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COMPUTED TOMOGRAPHY AND THE MEASUREMENT OF ENAMEL THICKNESS IN EXTANT HOMINOIDS: IMPLICATIONS FOR ITS PALAEONTOLOGICAL APPLICATION

by

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ABSTRACT

Isolated permanent lower molars of *Homo sapiens*, *Pan troglodytes* and *Gorilla gorilla* were imaged by computed tomography (CT) using a 1,5 mm thick section through the mesial cusps. The teeth were examined dry and immersed in water. Measurements of enamel thickness were made on enlargements of hard copy images. Following CT examination, the crowns were sectioned in the same plane, and the cut faces with maximum dentine content were micrographed for measurement using a scanning electron microscope (SEM). Enamel thickness measurements from the CT images were noticeably exaggerated compared to the ideal (sectioned) values, and the CT values for dry specimen images were even larger than those for wet specimen images. These results indicate that CT cannot be employed to measure enamel thickness with any degree of reliability in modern specimens. There is no close correspondence between the SEM and CT values; therefore, the latter cannot even be used to predict the actual values. Thus, the application of CT in the measurement of enamel thickness in fossils is rather dubious.

INTRODUCTION

Anthropologists have long recognized the importance of tooth enamel thickness in the analysis of Miocene hominoid fossils (e.g., Jolly 1970; Simons and Pilbeam 1972; Kay 1981; Martin 1985; Gantt 1986), and several recent studies have pointed to its significance in the interpretation of the early hominid fossil record (Beynon and Wood 1986, 1987; Grine and Martin 1988). Robinson (1956), who was the first and, until quite recently, the only worker to have published measurements of early hominid tooth enamel thickness, recorded maximum and minimum measurements for six naturally fractured *Paranthropus* molars from Swartkrans. He also claimed (1956: 21) that "*Australopithecus* does not appear to differ markedly in this respect," although no data was provided for that taxon. Based upon measurements of several broken teeth, Gantt (1986: 466) has claimed that both *Australopithecus* and *Paranthropus* possess "significantly" thicker enamel than any other hominoid, including modern humans. As noted by Grine and Martin (1988), however, the sources of Gantt's data are unclear, and Beynon and Wood (1986) have noted inconsistencies in his published values.

The first comparative analysis of enamel thickness in fossil hominid taxa was undertaken by Beynon and Wood (1986), who employed linear measurements of occlusal, cusp tip and lateral enamel in naturally fractured cheek-teeth attributed to *P. boisei* and "early" *Homo* (*H. habilis* and *H. erectus*) from eastern Africa. That study also represents the first attempt to obtain relative enamel thickness measurements from estimates of tooth size. They recorded that the size-corrected values for cusp tip and occlusal enamel in *P. boisei* were significantly larger than the corresponding values in their *Homo* sample. Beynon and Wood (1986), however, noted that their techniques of size correction were rather crude, and that measurements of naturally fractured enamel should be related to more accurate measures obtained from sectioned specimens. Grine and Martin (1988) obtained measurements of enamel thickness for sectioned permanent molars of *P. boisei*, *P. robustus* and *A. africanus*. As a result, they were able to provide the first reliable size-corrected (i.e., relative) thickness values for these taxa. Grine and Martin (1988) found that *A. africanus* has enamel of the same relative thickness as modern humans, while *Paranthropus* specimens possess relatively thicker enamel. That study, however, was constrained by very small fossil samples (two molars each of *A. africanus*, *P. robustus*, and *P. boisei*). Despite the fact that the technique employed by Grine and Martin (1988) resulted in the loss of only a 70µm thick section of tooth crown, it is unlikely that statistically adequate samples of Plio-Pleistocene hominid teeth will be available for sectioning until the numbers of available fossils that can be sampled have been increased substantially.

As one approach to increase sample size, Sperber (1985) used lateral radiographs to measure enamel thickness in unworn fossil hominid molars. Gantt (1977), however, had previously noted that measurements from x-rays cannot be considered accurate because they may vary by up to 50% from the true values obtained from thin sections of the same teeth. While Sperber (1985) recognized some of the limitations on accuracy imposed by this indirect method of measurement, he nevertheless concluded that *Paranthropus* molar enamel was generally thicker than that of *A. africanus*, which, in turn, exceeded modern human enamel thickness.

Within the last few years, computed tomography (CT) has become increasingly utilized as a noninvasive tool by which to investigate the internal structure of hominid fossils (Wind 1984; Wind and Zonneveld 1984; Conroy and Vannier 1985, 1987, 1991; Zonneveld and Wind 1985; Daegling 1989; Grine *et al.* 1989; Zonneveld *et al.* 1989; Daegling and Grine 1990, 1991; Floch-Prigent 1989; Conroy *et al.* 1990). Zonneveld and Wind (1985) recorded a maximum occlusal enamel thickness of 3,3 mm from a CT scan of a worn *P. robustus* M^2 from Kromdraai, and Zonneveld *et al.* (1989) recorded a maximum thickness of 2,6 mm from a parasaggital CT section through the M^2 of a *P. robustus* specimen from Swartkrans. Conroy and Vannier (1991) have recently used CT scanning to measure maximum enamel thickness in sections through the mesial cusps of lower molars from Sterkfontein and Swartkrans; they also have reconstructed enamel volume for some teeth.

