Molar crown thickness, volume, and development in South African Middle Stone Age humans

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One highly debated issue in palaeoanthropology is that of modern human origins, particularly the issue of when 'anatomically modern humans' (AMH) from the African Middle Stone Age became fully modern. While studies of cranial and external dental morphology suggest a modern transition occurred 150 000–200 000 years ago, little is known about dental development or enamel thickness in AMH. Studies of early members of the genus *Homo* suggest that the modern, prolonged condition of tooth growth arose late in human evolution, and that the enamel thickness of earlier hominins may not be homologous to the modern condition. This study represents the first integrated investigation of molar crown enamel thickness, volume, and development in fossil hominins, aimed at determining whether differences between AMH and living populations can be detected in these traits. Using high-resolution micro-computed tomography, we demonstrate similarities in enamel thickness and crown volumes between fossil and modern populations. Additionally, long-period growth line numbers and estimates of crown formation times for AMH molars fall within modern human ranges. These findings suggest that tooth structure and growth have remained constant for more than 60 000 years, despite the known geographical, technological, and ecological diversity that characterizes later stages of human evolution.

Introduction

A current debate in palaeoanthropology centres on the issue of modern human origins, particularly the question of when 'anatomically modern humans' (AMH) from the African Middle Stone Age (MSA) became fully modern.[1,2] Fossil *Homo* in Africa appears to have undergone a morphological transition from a more primitive form (i.e. *Homo heidelbergensis/Homo rhodesiensis*) to a more modern form (*Homo sapiens*) between 150 000 and 200 000 years ago.[3,4] This evidence is based primarily on external cranial and dental features. Little is known about internal aspects of tooth structure such as tissue thickness/distribution, or patterns of growth, including the speed and duration of development. Studies of incremental dental development in early *Homo* show a pattern more similar to African apes than modern humans.[5] Aspects of *Homo heidelbergensis* development also differ when compared to Upper Palaeolithic/Mesolithic populations.[6] Research on brain growth in early *Homo* also suggests a more rapid period of early development than in modern populations.[7] Given dietary changes and technological innovations during the Late Pleistocene and the Holocene, as well as dental size reduction in modern populations, it is unclear whether dental tissue thickness and development may have undergone corresponding changes, and when the unique, prolonged pattern of growth and development originated.

This study represents the first combined investigation of molar enamel thickness, crown tissue volumes, and enamel development in a fossil hominin taxon, aimed at determining whether differences between AMH and living populations can be detected. Micro-computed tomographic (mCT) image data were collected from several molars from the South African MSA localities of Die Kelders and Equus caves; these specimens are from approximately 60 000–80 000 and 33 000–94 000 yr BP, respectively.[8,9] Aspects of dental development were assessed from high-resolution casts, mCT scans, and confocal microscopy. Data on enamel thickness, crown volumes, and enamel development were compared with a large sample of modern humans from several geographical regions.[10–12]

Methods

Dental remains from three MSA localities were examined: Die Kelders Cave, Equus Cave, and Blombos Cave.[8,9,13,14] Unworn and lightly worn molar teeth were selected for imaging with conventional laboratory mCT (ScanCo mCT 20, Stony Brook University) or synchrotron mCT on the beamline ID 19 at the European Synchrotron Radiation Facility (Grenoble, France) with a voxel size of 16 mm. The use of a third-generation synchrotron for mCT of fossil teeth provides several advantages over laboratory mCT, including a monochromatic beam, rapid scan time, a high signal to noise ratio, and parallel beam geometry, leading to higher quality resultant images.[15,16] Nonetheless, these two scanning systems yield comparable data for fossil teeth that are not substantially remineralized during fossilization,[17] and both systems produce accurate dental measurements.[15,18] Although more than 50 teeth were examined from the three localities, only four unworn or lightly worn permanent molars were available for the study of enamel thickness, tissue volumes, and crown formation (SAM-AP 6242, 6277, 6282; EQ H5). Enamel thickness was quantified via traditional two-dimensional (2D) methods[19] for comparison with previous studies, as well as by newly developed three-dimensional methods,[10,15,20] which represent a whole-tooth approach, and capture the distribution of enamel thickness across the entire molar crown.

For 2D data, analogous (ideal) planes of section through the mesial and distal cusps were recorded from volume models of each tooth using VoxBlast software (Vaytek, Inc., Fairfield, IA, U.S.A.). The orientation of each image stack was first transformed so that individual images were plane-parallel to the plane defined by three dentine horn tips (those of the protoconid, metaconid, and hypoconid). A perpendicular plane of section was then recorded through the dentine horns of the protoconid and metaconid, as was a second plane through the hypoconid and entoconid dentine horns, and 2D data were recorded on these sections (Fig. 1). Several aspects of each cross section were measured using a digitizing tablet interfaced with SigmaScan software (SPSS Science, Inc.): the area of the enamel cap, the length of the enamel–dentine junction, and the area of dentine. Average and relative enamel thickness were calculated; average enamel thickness is the area of the enamel cap divided by the length of the enamel–dentine junction; relative enamel thickness is the quotient of average enamel thickness and the

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square root of the dentine area, multiplied by 100.[19] Slight reconstructions were made prior to measurement in sections that showed light to moderate wear or a minimal amount of missing cervical enamel.

