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Enamel thickness and the topography of the enamel–dentine junction in South African Plio-Pleistocene hominids with special reference to the Carabelli trait

This study explores the internal morphology of early hominid teeth using high-resolution computed tomography. Data on Carabelli feature size, enamel thickness, and the topography of the enamel–dentine junction are considered together in order to examine the relationship among these variables in the maxillary molars of gracile and robust australopithecines from South Africa. In particular, one aim is to investigate the degree to which Carabelli feature size influences enamel thickness in the plane of the mesial cusps. The results demonstrate that maxillary molars attributed to *Australopithecus africanus* from Sterkfontein, Taung and Makapansgat possess larger Carabelli features and thinner enamel along the lingual wall of the protocone than do specimens attributed to *Paranthropus robustus* from Swartkrans and Kromdraai. Distinct differences in the position of the Carabelli feature at the level of both the enamel-dentine junction and tooth crown surface between early hominid species may help explain the observed disparity in enamel thickness at that region of the tooth crown as well as offer clues to the functional role of Carabelli's cusp. As the size and position of the Carabelli feature affects the linear thickness of enamel at this one particular region of the tooth crown, future comparative studies focusing on taxa that possess moderate to strong development of the Carabelli complex should use the linear thickness of enamel taken close to the protoconal dentine horn or at the maximum projection of the Carabelli's cusp.

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Introduction

The aim of this study is to examine the internal architecture of early South African hominid maxillary molars relevant to an understanding of the relationship between the thickness of the enamel and the development of Carabelli's cusp at both the tooth crown surface and the enamel–dentine junction (EDJ). Paleoanthropologists have long recognized that the maxillary molars of australopithecines sometimes possess an additional cusp, or cuspule, on the lingual surface of the protocone (Robinson, 1956; Frisch, 1965; Tobias, 1967; Sperber, 1974; Wood & Engleman, 1988). The degree to which these protoconal cinguli, or Carabelli's cusps, are developed differs in a systematic manner between taxa: feature expression is stronger in *Australopithecus africanus* than in *Paranthropus robustus* (Sperber, 1974). Thus, the expression of the Carabelli trait as a prominent lingual cingulum in *A. africanus* in contrast with the lingual pit or absence of the trait in *P. robustus* serves to differentiate the two species (Figure 1). Despite its apparent

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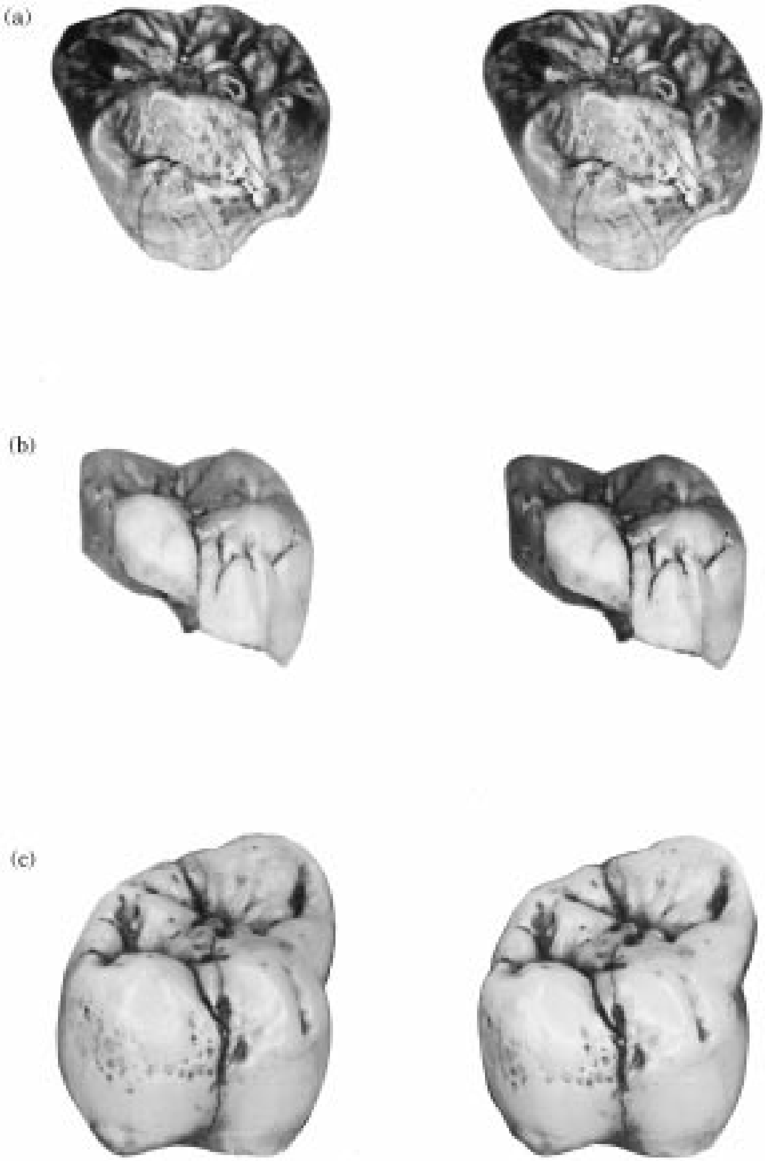

Figure 1. Stereophotographs of Carabelli cusp development. (a) Mesio-lingual view of Sts 37 (left M^3) attributed to *A. africanus* and showing strong development of the Carabelli feature in the form of a cingulum; mesial is to the left. (b) Lingual view of Sts 23 (right M^2) attributed to *A. africanus* with the Carabelli complex exhibiting a more cusp-like appearance; mesial is to the right. (c) Lingual view of SK 13 (right M^2) attributed to *P. robustus* and showing relatively weak development of the Carabelli complex; mesial is to the right.

usefulness as a taxonomically informative character, assessments of the degree of expression of the Carabelli trait have traditionally been confined to subjective, qualitative assessments, i.e., a pit, groove, bulge, or tubercle (e.g., Garn *et al.*, 1966; Wood & Engleman, 1988; Reid *et al.*, 1991). That is, until a recent study quantified the size of the

Carabelli feature in a large sample of early South African australopithecines ($n=65$) and demonstrated that, on average, Carabelli cusp sizes are greater for *A. africanus* than for *P. robustus* at each tooth position and increase from first to third maxillary molars in both groups (despite a large degree of variation for each molar) in contrast to the pattern in modern humans (Reid & van Reenan, 1995).

While Reid's & van Reenan's study is important for documenting differences in crown morphology between early hominid teeth, it is unable to address questions concerning the potential impact of Carabelli cusp size on measures of enamel thickness. From the data available at present, it is clear that *P. robustus* molars possess relatively more enamel overall and, in particular, thicker enamel along the lingual wall of the protocone which is the region of the crown where Carabelli's cusp occurs (e.g., Robinson, 1954; Grine & Martin, 1988; Conroy, 1991; Macho & Thackeray, 1992). Macho & Thackeray (1992) noted that the presence of a Carabelli's cusp may have exaggerated linear measurements of enamel thickness along the lingual wall of the protocone in these early hominid species. Given the lack of quantitative data on the Carabelli trait at that time, it was not noted to what extent, if any, both the size of this accessory feature and its position relative to the occlusal plane at the crown surface and EDJ impact on similarities and/or differences in enamel thickness between australopithecine species at that specific region of the enamel cap. Thus, an analysis of these two variables in a large sample of early hominid molars may not only shed light on previously observed disparities in enamel thickness but offer a possible explanation to supplement theories concerning the functional role of this accessory cusp.