Although CT has been employed successfully for the measurement of cortical bone thickness and area in modern and fossil specimens (Jungers and Minns 1979; Ruff and Leo 1986; Daegling 1989; Daegling and Grine 1990, 1991), its accuracy depends on a variety of factors such as specimen density, size and shape. To date, the precision with which tooth enamel thickness can be measured by CT has not been established for recent materials, let alone fossils. In view of the potential problems that can be encountered in the use of CT for quantification (Brooks and DiChiro 1976; McCullough 1977; Joseph 1981; Pullan *et al.* 1981; Ruff and Leo 1986; Daegling 1989), the present study was undertaken to investigate the efficacy of CT for the measurement of enamel thickness in modern hominoids as a guide to its possible palaeontological application.

MATERIALS AND METHODS

Isolated permanent lower molars of modern humans and African apes were chosen to compare enamel thickness measurements obtained from CT and mechanical sectioning. These samples were selected, not only because they display significant differences in enamel thickness (Martin 1985; Grine and Martin 1988), but also because they approximate the overall sizes of fossil hominid teeth. Ten unworn teeth of *Homo sapiens* (M_1=1, M_2=3, M_3=6), three unworn or slightly worn specimens of *Pan troglodytes* (M_1=1, M_2=2), and three unworn or slightly worn molars of *Gorilla gorilla* (M_1=3) were chosen for examination. The inclusion of worn teeth presents no difficulty, since the object of this study was to establish the correspondence between measurements obtained from CT and mechanical sectioning, rather than to provide pristine enamel thickness values for these taxa. Each crown was imaged first by CT, using an x-ray slice through the tips of the mesial cusps, and then after mechanical sectioning in the same plane. An unworn M^3 of *Homo sapiens* that was mechanically sectioned prior to CT examination was employed as a "standard" by which to establish the optimum window level and width settings for CT imaging.

The tips of the protoconid and metaconid on each tooth were marked in ink to facilitate alignment for CT and mechanical sectioning. For CT examination, the tooth roots were pushed firmly into a length of 3M strip caulking that was stuck to the base of a large plastic container (21 x 16,5 x 7 cm; Omega Barfel 2L.A346/2). This permitted each crown to be properly positioned with reference to the coronal and horizontal planes, and it enabled the teeth to be examined both in air (dry) and immersed in water (wet).

Specimens were examined immersed in water in order to minimize beam-hardening artifacts that result from the differential attenuation of heterogeneous x-ray beams (Brooks and DiChiro 1976; Sumner *et al.* 1985; Daegling 1989). Beam hardening in dense materials, such as dentine and enamel, results in beam attenuation that may not be strictly proportional to the thickness of the object being traversed. Its effect is accentuated when the difference between the attenuation coefficients of adjacent media is increased (Rao and Alfidi 1981). Modern CT scanners are calibrated so that the attenuation coefficient of air is -1,000 and that of water is zero; bone values vary from +500 to +2,000 (Ruff and Leo 1986). Although a clearer image of the outer margins of a tooth crown may be obtained through its immersion in water, specimens were also examined dry, since it may not be advisable to place fossils in water.

Specimens were examined in a GE model 9800 scanner, and each tooth was aligned independently in the gantry so that the laser alignment light passed across the ink spots on the cusp tips. The calibration of the the laser alignment system of the scanner used in this study is checked monthly so as to ensure that the CT section plane and the light beams are precisely aligned. Each CT image was generated using a 1,5 mm thick slice with a 4 second exposure at 170 MA and 120 kV; the bone reconstruction algorithm was used. A 13 cm field of view and a 2,75x magnification factor were employed. The teeth were examined dry, and then wet. The previously sectioned "standard" was used to determine the most precise window level and width settings by measuring the total buccolingual (BL) diameter of the image as well as the linear diameter of the enamel cap from the tips of the dentine horns to the tips of the cusps on the CRT display. Width and level settings may substantially effect the reliability of an image when objects approach the extremes of the Hounsfield scale, and high density objects are especially sensitive to window level variation because of the "point spread effect" (Joseph 1981; Ruff and Leo 1986). Thus, as has been aptly noted by Ruff and Leo

TABLE 1.

Buccolingual (BL) crown diameters recorded from wet CT images and SEM micrographs.

	N	$\overline{X}$	SD	SE	CV%	Obs. Range
Human sample						
CT	10	10,20	0,53	0,17	5,20	9,51-11,14
SEM	10	10,13	0,52	0,16	5,13	9,54-10,95
Ape sample						
CT	6	12,33	1,62	0,66	13,14	9,91-14,50
SEM	6	12,42	1,99	0,81	16,02	9,59-14,97

(1986) and Daegling (1989), the cleanest ("prettiest") CT image does not necessarily equate to the most accurate image. Window settings of 1500L and 4000W for wet specimens, and 1000L and 4000W for dry specimens* were determined to be the most reliable for accurate imaging by means of the previously sectioned "standard."

Hard copy images consisting of a 512^2 pixel matrix were obtained for each section at an enlargement of 2,75x to enable the image contours to be traced precisely in ink on a clear acetate sheet. Following Daegling (1989), each hard copy sheet included scale grids along the vertical and horizontal axes to control for possible hard copy image distortion, or "flattening." Each tracing was enlarged to a final magnification of 5,5x for measurement.