For three-dimensional (3D) data, the mCT image stacks of each tooth were subjected to median and anisotropic diffusion filters to facilitate tissue segmentation via pixel value thresholding.[20]

Volumes were calculated based on the number of voxels representing each tissue after threshold segmentation with 3D Slicer software[21] (Fig. 2). Surface areas were also calculated from models created with 3D Slicer software. The following variables were quantified: total coronal volume, enamel volume, dentine volume (also contains the volume of the coronal pulp chamber), basal area (BA) (defined as the area of the dentine and pulp contained by the most apical continuous ring of enamel at the molar cervix[10]), outer enamel surface area (OESSA), enamel–dentine junction surface area (EDJSA) (calculated by measuring the entire surface area of the coronal dentine, and then subtracting BA[20]), total specimen surface area (= BA plus OESSA), enamel surface area (= OESSA plus EDJSA), total dentine surface area (= EDJSA plus BA), average enamel thickness (AET) (= enamel volume divided by EDJSA), and relative enamel volume (= AET divided by the cube root of dentine volume,[10,15] multiplied by 100).

Developmental data were also collected on several additional naturally-fractured teeth from Blombos Cave (SAM-AP/AA 6292, 6295, 6302, 6303), which were examined with tandem scanning reflected (confocal) light microscopy.[22] High-resolution impressions of the four unworn or lightly worn molar teeth discussed above were made using Coltene President impression materials, and casts were made with Epo-Tek epoxy resin. Stereomicroscopy (×50 magnification) was used to determine the number of perikymata (manifestations of long-period growth lines on tooth surfaces) (Fig. 3), and linear enamel thickness was quantified from virtual sections (mCT slices) of the mesial and distal cusps. Confocal microscopy of naturally-fractured teeth did not reveal any evidence suggesting that daily secretion rates or long-period line periodicities are different from modern human population ranges. Thus, regressed estimates of cuspal formation time from linear thickness[5] were coupled with an estimated periodicity of 8 days multiplied by the number of long-period lines for each cusp to estimate cusp-specific crown formation time. The estimated periodicity of 8 was

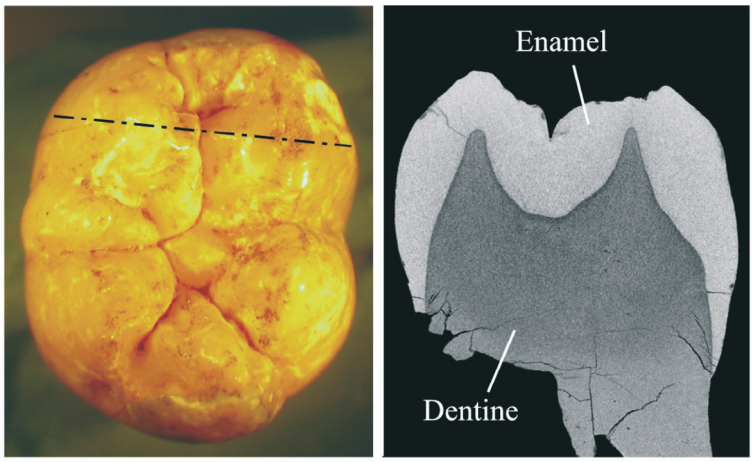

Fig. 1. Right lower first molar from Equus Cave, South Africa (EQ H5) shown as a stereomicroscope overview (left) with a dotted line indicating the orientation of the virtual plane of section (right), which is a synchrotron mCT image of the ideal mesial plane of section (coursing through the tips of the dentine horns of the mesial cusps). This non-destructive technique permits quantification of the linear thickness of enamel as well as the relative enamel thickness and tissue volumes.[10,15,20]

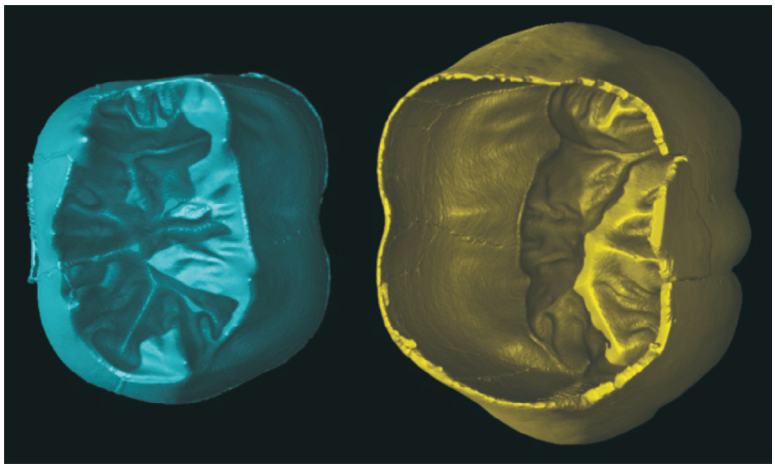

Fig. 2. Virtually separated coronal dentine (left) and enamel cap (right) of the right lower first molar illustrated in Figs 1 and 3. A small amount of enamel is missing on the lingual cervix. The volume and surface area of each of these tissues was calculated, which was used to calculate the 3D average and relative enamel thickness (see text).