Throughout the life of a tooth, the EDJ preserves the form of the basement membrane of the inner enamel epithelium and thus, it has been argued, may preserve features of an older genetic heritage (Butler, 1956; Korenhof, 1962, 1980). Therefore, valuable phylogenetic and taxonomic information can be obtained through comparative analyses of EDJ morphology among early hominid taxa. Differences in the topography of the EDJ and tooth crown surface have been documented in modern humans (Kraus, 1952; Butler, 1956, 1967; Kraus & Jordan, 1965; Sakai, 1967; Kimura *et al.*, 1977), Plio-Pleistocene hominids (Macho & Thackeray, 1993) and certain extant primates (Corruccini, 1987*a*,*b*; Corruccini & Holt, 1989). Few studies have sought to examine the internal morphology of molars, including the topography of the EDJ, in the region of Carabelli's cusp in early hominids. Studies of EDJ morphology at the region of the Carabelli feature in primates and modern humans demonstrate that the expression of an incomplete or complete lingual cingulum along the EDJ is not necessarily correlated with a cingulum or cusp at the tooth crown surface (Korenhof, 1982; Corruccini & Holt, 1989). To date, it is unknown whether the morphology of these accessory crown features present in South African hominid teeth are mimicked at the level of the EDJ.

Until recently, it has only been possible to examine the internal architecture of teeth, including the morphology of the EDJ, through either histological sections (e.g., Gantt, 1977; Martin, 1983; Grine & Martin, 1988; Macho, 1994) or by separating the enamel cap from the underlying dentine core (e.g. Kraus, 1952; Korenhof, 1960; Nager, 1960; Achermann, 1970; Sakai, 1967; Corruccini, 1987*a*); however, neither technique is recommended for investigations of large samples of rare and important fossil specimens. It is necessary, therefore, to use noninvasive methods such as plain-film radiography or computerized tomography (CT) to examine the topography of the EDJ in early hominid teeth. Simons & Pilbeam (1972) and Gantt (1977) both commented on the inefficacy of plain-film radiography for accurately determining the position of the EDJ. The unique ability of CT for safely visualizing the internal anatomy of precious fossil material in any plane of interest (e.g., Conroy & Vannier, 1984, 1987, 1991*a*,*b*; Conroy *et al.*, 1990; Conroy, 1991; Daegling & Grine, 1991; Macho & Thackeray, 1992, 1993; Spoor, 1993; Spoor *et al.*, 1994; Schwartz *et al.*, 1995; Thackeray & Schwartz, 1995; Schwartz & Conroy, 1996; Schwartz, 1997) makes it possible to study the relationship between enamel thickness, Carabelli feature size, and topography of the EDJ in the maxillary molars of South African Plio-Pleistocene hominids. This study therefore represents the first attempt at relating the morphology of the Carabelli feature with other aspects of the internal anatomy of the early hominid dentition. In particular, the goals of this study are to investigate the potential influence of both Carabelli feature size and its position along the lingual wall of the protocone on the distribution of enamel thickness across the mesial cusp region and to determine whether Carabelli features are similarly expressed at the level of the EDJ, or whether complete or incomplete lingual cingula are present at the EDJ and not at the tooth crown surface.

Material and methods

Total furrow lengths associated with the Carabelli feature are used as an objective measure of Carabelli cusp size thereby facilitating comparisons between taxa. Measurements of Carabelli furrow length and the expressivity of the Carabelli trait are related such that a greater furrow length implies a better developed Carabelli's cusp. All data on Carabelli furrow length are taken from Reid & van Reenan (1995) and are recorded from digitized, stereomicroscopic photographs of the palatal surfaces of the protocone (see Reid & van Reenan, 1995 for a more detailed explanation). Table 1 lists the specimens used to obtain data on the size of the Carabelli feature ($n=65$), as estimated by total furrow length. This subsample consists of permanent maxillary molars attributed to *A. africanus* from Sterkfontein and Makapansgat, and *P. robustus* from Swartkrans and Kromdraai. Also listed in Table 1 is the subsample of molars specimens (from Sterkfontein, Taung, Kromdraai and Swartkrans; $n=45$) used to obtain measurements of enamel thickness along the lingual wall of the protocone. The two separate subsamples of maxillary molars are not identical in composition, however, many teeth (bold type in Table 1; $n=21$) appear in both study samples. Many of the molars that preserve unworn Carabelli features possess moderately, or sometimes, heavily worn occlusal surfaces, and are therefore not used to measure enamel thickness. As a result, both pooled values of enamel thickness and Carabelli furrow length from each data set, as well as a subsample consisting of molars for which both variables are known, are used to make comparisons between species.

High-resolution CT is used to obtain cross-sectional images of the enamel cap in the plane of the mesial cusps in unworn or very slightly worn molars allowing measurements of enamel thickness to be recorded. Although an earlier attempt at recording enamel thickness in South African early hominid teeth employed CT as well (Macho & Thackeray, 1992), it is important to note that our study differs in two important ways. First, the sample used here is more inclusive than that used previously; only five molars attributed to *A. africanus* were included in the earlier study compared with the 26 molars of this species included in the present analysis thereby allowing for more detailed comparisons of the variation in enamel thickness at this region of the enamel cap among the molars of *A. africanus* and between teeth of this species and those of *P. robustus*. Second, Macho & Thackeray (1992) measured enamel thicknesses from hard copy CT images, a technique now known to be prone to mensurational inaccuracies related to the imprecision of locating the position of important measurement points such as the EDJ (see below).

A Philips Tomoscan SR7000, housed in the Johannesburg General Hospital, South Africa, was used throughout the investigation and the following scan parameters were kept constant throughout: 140 kVp tube voltage; 300 mAs (150 mA for 2 s). The thinnest possible slice thickness of 1·5 mm was used in conjunction with a table index of 1·0 mm (i.e., after each CT slice, the table was moved forward by 1·0 mm). This configuration resulted in an overlapping of successive CT scans. The incorporation of redundant data in this way serves to markedly reduce partial volume averaging artefacts. A field of view of 100 mm was used and in conjunction with a 512 × 512 display matrix yielding a pixel size of 0·19 mm in the imaging plane.

Each tooth was mounted to a sheet of perspex with plasticine and was situated with the cervical plane parallel to the perspex and perpendicular to the X-ray beam. In this position, the alignment light from the CT gantry was parallel to the plane of the mesial cusp tips. It is important to keep the region to be scanned perpendicular to the scan plane as obliquity can accentuate partial volume averaging thereby causing a reduction in image quality (Goodenough *et al*., 1981; Zonneveld & Vijverberg, 1984).