Following examination by CT, each crown was coated with a thin layer of epoxy (to prevent enamel spalling during sectioning), and sectioned using a Buehler Isomet with a 0,15 mm diamond wafering blade. The edge of the blade was positioned immediately distal to the ink marks on the cusp tips so that the mesial crown section would include the dentine horns. The mesial cut face was then ground and polished with 6 µm, 1µm and 0,25 µm diamond paste on a Buehler Microcloth to obtain the ideal, topography-free section with maximum dentine content (i.e., a section including the very tips of both dentine horns). The polished surface was lightly etched with 0,5% H_3PO_4 for 15 seconds to remove any smeared enamel, ultrasonicated in distilled water, air dried, mounted on an aluminum stub and coated with silver. These surfaces were micrographed at magnifications of between 7,5x and 11,5x using an AMRAY 1810D scanning electron microscope (SEM) at 10 or 20 kV in the secondary electron mode, and at 20 kV for the detection of backscattered electrons. Micrographs were recorded using Polaroid type 55 P/N film, and the positive contacts were employed for measurement.

Linear and area measurements on the CT tracings and micrographs were made using Bioquant System IV software interfaced with a SummaSketch II tablet. All values were recorded to the nearest 0,01 mm or 0,01 mm^2. As an additional means of control to ensure that the CT tracings were scaled accurately, the maximum BL crown diameter on the tracing was compared to the same diameter on the micrograph. These values were very similar for both the human and ape samples (Table 1), indicating that at least for this parameter, the CT images could be considered reliable indicators of crown size.

The BL diameter of each trigonid was also measured with vernier calipers prior to being sectioned; for the human sample this mean was 10,29 mm and for the ape sample it was 12,58 mm. In both instances, the mean obtained by direct crown measurement exceeds the BL average recorded from the micrographs (in the human sample the SEM value ranged from being 9,4% smaller to 2,0% larger than the direct measurement, and in the ape sample the SEM value ranged from being 5,6% smaller to 6,4% larger than the direct measurement). While the direct measurement of BL crown diameter might provide a reasonable rough guide by which to gauge the accuracy of a CT image, it cannot be considered wholly reliable or accurate, since the points that define the maximum breadth of the crown (or even part of the crown) may not lie in the plane that bisects the cusp tips.

Six measurements of enamel thickness were recorded on each tracing and micrograph (Figure 1). These measurements are as defined by Grine and Martin (1988). Measurement "a" is the total area of the crown section, measurement "b" is the area enclosed by the enamel-dentine junction (EDJ), measurement "c" is the area of the sectioned enamel cap, and measurement "e" is the perimeter length of the EDJ from the buccal to the lingual cervix. Measurement "k" is the linear thickness of enamel on the buccal side of the protoconid measured perpendicular to the EDJ from a point at which a line drawn parallel to one between the tips of the dentine horns and tangent to the lowest point of the EDJ between the cusps intersects the EDJ at the side of the crown. Measurement "l" is the linear thickness of the enamel on the lingual side of the metaconid as defined by the same method.

The proportional contribution of the enamel cap to the entire crown section may be expressed by (c/a) x 100. Overall relative enamel thickness may be expressed by the formula $[(c/e)/\sqrt{b}] \times 100$, and relative buccal and lingual enamel thicknesses may be expressed by (k/e) and (l/e) respectively (Grine and Martin 1988).

RESULTS

The proportional enamel cap areas determined from wet and dry CT images, and SEM micrographs are recorded in Table 2. The human values from SEM are similar to those recorded by Grine and Martin (1988) for a separate sample of six human lower molars ($\overline{X}$ = 42,92, SD = 5,68, Range = 34,0-48,8). The values derived from CT images are noticeably greater, and the wet CT image values are closer to the ideal sectioned values than the dry CT values. The wet CT values are, on average, about 34% larger than the true values, while the dry CT values are, on average, nearly 7% larger again. Individual values from wet CT images overestimated proportional enamel thickness by anywhere from about 16% to 47%, while individual dry CT image values were exaggerated by about 24% to 55%. The same pattern applies to the

* The window level values for dry and water immersed specimens reported in Grine (1991) were inadvertently transposed.

