988). Mean values for enamel cap areas in sectioned lower molars were 11,52 in *Pan* (n=8), 23,81 in *Gorilla* (n=8), 20,04 in *Pongo* (n=9), and 20,07 in *Homo* (n=6). Mean values for EDJ length were 17,83 in Pan (n=8), 26,03 in *Gorilla* (n=8), 19,46 in *Pongo* (n=9), and 15,22 in *Homo* (n=6). Average enamel thickness (c/e) of lower molars was 0,63 in *Pan*, 0,92 in *Gorilla*, 1,05 in *Pongo*, and 1,32 in *Homo*.

Grine and Martin (1988) were only able to section 4 australopithecine teeth through the mesial two cusps (Stw 184, Stw 402, KB 5223, SKX 21841). They report values for c, e and c/e for each specimen as follows:

Stw 284:	46,30	25,59	1,81
Stw 402:	38,67	21,69	1,78
KB 5223:	31,71	19,56	1,62
SKX 21841:	62,01	23,64	2,62

The relative enamel thickness values of 1, 81 and 1,78 for the two *A. africanus* specimens from Sterkfontein (Stw 284, Stw, 402) fall within the 95% confidence limits of the *A. africanus* sample reported here and beyond the 95% confidence limits of the *A. robustus* sample (Table 4); the value of 1.62 for the Kromdraai *A. robustus* specimen (KB 5223) is almost identical to the mean value for *A. africanus* reported here and lies outside the 95% confidence interval for *A. robustus;* and the value of 2,62 for the Swartkrans specimen (SKX 21841) is beyond the 95% confidence interval for *A. robustus* reported here.

These data also make it clear that relative enamel thickness is greater in both gracile and robust australopithecines than in any extant hominoid, including *Homo*.

As noted by the quotation cited at the beginning of this paper, a most useful measure of the amount of enamel on a tooth would be the total volume of the tissue expressed as a relative thickness by dividing the enamel volume by the surface area of the enamel/dentine junction over which it formed (Martin 1985). I have done this experiment

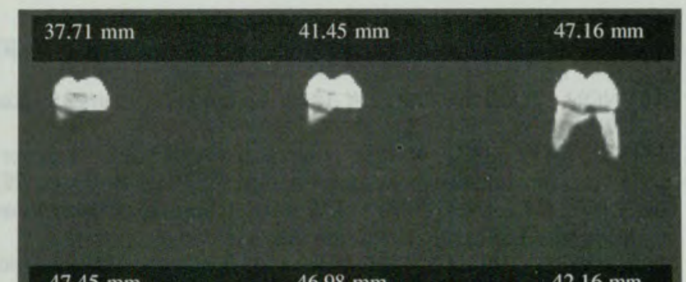

Figure 7. A sample of 9 contiguous 1mm CT scans of (out of a total of 20) SK 6 taken in the buccolingual plaine. Enamel cap area (mm^2) of each section is given.

on one specimen, the RM_2 of SK 6. Contiguous 1 mm thin CT slices were taken through the entire tooth in the buccolingual plane (Figure 7). The total enamel cap volume was calculated by summing the individual enamel cap section volumes (area of section x slice thickness). The total surface area of the enamel/dentine junction over which the enamel cap formed was calculated by summing the individual EDJ areas (EDJ length x slice thickness). The ratio of total enamel cap volume to enamel-dentine junction area for this specimen turns out to be 2,23 mm. The fact that the c/e ratio for a single CT section of this tooth is somewhat similar (2,43 mm; Table 1) gives us some hope that single CT slices (or sections) through the mesial cusps of hominid teeth may be reasonable first approximations of relative (or average) enamel thickness over the entire tooth.

CONCLUSIONS

Ultimately, a complete assessment of enamel thickness in early hominids will require further investigations and larger sample sizes. It is imperative to CT scan and archive as large a sample of gracile and robust australopithecines as possible in order to examine intra- and interspecific variation in enamel thickness of early hominids. CT scanning of relevant material, using methods described herein, can contribute to the resolution of these issues by making the previously hidden enamel dimensions more "visible" to investigators.

This study represents an important, albeit preliminary, first step in establishing a methodology for the non-invasive determination of enamel thickness in fossil hominids by computer tomography. It demonstrates the viability of the technique and the type of problem oriented approach that can be tackled using computed tomography in modern anthropological research (Conroy 1987; Conroy and Vannier 1984, 1985, 1986, 1987, 1988, 1991 a,b; Conroy *et al.* 1990).

Measurements derived from CT cannot, of course, be expected to have the same degree of precision as those taken directly from sectioned teeth; nevertheless, important insights into the functional morphology of early hominid teeth are still easily decipherable from the CT data. Given that the alternative to CT is the physical destruction of original hominid fossils, the slight loss in mensurational accuracy seems well worth the price.

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