Both raw and image data were saved to an optical disk and downloaded to a Gyroview computer terminal (Philips Medical Systems, 1991) which was equipped with the Gyroview-HR Software package (ISG Technology Inc., version 1.5.6., 1994). This setup allowed easy manipulation of 2- and 3-d image reconstructions, including multiplanar reformatting and post-processing enhancements (the Gyroview workstation is intended for the use of surgeons and radiologists to accurately depict and analyze subtle morphological detail from CT data and, essentially, functions as a CT console enabling the investigator to perform the majority of the functions available with the scanner itself). The Gyroview package also has some advancements which are not readily accessible on the scanner. For instance, it incorporates a facility to calculate images (from the raw data) with an extended Hounsfield scale so that window levels and widths can be extended well beyond the normal scale (O H to +3095 H) thus avoiding overflow phenomena caused by fossilization or beam hardening artefacts.

Morphometric studies focusing on such structures as mandibular cross sections (Daegling, 1989, 1990; Demes *et al*., 1990; Daegling & Grine, 1991; Schwartz & Conroy, 1996), humeri (Senut, 1985), femora (Ohman *et al*., 1997) and labyrinthine structures (Spoor, 1993; Spoor *et al*., 1994; Spoor & Zonneveld, 1995) obtained from CT scans have been well accepted, while those on enamel thickness (Zonneveld & Wind, 1985; Conroy, 1991; Macho & Thackeray, 1992; Spoor *et al*., 1993; Conroy *et al*., 1996) have been questioned (see Grine, 1991). One of the main reasons for this is the apparent inability of CT to clearly depict tissue interfaces such as the EDJ; the contact region between adjacent tissues presents itself as a blurred boundary on CT images causing difficulty in the positioning of measuring points. Radiologists have developed methods for locating tissue interfaces by utilizing data on the local attenuation values on either side of the interface. On CT images, a tissue interface is always represented by a gradual, rather than a discontinuous, change in CT numbers. This gradual transition of attenuation values across an interface is attributable to the limitations of the CT scanner's spatial resolution, as determined by the X-ray beam

Table 1 List of South African early hominid maxillary molars used in the analysis as well as data on the length of the furrow associated with Carabelli's cusps, the thickness of enamel along the lingual wall of the protocone and the relative position of the Carabelli cusp at both the level of the EDJ and the tooth crown surface

Specimen	Tooth type	Carabelli furrow length	Enamel thickness	EDJ topography[1]	Carabelli position[2]
P. robustus:					
SK 13	RM1	1·85			
SK 17	RM1	0·91			
SK 47	RM1	6·60			
SK 89	LM1		2·6		
SK 102	LM1	0·74	2·5	Concavity at level of RP	CC above level of RP
SK 829	LM1		2·2		
SK 832	LM1	3·09	3·1	Large concavity at level of RP	CC above level of RP
SK 839	RM1		2·2		
SK 839	LM1		2·1	Concavity above level of RP	CC above level of RP
KB 5063	RM1		2·8		
KB 5383	RM1		2·4		
SK 13	RM2	2·78			
SK 14	LM2	1·31			
SK 16	LM2	7·70			
SK 47	RM2	2·03			
SK 47	LM2	6·17			
SK 98	LM2		3·1		
SK 826a	LM2	0·67			
SK 831a	LM2	0·69			
SK 856	RM2	4·55			
SKW 14129	RM2		3·0	Slight concavity above RP	Little topography
SK 11	LM3	0·86			
SK 31	RM3	2·86	3·1		
SK 41	LM3	10·3	3·4	Little topography	CC above level of RP
SK 105	LM3	2·97	3·1	Concavity at level of RP	CC above level of RP
SK 831a	LM3	3·52			
SK836	LM3		2·7		
SK 3975	LM3	13·1	3·1	Slight concavity above level of RP	CC above level of RP
SK 3977	RM3		3·3		
SKW 21841	RM3		2·9	Slight concavity below level of RP	CC above level of RP
TM 1517	RM3		3·3		
TM 1603	LM3	1·07	3·0		
KB 5222	LM3	1·32			
A. africanus:					
Sts 1	RM1	3·09			
Sts 1	LM1	3·91			
Sts 8	LM1	0·54			
Sts 24a	RM1	6·72	1·5	Slight concavity at level of RP	Small CC at level of RP
Sts 52a	RM1	0·64			
Sts 52a	LM1	0·51			
Sts 56	LM1	10·9			
Sts 57	LM1	3·48			
Stw 59	RMi	2·44			
Stw 156	LM1		2·2		
Stw 157	RM1		2·3		
Stw 252j	LM1	1·82	2·7		
Stw 402	RM1		1·7	Little topography	Little to no CC
Stw 447	RM1	1·84	2·1		

Table 1 ***Continued***

Specimen	Tooth type	Carabelli furrow length	Enamel thickness	EDJ topography^1	Carabelli position^2
A. africanus: (continued)					
Stw 450	RM1	11·2	2·8	Little topography	CC above level of RP
Taung	RM1		1·4		
Taung	LM1		1·6		
TM 1601e	LM1		1·5		
Sts 1	LM2	6·49		Slight concavity at level of RP	Small CC below level of RP
Sts 8	LM2	6·47	1·6	Slight concavity above level of RP	CC below level of RP
Sts 17	RM2	2·51			
Sts 22	LM2	8·03			
Sts 30	RM2	5·95			
Sts 32	LM2	2·37			
Sts 37	LM2	7·23	2·8		
Sts 52a	RM2	0·81			
Sts 52a	LM2	3·14			
Sts 56	LM2	7·53			
Sts 73	RM2	6·95			
Stw 183	LM2		2·4	Little topography	Little topography
Stw 188	RM2	9·57	2·1	Slight concavity above level of RP	Small CC above level of RP
Stw 252k	LM2	7·27	1·8	Slight concavity at level of RP	CC above level of RP
Stw 284	LM2		2·5	Slight concavity at level of RP	Small CC slightly above RP
Sts 8	LM3	10·7			
Sts 17	RM3	10·7			
Sts 31	LM3	3·55			
Sts 37	LM3	11·0		Large concavity below level of RP	Large CC below level of RP
Sts 52a	RM3	3·85			
Sts 52a	LM3	7·18			
Stw 2	RM3		1·9		
Stw 18c	RM3	9·70			
Stw 43	RM3	9·23			
Stw 53b	RM3	3·63			
Stw 53b	LM3	5·05			
Stw 92	LM3	13·9	2·4	Slight concavity at level of RP	CC below level of RP
Stw 128	RM3	13·2	1·7	Little topography	Small CC below level of RP
Stw 140	LM3	2·86			
Stw 179	LM3		2·1		
Stw 189	LM3	4·77	2·3	Little topography	CC below level of RP
Stw 204	LM3	2·22	2·3	Little topography	CC below level of RP
Stw 252h	RM3		2·7	Slight concavity below level of RP	CC below level of RP
Stw 252l	LM3	8·16	2·3	Concavity below level of RP	CC below level of RP
Stw 277	LM3	14·1	2·09	Little topography	CC below level of RP
TM 1511	RM3		2·8	Slight concavity below level of RP	CC below level of RP
MLD 28	LM3	2·92			
MLD 44	LM3	9·45			

Specimens in bold type include data on enamel thickness and Carabelli size. All measurements are in mm.