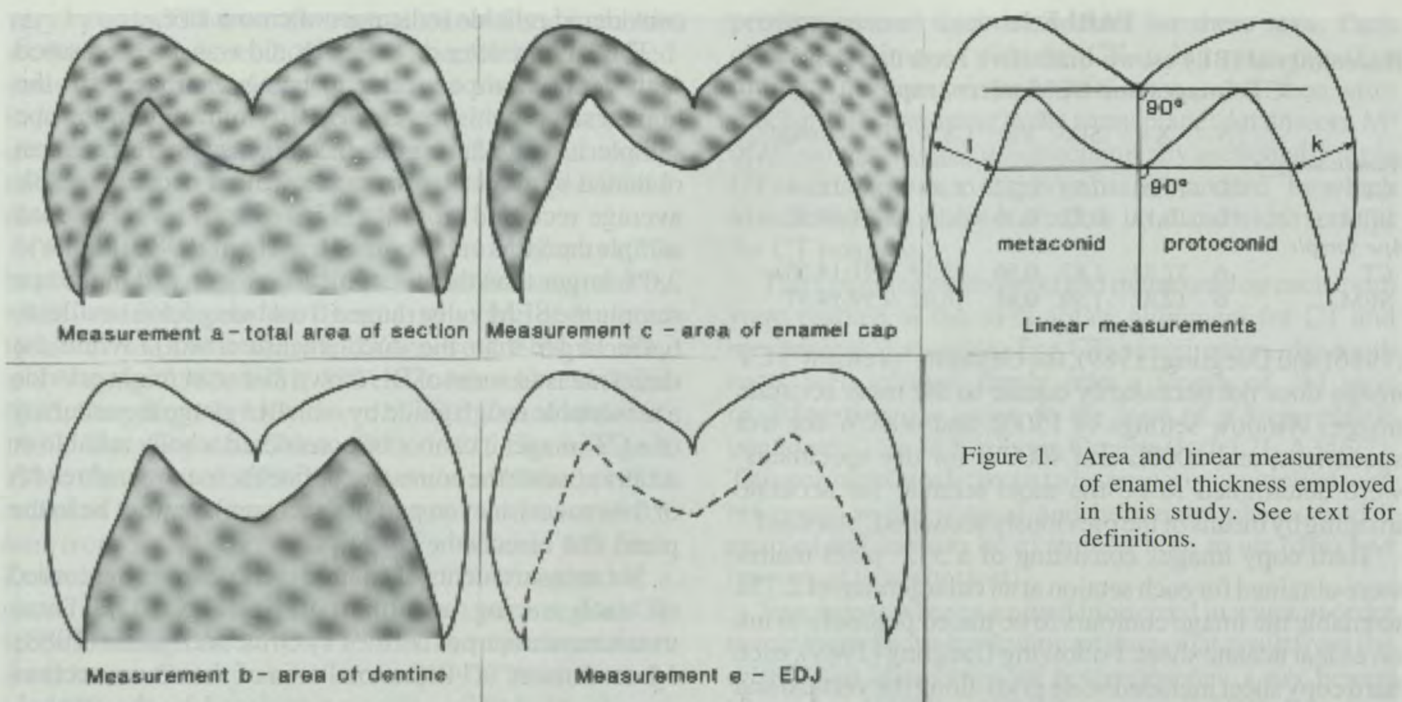

Figure 1. Area and linear measurements of enamel thickness employed in this study. See text for definitions.

TABLE 2.
Proportional enamel thickness [(c/a) x 100] values recorded from wet and dry CT images and SEM micrographs.

	N	$\bar{X}$	SD	SE	CV%	Obs. Range
Human sample						
CT wet	10	52,91	3,77	1,19	7,13	47,48- 59,97
CT dry	10	55,81	4,58	1,45	8,21	50,13- 61,62
SEM	10	39,77	3,63	1,15	9,13	32,47- 44,62
% Diff. CTw-SEM	10	133,70	11,28	3,57	33,47	115,76-146,55
% Diff. CTd-SEM	10	141,37	12,00	3,79	8,49	123,47-155,16
Ape sample						
CT wet	6	34,49	4,39	1,79	12,73	27,20- 39,74
CT dry	6	38,05	4,45	1,82	11,70	32,98- 43,22
SEM	6	24,61	4,37	1,78	17,76	18,85- 30,59
% Diff. CTw-SEM	6	141,53	13,67	5,58	32,92	124,81-163,69
% Diff. CTd-SEM	6	163,92	17,47	7,13	10,66	141,71-183,08

TABLE 3.
Relative enamel thickness [(c/e)/ √b x 100] values recorded from wet and dry CT images and SEM micrographs.

	N	$\bar{X}$	SD	SE	CV%	Obs. Range
Human sample						
CT wet	10	38,49	5,90	1,87	15,33	31,28- 50,37
CT dry	10	45,31	8,22	2,60	18,14	35,75- 54,31
SEM	10	21,10	3,08	0,97	14,60	15,20- 24,49
% Diff. CTw-SEM	10	185,79	32,61	10,31	17,55	139,39-238,38
% Diff. CTd-SEM	10	216,13	33,12	10,47	15,32	161,23-268,86
Ape sample						
CT wet	6	17,94	3,14	1,28	17,50	13,26- 22,60
CT dry	6	21,56	3,63	1,62	16,84	17,30- 26,07
SEM	6	10,83	2,30	0,94	21,24	7,94- 13,87
% Diff. CTw-SEM	6	167,51	19,37	7,91	11,56	146,48-202,88
% Diff. CTw-SEM	6	213,72	33,04	13,49	15,46	166,34-253,42

combined *Pan* and *Gorilla* sample, although here the discrepancy is even larger. In this sample, wet CT images resulted in proportional enamel thickness being overestimated by 25% to 64%, and dry CT images were exagerated by 42% to 83%.

The "standard" specimen provided a proportional enamel thickness value of 37,00 from the SEM micrograph; the corresponding wet and dry CT values were 42,96 and 45,92 respectively based on the most reliable settings. The wet CT value is 16% larger than the true SEM value, and the dry CT value is 7% greater than the wet CT value. Thus, despite the fact that the total BL diameter of the section and the linear enamel measurements were very nearly the same for the SEM and CT images, the latter still yielded noticeably greater values for proportional enamel thickness.

Relative enamel thickness values from SEM micrographs as well as wet and dry CT images are recorded in Table 3. The human sample values from SEM are comparable to those recorded by Grine and Martin (1988) for a different human sample ($\bar{X}$= 25,90, SD = 5,66, Range = 17,4-32,3). The CT images, however, yield gross overestimates of the ideal values for both thin and thickly enamelled teeth. Here too, the wet CT values are somewhat more accurate than those from dry CT images. Within the human sample, the wet CT values are, on average, 85% larger than the ideal values, while the dry CT values are about 21% greater again. In the ape sample, wet CT values are exaggerated by an average of 68%; dry CT values are 27% larger than the wet CT values.

The unpredictable nature of CT exaggeration is revealed by correlation analysis of individual relative enamel thickness [(c/e)/√b x 100] values obtained from wet CT images and SEM micrographs. In the combined ape+human sample R^2 = 0,39, for the human sample alone R^2 =0,03, and for the ape sample alone R^2 = 0,39.

TABLE 4.
Total section area (a), dentine area (b), enamel cap area (c), and enamel-dentine junction length (e) recorded from wet CT images and SEM micrographs.

	N	$\overline{X}$	SD	SE	CV%	Obs. Range
Total Section Area (a)						
Human sample						
CT Wet	10	55,90	8,22	2,60	14,70	39,0- 68,6
SEM	10	59,98	7,10	2,25	11,84	51,5- 73,0
% Diff.	10	93,24	9,57	3,03	10,26	74,1-102,6
Ape sample						
CT Wet	6	70,29	19,89	8,12	28,30	46,0- 90,5
SEM	6	76,78	25,75	10,51	33,54	48,3-108,4
% Diff.	6	92,93	8,21	3,35	8,83	84,8-105,2
Dentine Area (b)						
Human sample						
CT Wet	10	26,44	5,14	1,63	19,44	17,1- 35,7
SEM	10	36,15	4,93	1,56	13,64	28,5- 43,8
% Diff.	10	73,25	11,08	3,51	15,13	53,4- 88,5
Ape sample						
CT Wet	6	46,66	15,72	6,42	33,69	27,7- 65,9
SEM	6	58,55	21,99	8,98	37,56	33,5- 88,0
% Diff.	6	80,67	6,31	2,58	7,82	77,8- 91,2
Enamel Cap Area (c)						
Human sample						
CT Wet	10	29,46	4,12	1,30	13,99	21,9- 37,2
SEM	10	23,83	3,45	1,09	14,48	19,7- 29,9
% Diff.	10	124,27	13,26	4,19	10,67	106,3-145,6
Ape sample						
CT Wet	6	23,63	4,75	1,94	20,10	18,3- 30,7
SEM	6	18,23	4,49	1,83	24,63	13,1- 25,8
% Diff.	6	131,78	19,76	8,07	14,99	119,1-160,0
Enamel-Dentine Junction Length (e)						
Human sample						
CT Wet	10	15,11	1,54	0,49	10,19	12,0- 17,6
SEM	10	18,94	1,46	0,46	7,71	16,9- 21,5
% Diff.	10	79,96	7,48	2,37	9,35	66,3- 89,2
Ape sample						
CT Wet	6	19,93	3,23	1,32	16,21	15,4- 23,0
SEM	6	22,77	3,44	1,40	15,11	18,4- 27,4
% Diff.	6	87,44	11,02	4,50	12,60	83,4- 94,2

TABLE 5.
Linear enamel thickness recorded from wet CT images and SEM micrographs for lingual (l) and buccal (k) sides.

	N	$\overline{X}$	SD	SE	CV%	Obs. Range
Lingual (l)						
Human sample						
CT wet	10	1,58	0,20	0,06	12,66	1,20- 1,84
SEM	10	1,15	0,18	0,06	15,65	0,83- 1,40
% Diff.	10	138,51	16,97	5,37	12,25	109,02-162,50
Ape sample						
CT wet	6	1,40	0,08	0,03	5,71	1,25- 1,49
SEM	6	1,00	0,09	0,04	9,00	0,88- 1,13
% Diff.	6	141,42	16,14	6,59	11,41	116,82-159,09
Buccal (k)						
Human sample						
CT wet	10	2,02	0,29	0,09	14,36	1,55- 2,39
SEM	10	1,61	0,23	0,07	14,29	1,30- 2,00
% Diff.	10	125,99	13,26	4,19	10,52	113,95-157,45
Ape sample						
CT wet	6	1,40	0,26	0,11	18,57	1,03- 1,69
SEM	6	1,05	0,21	0,09	20,00	0,77- 1,29
% Diff.	6	133,40	6,68	2,72	5,01	126,80-144,94

TABLE 6.
Relative enamel thickness values recorded from wet CT images and SEM micrographs for buccal enamel (k/e) and lingual enamel (l/e).