[1] Examined at the point where the reference line, R–R′ (see Figure 3), intersects the EDJ along the lingual wall of the protocone.

[2] Refers to the position of the Carabelli cusp along the lingual wall of the protocone at the tooth crown surface. Abbreviations: CC = Carabelli's cusp; RP = reference plane R–R′.

geometry. The precise position of tissue interfaces can be exactly determined and is calculated by analyzing the CT numbers of both tissues, through a technique known as the half maximum height (HMH) (Ulrich *et al.*, 1980; Baxter & Sorenson, 1981;

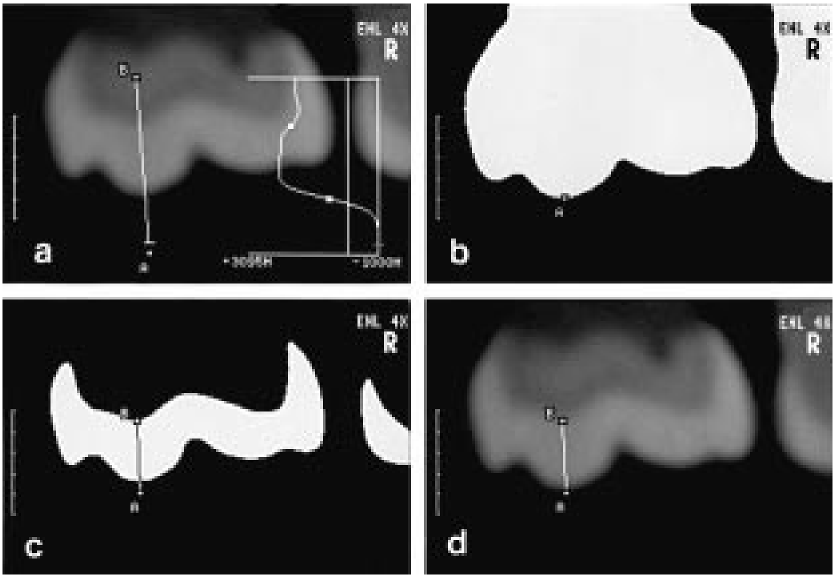

Figure 2. High-resolution CT scan of TM 1517 (*P. robustus*, right M^3) demonstrating the half-maximum height (HMH) technique to measure enamel thickness. (a) Mesiodistal CT scan with the line A–B drawn through the estimated position of the dentine horn and cusp tip. The graph of the CT number transition (in Hounsfield units) along line A–B appears on the right and shows the gradual change from dentine (about 2200 H), through enamel to air (–1000 H). The points indicate the midpoint of the CT number transitions associated with each interface and are referred to as the HMH CT values. (b) Visualizing the true position of the cusp tip to place measurement point A is accomplished by thresholding for the local HMH value, i.e., setting the window width to 1 H and the window level to the HMH value associated with the air–enamel CT number transition. (c) This procedure is repeated to set the measurement point B along the EDJ, this time using the HMH value associated with the enamel–dentine tissue interface. (d) the new line A–B represents the thickness of enamel at the cusp tip. Scale bar = 5 mm. (Photo courtesy of Fred Spoor.)

Seibert *et al.*, 1981; Eubanks *et al.*, 1985; Magnusson, 1987; Spoor, 1993; Spoor & Zonneveld, 1995; Spoor *et al.*, 1993; Ohman *et al.*, 1997). Moreover, experimental studies have shown that objects larger than 1·0 mm can be measured with an error range of ± 0·1 mm; objects smaller than 1·0 mm are overestimated owing to the limited spatial resolution of the scanner (Spoor, 1993; Spoor & Zonneveld, 1995; Spoor *et al.*, 1993). HMH CT values have been used to test the accuracy of CT-based measurements for quantifying the dimensions of the spinal cord and related structures (Seibert *et al.*, 1981; Eubanks *et al.*, 1985), enamel thickness in the molars of modern humans and certain fossil mammals (Spoor *et al.*, 1993), and labyrinthine structures of extant primates (Spoor, 1993; Spoor & Zonneveld, 1995). Results from these studies provide strong evidence for the efficacy of HMH CT values for accurately determining the precise position of tissue interfaces, thereby allowing accurate measurements to be recorded.

HMH CT numbers are used to measure enamel thickness in this study. Cross-sectional CT images in the plane of the mesial cusps are generated according to the procedures outlined above. For illustrative purposes, Figure 2 shows a mesio-distal CT image through a fossil hominid maxillary molar. The line A–B is drawn through the estimated position where enamel thickness is to be measured (in this instance, across the cusp tip) and the CT console automatically generates a CT number profile (pictured on the right of the image) corresponding to that line. The CT number profile, expressed in Hounsfield units, depicts the changes in density traveling along the line from air (point A), through the enamel cap, across the EDJ, and into the dentine core (point B). The length of the number profile moving from one tissue into another is proportional to differences in tissue density. For instance, the slope corresponding to the air–enamel transition is longer than that for the enamel–dentine transition as the difference between density values for air and enamel is greater than that between enamel and dentine. The midpoint along each slope in the profile is the HMH CT number [Figure 2(a)]. Though the boundary corresponding to the interface on the CT image is blurred, its exact position can be located along the slope of the CT number profile by thresholding (i.e., level-slicing) for the HMH CT number, which is achieved by setting the window width to 1 H and the window level to the appropriate HMH CT value. By doing so, the interface is depicted as a black–white transition thereby allowing the easy placement of measurement point A on the pixel corresponding to the true position of the cusp tip [Figure 2(b)]. This process is then repeated to position the measurement point B along the EDJ [Figure 2(c)]. The repositioned line A–B now corresponds to the thickness of enamel at that particular region of the tooth crown [Figure 2(d)].

Earlier investigations into the internal morphology of teeth using high-resolution CT relied on hard copy outputs of enamel cap cross sections to record measurements of enamel thickness (Macho & Thackeray, 1992), or image analysis programs that compress the 12-bit CT number scale (4096 values) to 8 bits (256 values) by lumping the CT numbers for each grey scale, thereby markedly reducing resolution (Conroy, 1991). Relying on measurements derived from hard copy images is not advisable since it is only possible to threshold for one tissue interface for any given hard copy image. While one interface (e.g., the EDJ) may be accurately resolved by thresholding for the appropriate HMH CT value, it is unlikely that the remaining interface (in this case, the air–enamel transition) will be imaged at the proper HMH CT value [see Figure 2(c)]. This problem is especially pronounced in CT analyses of fossil teeth due to the large disparity in HMH CT values associated with the two relevant tissue boundaries. Incorrectly resolved tissue interfaces can translate into measurement errors which exceed 1·0 mm (Spoor *et al.*, 1993). Thus, the magnitude of error resulting from analysis of hard copy images is too great given the range of enamel thickness present in hominoid and hominid teeth.