	N	$\overline{X}$	SD	SE	CV%	Obs. Range
Relative Buccal (k/e)						
Human sample						
CT Wet	10	13,48	2,24	0,71	16,62	10,0- 16,7
SEM	10	8,48	0,87	0,28	10,26	6,9- 9,8
% Diff.	10	159,02	23,00	7,27	14,46	127,0-192,0
Ape sample						
CT Wet	6	7,05	0,83	0,34	11,77	5,5- 8,0
SEM	6	4,62	0,56	0,23	12,12	3,7- 5,3
% Diff.	6	152,83	8,60	3,51	5,63	144,0-169,3
Relative Lingual (l/e)						
Human sample						
CT Wet	10	10,62	2,39	0,76	22,50	8,0- 15,4
SEM	10	6,09	0,93	0,29	15,27	4,4- 7,3
% Diff.	10	175,18	31,04	9,82	17,72	124,1-237,1
Ape sample						
CT Wet	6	7,19	1,37	0,56	19,05	5,4- 9,3
SEM	6	4,42	0,50	0,20	11,31	4,1- 5,4
% Diff.	6	159,99	20,54	8,39	12,84	130,8-185,6

Thus, on the basis of the data for the combined ape and human sample, one could predict a CT value from an ideal value with only about 38% greater accuracy than if there was absolutely no relationship betwen these values.

The "standard" specimen yielded relative enamel thickness values of 20,09 for SEM, 24,23 for wet CT, and 28,42 for dry CT. While its CT values are closer to the ideal value than in the other specimens comprising the sample, the wet CT value is still 16% larger than the SEM value, and the dry CT value is some 7% larger still.

The individual area and linear measurements from which the proportional and relative thickness values were calculated are recorded in Table 4. The SEM and CT images yielded similar total section areas. The latter are slightly smaller on average in both the ape and human samples, being from about 74% to about 105% of the SEM values. Dentine area also tends to be smaller when measured from CT images, and in this instance the difference is somewhat greater than with the total section area. In the ape and human samples, CT image values are some 53% to 91% of the SEM image values for dentine area. Similarly, the length of the EDJ tends to be somewhat shorter on CT than on SEM images. While total section area measurements tend to be smaller on CT images, the dentine area and EDJ length values tend to be even smaller still, resulting in enamel cap areas that are exaggerated when compared to the true SEM measurements.

Linear enamel thickness measurements for the buccal and lingual sides of the crown as determined from CT images and SEM micrographs are recorded in Table 5. For these diameters, the human sample values are comparable to those recorded by Grine and Martin (1988) for a different human sample. The values determined from wet CT images are, on average, about 40% larger than the SEM values for the lingual side of the crown, and