For the purposes of this study, measurements of enamel thickness are taken along the lingual wall of the protocone and are recorded relative to the reference plane R–R′ drawn parallel to the buccal and lingual cervical margins and tangential to the most inferior extent of the EDJ in the occlusal basin. The intersection of the reference plane and the EDJ on the lingual slope of the protocone defines the point where enamel thickness measurements are recorded (Figure 3). As this is the same methodology used by Macho & Thackeray (1992), it enables us to determine whether the presence of a Carabelli's cusp affects observed differences in enamel thickness between taxa and, ultimately, whether this is the optimum point for measuring the linear thickness of enamel at this region of the tooth crown. All linear measurements are recorded directly from the Gyroview workstation, not hard copy images, using the HMH technique outlined above.

Assessments of the topography of the EDJ and outer enamel surface are made by generating line drawings from CT images of the enamel caps. Given the problems associated

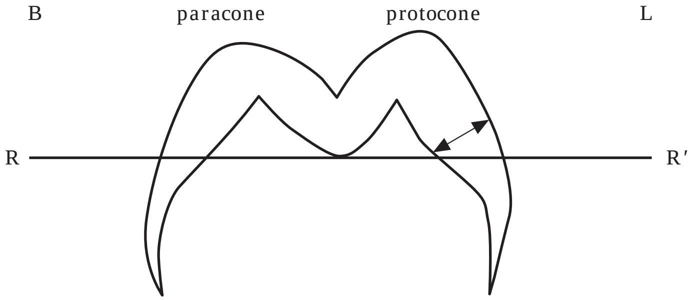

Figure 3. Schematic drawing of a CT-generated cross section of a maxillary molar. The intersection of the reference plane (R–R′) with the lingual slope of the EDJ defines the point at which enamel thickness measurements are recorded (arrow). B = buccal, L = lingual.

with images thresholded to depict only one interface accurately, the line drawings of the enamel cap used here are made using two different thresholds, one for the EDJ and one for the air–enamel interface. This is the only way to accurately portray the position of both boundaries in CT images and therefore the only way of obtaining images of the true extent of the enamel cap with maximum accuracy. In this way, the topography of the EDJ and outer enamel surface in the region of the Carabelli's cusp can be visualized simultaneously allowing us to determine the positional relationship of the reference line and the Carabelli feature at both the EDJ and tooth crown surface.

It is important to note that estimates of Carabelli furrow length record the extent of this feature predominantly in the mesiodistal plane while enamel thickness is recorded in the bucco-lingual plane. It may therefore seem inappropriate to compare these seemingly dissimilar data. Additionally, many of the hominid teeth used in this analysis possess Carabelli features that do not lie completely in the plane of the mesial cusps. As such, it is possible that a buccolingual CT scan in the plane corresponding to the tips of the paracone and protocone will not incorporate the full extent of this feature. As the main goal of this study is to determine the impact of Carabelli cusp size and position on measurements of enamel thickness, which by convention is recorded in the plane of the paracone and protocone, it is appropriate to consider the extent of the Carabelli feature occurring in this plane only, even though the fair portion of the accessory caspule may lie in a plane either mesial or distal to the one analyzed here.

Results

Table 1 lists the length of the Carabelli furrow, the thickness of enamel along the lingual wall of the protocone, the topography of the EDJ and the position of the Carabelli feature at the tooth crown surface for each specimen. For each tooth category, descriptive statistics of Carabelli furrow length and enamel thickness for each taxon are listed in Table 2. For both early hominid species, variation in Carabelli feature size is greater than for measurements of enamel thickness. It is interesting to note that variation in enamel thickness decreases posteriorly along the molar series in each species while the variation associated with the size of the Carabelli feature increases posteriorly most notably in molars of *P. robustus*. Mean values for Carabelli furrow length are greater in *A. africanus* at each tooth position. Carabelli feature size increases distally along the tooth row in both taxa, although *P. robustus* molars are characterized by smaller increases between

Table 2 **Descriptive statistics for Carabelli cusp size and enamel thickness along the lingual wall of the protocone in maxillary molars of South African australopithecines. All measurements are in mm**

		Carabelli size				Enamel thickness			
		n	Mean	S.D.	Range	*n*	Mean	S.D.	Range
A. Total sample:									
P. robustus	M^1	5	2·64	2·40	0·74–6·60	8	2·5	0·3	2·1–3·1
	M^2	8	3·24	2·64	0·67–7·70	2	3·1	—	3·0–3·1
	M^3	8	4·50	4·61	0·86–13·1	9	3·1	0·2	2·7–3·4
A. africanus	M^1	12	3·92	3·76	0·51–11·2	10	2·0	0·5	1·4–2·8
	M^2	13	5·72	2·63	0·81–9·57	6	2·2	0·5	1·6–2·8
	M^3	19	7·69	4·01	2·22–14·1	10	2·3	0·3	1·7–2·8
B. Subsample of molars with both variables:									
P. robustus	M^1	2	1·92	—	0·74–3·09	2	2·8	—	2·5–3·1
	M^2	0	—	—	—	0	—	—	—
	M^3	5	6·06	5·30	1·07–13·1	5	3·1	0·2	3·0–3·4
A. africanus	M^1	4	5·40	4·50	1·82–11·2	4	2·3	0·6	1·5–2·8
	M^2	4	7·64	1·34	6·47–9·57	4	2·1	0·5	1·6–2·8
	M^3	6	9·39	5·12	2·22–14·1	6	2·2	0·3	1·7–2·4

adjacent molar types. To state that Carabelli size increases towards M^3 may seem inappropriate as this is based on mean values for each molar position, each of which is associated with quite a large degree of variation. However, this overall trend is borne out by data for an *A. africanus* specimen (Sts 8) which preserves intact Carabelli features on all three molars: values for furrow length increase from M^1 (0·55 mm) to M^2 (6·47 mm) to M^3 (10·7 mm).

On average, *P. robustus* specimens possess thicker enamel at the site of the Carabelli feature, i.e., on the lingual wall of the protocone, than their gracile counterparts at each tooth position with the most marked disparity occurring in M^2 and M^3. *P. robustus* exhibits a substantial increase in enamel thickness from M^1 to M$^{2/3}$ whereas *A. africanus* molars remain fairly constant for this trait (Table 2; Figure 4).

When an analysis of molars where both Carabelli feature size and enamel thickness are known is performed, it is evident that, on average, Carabelli size continues to show an increase towards the posterior molars in both taxa, though the ranges of variation are somewhat smaller than that for the total sample (Table 2). Data on enamel thickness are difficult to interpret as samples are very small, especially for *P. robustus*, although both species seem to exhibit the same trends as in the analysis of pooled samples.

Ideally, an examination of the correlation between enamel thickness and the degree of Carabelli cusp development is desirable; this comparison would be especially informative on those specimens where both variables are available so that the covariation can be explored directly instead of using mean values from pooled samples. Results based on correlations would be suspect given the small samples for each molar category, and non-significance would generally be expected; for six *A. africanus* M^{3}s and five *P. robustus* M^{3}s, r values would have to be at least 0·900 and 0·980, respectively, to be statistically significant.[1] The possibility of

[1] M^1 and M^2 of *A. africanus* have low positive correlations (r=0·11 and 0·14, respectively) which become negative for M^3 (r= − 0·48). As in *A. africanus*, M^{3}s of *P. robustus* exhibits the highest correlation but has the opposite sign (r=0·55). Results for the anterior molars of this taxon remain unknown as too few teeth are present.

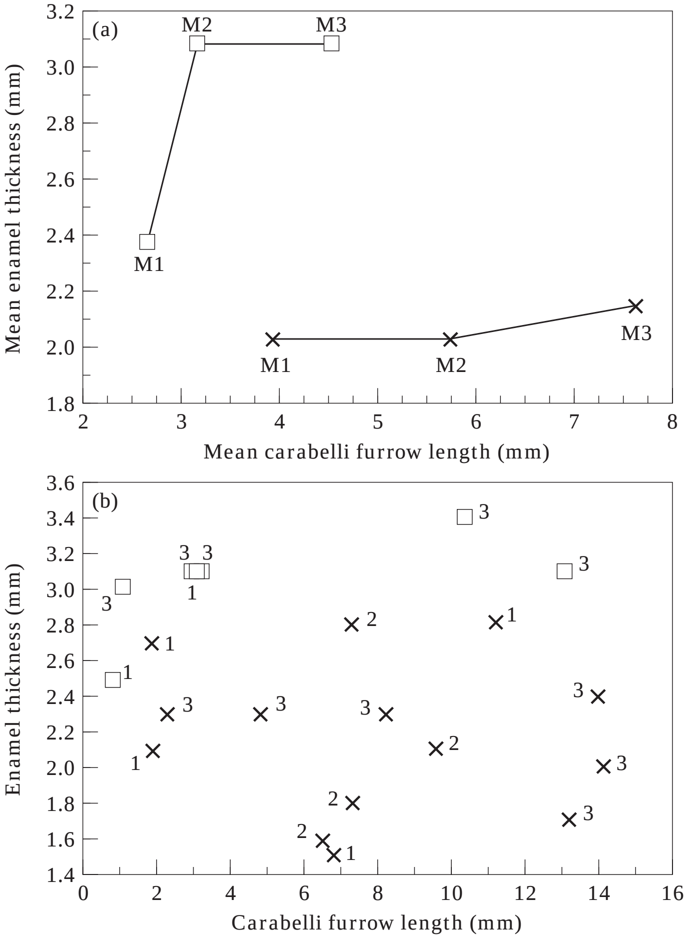

Figure 4. (a) Bivariate plot of mean Carabelli feature size, as estimated by Carabelli furrow length, versus the mean linear thickness of enamel at the lingual wall of the protocone for maxillary molars of South African Plio-Pleistocene australopithecines. Error bars are excluded for clarity. (b) Bivariate plot of Carabelli furrow length (CFL) and enamel thickness (ET) by tooth type for the subsample of molars (see text) attributed to *A. africanus* and *P. robustus*. $1 = M^1$, $2 = M^2$, $3 = M^3$. *A. africanus* molars are depicted by an ‘‘×’’ while *P. robustus* molars are open squares.

some correlation pattern within each tooth category existing between the two variables can be investigated by plotting all of the individual teeth for which these parameters are known [Figure 4(b)]. From the plot it seems that no clearly discernible pattern is present (aside from *A. africanus* molars possessing thinner enamel) when separated by tooth type with the exception that variation in Carabelli feature size seems to be greatest in M^3. It should be borne in mind, however, that results based on each tooth category separately should be treated cautiously as samples sizes are small at best.

The results for the topography of the EDJ and tooth crown surface, and their position relative to the reference line, at the site of the Carabelli feature are included in Table 1. In the area of this accessory cusp(ule), the EDJ exhibited either: (1) no apparent topography; (2) a slight depression (concavity) at the level of the EDJ directed towards the pulp cavity; or (3) a large concavity at the level of the EDJ. A concavity at the level of the EDJ is usually associated with a slight to large tubercle situated just cervically along the EDJ (see Figure 5). The tooth crown surface exhibited either little to no topography or a tubercle associated with the Carabelli cusp. Specimens belonging to both early hominid taxa exhibit each of the aforementioned topographies, although the majority of the *P. robustus* specimens possess a slightly deeper concavity of the EDJ at the level of the EDJ associated with the Carabelli feature (Table 1; Figure 5).

Discussion

Korenhof (1982) suggested that the topography of the EDJ is not necessarily correlated with the topography of the tooth crown in modern human teeth. In other words, features expressed at the EDJ may not be similarly expressed at the tooth crown. While the size of the Carabelli feature has served as a taxonomic marker in early hominid systematics, previous studies have been unable to assess whether the Carabelli feature is also expressed at the EDJ in early hominid maxillary molars. Hominid dental specimens with large Carabelli features at the tooth crown surface in the plane of the mesial cusps are not always characterized by large protrusions, or tubercles, at the EDJ in the same plane (see Table 1). Likewise, early hominid maxillary molars with small Carabelli features on the tooth crown in the plane of the mesial cusps can also possess very prominent concavities or cingula at the level of the EDJ.

Macho & Thackeray (1992) found that the enamel along the lingual wall of the protocone is relatively thicker than that along the buccal wall of the paracone for all South African hominid specimens and that this may represent some functional response to increased loading on the lingual cusps of maxillary molars. They also note that this relationship could be an artefact of the presence of Carabelli cusps, thereby inflating measures of enamel thickness in all early hominid specimens at that region of the enamel cap. Since *A. africanus* maxillary molars possess much larger Carabelli features at all tooth positions, they should also possess thicker enamel at that region of the enamel cap. For each tooth position, however, *A. africanus* possesses markedly thinner enamel than *P. robustus* along the lingual wall of the protocone, especially in M^2 and M^3 (see Figure 4). Thus, the pattern is opposite to what one might expect given knowledge of Carabelli feature size indicating that functional and developmental mechanisms, or the topography of the enamel cap relative to the point at which measurements of enamel thickness are taken, may provide additional information to help explain the differential morphology observed in this study.