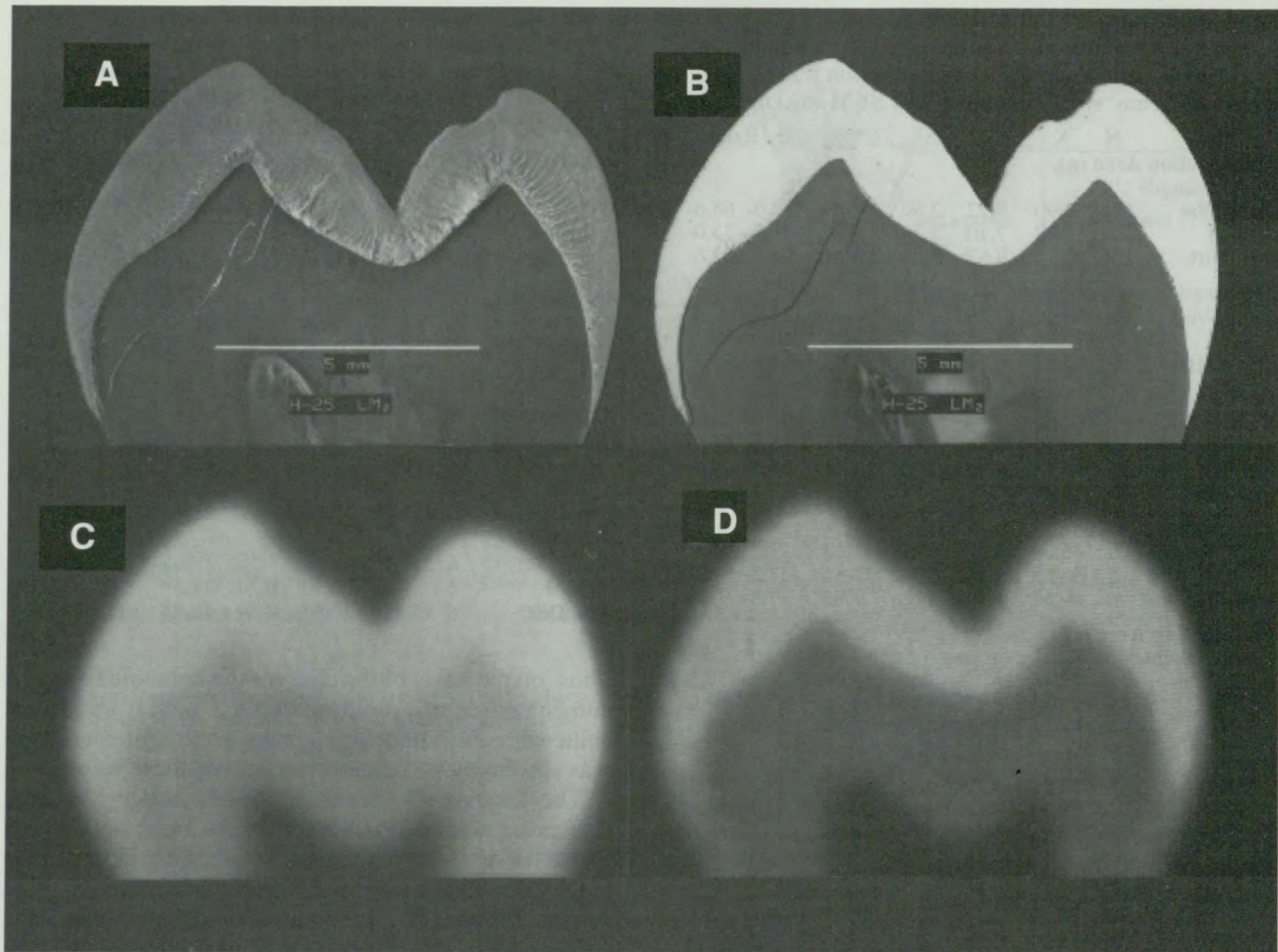

Figure 2. Comparison of scanning electron micrographs (A,B) of sectioned faces and CT images (C,D) through the mesial cusps of a LM_2 of *Homo sapiens*. Micrograph (A) is a secondary electron image at 20kV, (B) is a back scattered electron image at 20kV that highlights the enamel cap by atomic number contrast. The CT images are of a water immersed tooth; for image (C) L=900, W=4000; for image (D) L=1500, W=4000. Note the loss of the cervical margins in the CT images, and the difference in enamel thickness at different window level settings. In this instance, the shapes of the dentine horns are similar in the SEM and CT images.

about 30% larger for the buccal enamel. These percentage differences correspond roughly to the differences between wet CT image and ideal values for proportional enamel thickness (Table 2). The CT values range from being some 9% larger to about 62% larger than the real diameters. Here too, it is evident that there is not a close correspodence between CT and real values for individual specimens.

The relative thickness values for buccal and lingual enamel, as determined from the linear measurements are recorded in Table 6. As would be expected from the fact that the linear enamel thickness measurements tend to be exaggerated in CT images, while the EDJ length tends to be under-represented in these same images, the CT values for relative buccal and lingual enamel thickness are noticeably exaggerated. These values are on the order of 56% too large for buccal enamel, and 68% too large for lingual enamel. In both the ape and human samples, the discrepancy is greater with regard to the lingual side of the crown, where the enamel is thinner (Table 6; see also Grine and Martin 1988).

DISCUSSION AND CONCLUSIONS

Enamel thickness measurements by CT are noticeably exaggerated compared to the true values recorded from images that were obtained by mechanical sectioning. The values from CT sections that were recorded for water immersed teeth are somewhat closer to the ideal values than are those for CT images of crowns surrounded by air. This suggests that beam hardening artifacts (Brooks and DiChiro 1976; McCullough 1977; Rao and Alfidi 1981) have affected the dry specimen images more than those obtained for water-immersed teeth.

Beam hardening may also be a factor in the exaggeration of the CT images of water immersed teeth, although the similarity in the total BL diameters of the wet CT and SEM sections indicates that other factors may be primarily