Several factors might account for the presence of thicker enamel on the lingual wall of maxillary molars in robust australopithecines. The relatively thicker enamel at the site of the Carabelli feature may be a result of developmental differences in crown formation between the two hominid groups. Robust australopithecines, although larger-crowned and thicker-enamelled, seem to develop their permanent tooth crowns in a shorter period of time than gracile australopithecines and *Homo* (Beynon & Wood, 1987; Beynon & Dean, 1988). This is due to two main factors: (1) a large daily incremental rate; and (2) a fast enamel-extension rate. These two mechanisms acting in concert could result in thicker enamel along the walls of the robust australopithecine teeth. One possible reason for an increase in enamel thickness in this particular area of the tooth crown is to withstand enhanced crushing and grinding activity in the robust forms (Grine, 1981). Interpretations of enamel thickness within a developmental context are difficult,

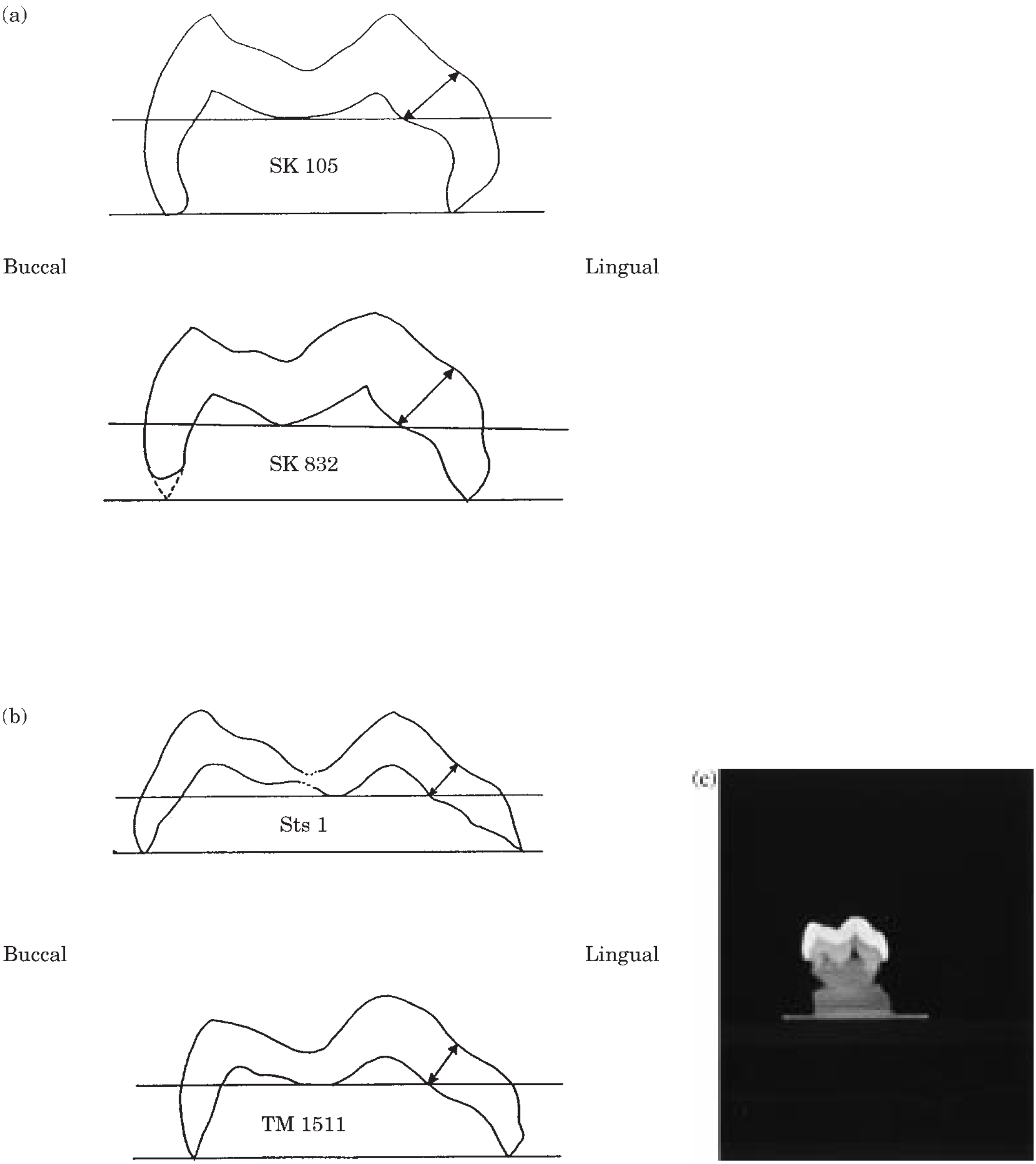

Figure 5. Enamel cap profiles across the mesial cusp region in *P. robustus* and *A. africanus* maxillary molars. Arrows indicate the position at which linear measurements of enamel thickness are taken along the lingual wall of the protocone. (a) Profiles for two representative robust australopithecine maxillary molars: SK 105 (left M^3) and SK 832 (left M^1). Note the position of the Carabelli feature on the tooth crown surface and its associated concavity (and tubercle) at the EDJ above the level of the reference plane. (b) Profiles for two representative gracile australopithecine maxillary molars: Sts 1 (left M^2) and TM 1511 (right M^3). Note the presence of the Carabelli feature on the tooth crown surface as well as its associated topography along the EDJ at or below the level of the reference plane. Lingual is to the right on all profiles. (c) For comparison with Figure 5(a), a bucco-lingual CT scan through the plane of the mesial cusps of SK 832 (left M^1).

however, given the likelihood that many combinations of developmental events (including not only differences in the secretory *rate* but differences in the secretory *period* as well) contribute to increases in enamel thickness along with the possibility that each combination differs between taxa.

It is clear that in some complicated way developmental factors account for the disparities in enamel thickness at the site of the Carabelli feature. However, given the point at which enamel thickness was recorded in this study, it is also conceivable that: (1) the topography of the EDJ in the region of the Carabelli cusp; and/or (2) the position of the Carabelli feature along the lingual slope of the protocone, may differ in a systematic manner between hominid groups and thus account for the disparity in enamel thickness between the two australopithecine species analyzed here.

Based on the results of this study, there seems to be no clear relationship between the size of the Carabelli feature, as estimated by Carabelli furrow length, and the topography of the EDJ directly corresponding to that region of the tooth crown. That is, large Carabelli features at the crown surface are not always indicative of prominent cingula at the EDJ in the plane of the mesial cusps, nor does a lack of cingula at the crown surface preclude the possibility of a distinct concavity at the EDJ in the same plane. What may be important is the relative positions of Carabelli features at the crown surface and EDJ to one another and relative to the occlusal surface. Given the methodology used by Macho & Thackeray (1992) and in this study, measurements of enamel thickness will be markedly increased if: (1) a noticeable Carabelli feature is present at the tooth crown surface at or slightly above (i.e., occlusal to) the level of the reference plane; (2) a noticeable concavity is present at the level of the EDJ at or slightly above the level of the reference plane; or (3) a large or small Carabelli feature occurs in conjunction with a concavity of the EDJ at or slightly above the level of the reference plane. The majority of the *P. robustus* maxillary molars exhibit a slight to large concavity of the EDJ at or above the reference line (six of eight molars; 75·0%) in association with a noticeable Carabelli feature at or slightly above the level of the reference plane (seven of eight molars; 87·5%) [Table 1; Figure 5(a)]. On the other hand, half of the *A. africanus* molar sample exhibit a concavity of the EDJ either at or below (i.e., cervical to) the level of the reference plane (nine of 18 molars; 50·0%) while the majority possess a Carabelli feature on the tooth crown surface positioned cervical to the reference plane (12 of 18 molars; 66·7%) [Table 1; Figure 5(b)]. Therefore, the more occlusally positioned Carabelli feature both at the crown surface and the EDJ in *P. robustus* results in the full thickness of this accessory cusp being incorporated into the linear measurement of enamel thickness recorded along the lingual wall of the protocone [see arrows in Figure 5(a)]. Gracile australopithecines, on the other hand, tend to exhibit more cervically positioned Carabelli features at both the level of the EDJ and tooth crown surface. This differential organization of the enamel cap in the region of the Carabelli feature between the two early hominid groups would seem to offer a possible explanation, or at the very least, supplement pre-existing mechanisms to explain differences in enamel thickness at one particular region of the enamel cap as defined here and in an earlier study (Macho & Thackeray, 1992).