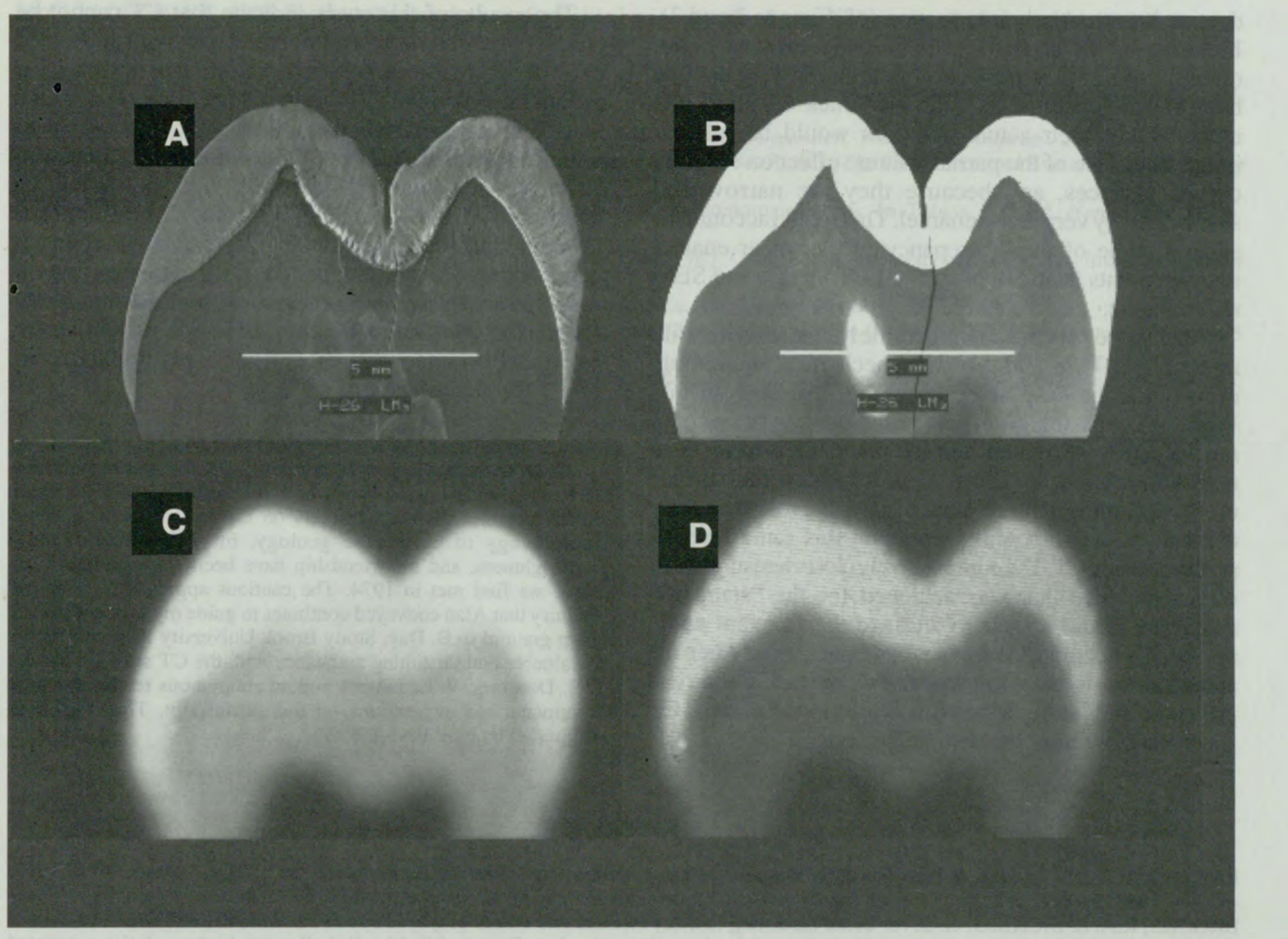

Figure 3. Comparison of scanning electron micrographs (A,B) of sectioned faces and CT images (C,D, through the mesial cusps of a LM_3 of *Homo sapiens*. Micrograph (A) is a secondary electron image at 20kV, (B) is a back scattered electron image at 20kV that highlights the enamel cap by atomic number contrast. The CT images are of a water immersed tooth; for image (C) L=900, W=4000; for image (D) L=1500, W=4000. Note the loss of the cervical margins in the CT images, and the difference in enamel thickness at different window level settings. Note also that in this specimen the dentine horns (especially the protoconid) have been blunted in the CT images because the CT section missed the tips of the horns.

responsible for the inaccuracies of the CT images. Partial volume effect would seem to be a likely factor, although the reconstruction algorithm may be at least partially responsible, since they tend to artificially enhance lucency near object borders (Joseph 1981).

The comparatively small size of the tooth crown and the density of enamel, coupled with the narrow apices of the dentine horns and the thin cervical enamel margins probably account for much of the distortion perceived in CT images (Figure 2 and 3).

The CT image is a planar (two dimensional) representation of a three dimensional (1,5 mm thick) slice. Thus, the pixels actually represent three dimensional voxels. Although the algorithm that is employed to produce the image assumes that each voxel uniformly attenuates the x-ray beam, this is almost certainly not the case where thin cervical margins and finely tapered dentine horns are concerned. This partial volume effect may be especially acute at object borders (Pullan *et al.* 1981). On CT scans, the thin, finely tapered cervical margins of the enamel cap, which are clearly seen in mechanically sectioned specimens, are not visualized. Rather, they take the form of blunt borders that are situated to the inside, rather than the outside of the level of the root margin as it approaches the crown (Figures 2 and 3). This has a rather profound effect on the measurement of relative enamel thickness – not only might the thickness of the enamel be exaggerated near the cervix, but the apparent inability to resolve the very thin enamel near the extremity of the margin also reduces the length of the EDJ and the total enclosed area, with a disporoprtionate loss of area under the EDJ.

The dentine horns in apes and humans are generally rather finely tapered at their apices, and they display a rather tight radius of curvature in the horizontal plane close to their tips. It is very possible to miss the tips of the dentine horns entirely in a section (cf. Figures 2 and 3). Indeed, most CT sections through cusp tips reveal blunt, obtusely angled dentine horn outlines. Even if the dentine horn tips are captured by a 1,5 mm thick CT slice, it is unlikely that their actual contours would be reliably imaged because of the partial volume effect on strongly curved surfaces, and because they are narrow and surrounded by very dense enamel. This would account for at least some of the discrepancy in the linear enamel measurements (k and l) taken from CT images and SEM micrographs.

Finally, the very tips of the dentine horns can be readily missed by 100 to 200 µm with mechanical sectioning, even when the cusp apices have been marked in ink. While it is possible to visualize the dentine horns on a mechanically sectioned surface when they have been narrowly missed, and then to polish/grind the surface until maximum dentine content is achieved, it is very difficult, if not impossible, to attain this same level of precision using CT. The comparatively close mensurational correspondence that was achieved for the "standard" specimen would appear to attest to the fact that while reasonably accurate CT images can be achieved when the actual dimensions are known (and when the CT slice can pass precisely along a previously sectioned plane), CT slices variably miss the dentine horn tips.

The results of this study indicate that CT cannot be employed to determine enamel thickness with the degree of reliability and accuracy that is required for comparative purposes. Although CT images may provide a rough visual impression of whether a tooth has thin enamel (e.g., a modern African ape) or thick enamel (e.g., a modern human), measurements of these images cannot be considered reliable. Certainly the use of such measurements in a comparative statistical analysis would lead to spurious conclusions. The employment of CT in palaeontology is potentially even more problematical because diagenetic factors that may affect the mineralization of fossil teeth can only but add to the factors that can confound the use of CT for quantification.

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