It has been suggested that the presence of accessory crown features may serve the function of increasing molar surface area in microdontic populations (Haeussler *et al.*, 1989). In an earlier study on a sample of extant southern Africans, it was shown that molar size, as estimated by crown base area, and the degree of expressivity of the Carabelli feature are directly correlated

(Reid *et al.*, 1991). The data presented in Reid & van Reenan (1995) and here suggest that the smaller molars of *A. africanus* (relative to *P. robustus*) are characterized by larger Carabelli features, and lend support to the results obtained by Haeussler *et al.* (1989). Thus, the size of the Carabelli feature may have been increased in the lineage leading to *A. africanus* through selective pressures relating to some functional role. In fact, Tobias (1967) has argued that the reduced Carabelli feature in the robust australopithecines represents a more advanced stage while the gracile australopithecines, with their larger lingual cingula, exhibit the more primitive stage in an overall trend towards reduction of the lingual cingulum. However, the presence of several different EDJ topographies in the region of Carabelli's cusp in both robust and gracile australopithecines may suggest that little phylogenetic information is contained in the morphology of this one particular region within teeth.

Functional explanations have also been offered to explain the presence and expressivity of accessory cuspules in modern human populations. The occurrence of certain tubercles on the tooth crown has been interpreted as providing additional enamel bulk in areas of early attrition (Townsend *et al.*, 1986, 1989; Macho & Moggi Cecchi, 1992). It is conceivable that the Carabelli trait became fixed in populations of large-toothed early hominids where high masticatory stresses and concomitant heavy wear necessitated additional enamel bulk. Given that human molar attrition is characterized by a helicoidal pattern of wear, where maxillary molars display a lingual slope of wear anteriorly and a buccal slope posteriorly (Tobias, 1980, 1991; Ward, 1981; Osborn, 1982; Richards & Brown, 1986; Smith, 1986), it might be expected that Carabelli cusps would be larger and more protrusive in the anterior-most molars. This would especially hold true for molars of *P. robustus* as the majority of *A. africanus* specimens do not seem to exhibit a helicoidal wear pattern (Tobias, 1980). As anterior maxillary molars of *P. robustus* possess smaller Carabelli cusps than their posterior counterparts, it is unlikely that the presence of this accessory cuspule is a compensation for the loss of tooth material resulting from a combination of heavy attrition and a helicoidal pattern of occlusion.

Molars of *P. robustus* may have required the recruitment of additional enamel bulk in the form of the Carabelli cusp once the level of wear obliterated the occlusal surface. As this accessory cuspule is situated more occlusally compared with that seen in *A. africanus*, it would become incorporated into the occlusal surface early on in the wear process. The smaller size of Carabelli's cusps in molars of *P. robustus* may indicate that this species may have not required much additional enamel bulk lingually as teeth attributed to this taxon have much larger occlusal areas and markedly thicker enamel compared with those of *A. africanus*. The plane of wear in molars of *A. africanus*, on the other hand, would not reach the level of the Carabelli feature until much later in the wear process as this accessory cusp is situated more cervically. As *A. africanus* molars possess relatively thinner enamel, it may have become more critical to recruit additional enamel, in the form of a larger Carabelli's cusp, for teeth to remain functionally competent throughout the lifetime of an individual.

Finally, we propose that it is inadvisable to measure enamel thickness where a reference place intersects the EDJ along the lingual wall of the protocone in the area of Carabelli's cusp(ule) as the placement of this feature can directly impact on observed differences in enamel thickness. Future comparative studies on enamel thickness patterning, especially in taxa which possess moderate to strong development of the Carabelli trait, should rely on measurements of enamel thickness recorded closer to the protocone dentine horn, as in Beynon & Wood (1986), Grine & Martin (1988) and Schwartz (1997, in prep.), thereby avoiding the potential impact of Carabelli feature size on the patterning of enamel thickness. Alternatively, enamel thickness could be measured at the point of maximum projection of the Carabelli feature in the plane of the mesial cusps, though as the results presented here demonstrate, this position will differ between molars attributed to both *A. africanus* and *P. robustus*. As the important point to consider is the comparison of enamel thickness data at homologous regions of the crown, either method is recommended over using a measure of enamel thickness recorded relative to a reference plane such as the one used here.

Summary and conclusions

For many years, paleoanthropologists have recognized distinct differences in the degree of expression of the Carabelli trait between South African robust and gracile australopithecines. Until recently, however, no quantitative data existed on Carabelli feature size. In this study, we have examined the relationship between Carabelli feature size, as estimated by the length of the associated furrow, EDJ topography and the linear thickness of the enamel cap along the lingual walls of the protocone. As in Korenhof's (1982) study on modern human maxillary molars, we report that the expression of an incomplete or complete lingual cingulum, or Carabelli's cusp, along the EDJ is not necessarily correlated with a cingulum or cusp at the crown surface in early South African hominids. Moreover, large Carabelli features at the tooth crown surface are not always correlated with prominent cingula at the EDJ and the lack of a cingulum at the crown surface does not preclude the possibility of a distinct concavity at the level of the EDJ. Different combinations of EDJ and crown surface topography are therefore possible in these two early hominid species making phylogenetic and/or ontogenetic inferences (*sensu* Butler, 1956 and Tobias, 1967) difficult based solely on data concerning the internal architecture of hominid teeth presented here.

On average, robust australopithecines do possess smaller Carabelli features than their gracile counterparts at each tooth position and at the same time exhibit markedly thicker enamel along the lingual wall of the protocone. Functional and developmental mechanisms can and have been offered to explain these patterns; however, we propose that in part it is a more occlusally positioned Carabelli feature (relative to the reference plane from which enamel thickness data are recorded) at both the crown surface and the EDJ in the robust australopithecines which explains observed differences in enamel thickness between these taxa at that particular region of the enamel cap. This hypothesis can be tested more explicitly by measuring and comparing the height of the Carabelli complex above the cervical margin, or the depth of the feature below the occlusal plane, on the existing material. Furthermore, we emphasize that caution should be used when comparing enamel thickness among taxa that possess moderate to strong Carabelli features and recommend using the linear thickness of enamel taken close to the protoconal dentine horn (approximately 1·0 mm from the dentine horn) or at the maximum projection of the Carabelli feature in future comparative studies.

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