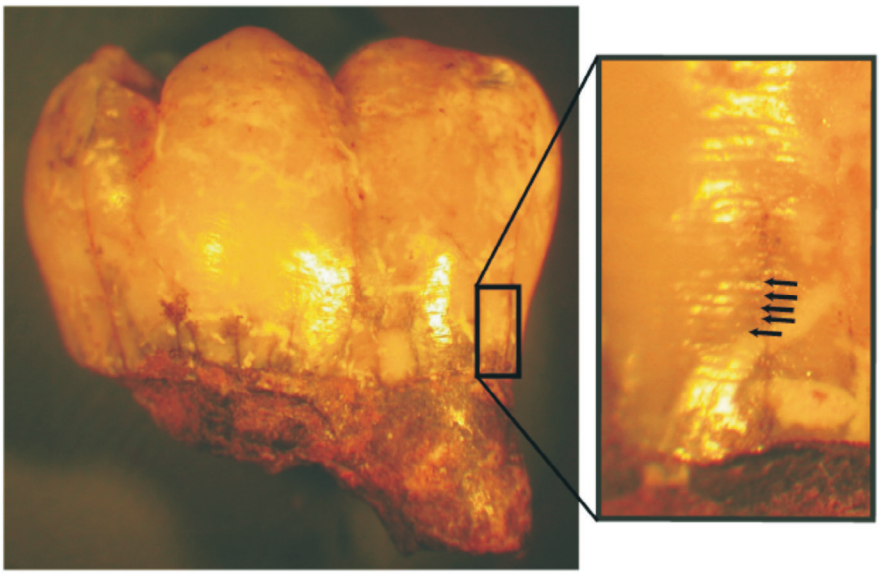

Fig. 3. Stereomicrographs of the fossil hominin tooth depicted in Figs 1 and 2, showing the clarity of perikymata, horizontal manifestations of long-period growth lines on the tooth surface (black arrows in the higher magnification image on the right).

Table 1. Two-dimensional enamel thickness in Middle Stone Age South African and modern human mandibular molars.

Tooth	Population	*n*	AET (mm)	Range	RET	Range
LM1	MSA	3	1.17	0.96–1.47	19.37	16.29–23.28
	Modern SA	17	1.09	0.80–1.40	17.21	13.31–22.62
	Modern Mix	55	1.07	0.80–1.40	16.99	11.76–22.62
LM3	MSA	1	1.27	–	26.35	–
	Modern SA	5	1.36	1.28–1.53	22.16	20.27–24.14
	Modern Mix	44	1.24	0.98–1.67	21.63	17.22–31.84

Tooth: LM1, lower first molars; LM3, lower third molars. Population: MSA, Middle Stone Age humans from South Africa; Modern SA, modern South Africans; Modern Mix, modern humans from four global populations.[12] *n*, sample size; AET, average enamel thickness in mm, calculated by dividing enamel cap area by the enamel–dentine junction length.[19] Range: minimum and maximum values. RET, relative enamel thickness, calculated by dividing AET by the square root of the dentine area and multiplying by 100.[19]

Table 2. Crown volume and area measurements in Middle Stone Age South African and modern human mandibular molars.

Variable	LM1			LM3	
	MSA	Modern	s.d.	MSA	Modern
Coronal volume (mm^3)	620.9	584.0	–	> 359.0	554.9
Specimen surface area (mm^2)	463.1	–	–	> 321.1	395.4
Enamel volume (mm^3)	271.7	279.4	37.7	> 169.5	247.7
Enamel surface area (mm^2)	589.3	–	–	> 407.4	481.8
Outer enamel surface area (mm^2)	384.7	–	–	> 259.1	325.8
Dentine volume (mm^3)	349.3	304.6	47.3	189.5	307.2
Dentine surface area (mm^2)	282.9	289.5	–	210.3	225.6
Basal area (mm^2)	78.4	77.6	4.3	62.0	69.6
EDJ surface area (mm^2)	204.6	211.9	23.7	148.3	156.0
Average enamel thickness (mm)	1.33	1.32	0.12	> 1.14	1.58
Relative enamel volume	18.86	19.59	–	> 19.91	23.33

Variables are explained in the text. LM1, lower first molars; LM3, lower third molars; MSA, Middle Stone Age human mean values from South Africa (*n* = 3 for LM1, *n* = 1 for LM3); Modern LM1, modern Japanese mean values; data taken or calculated for 13 LM1.[10] s.d., standard deviation of modern sample where given.[10] Data on modern third molars are from two North American teeth that were clinically extracted and reported here for comparison. Note: due to cuspal wear on the MSA LM3, values of enamel volume, enamel outer surface area, and the indices that contain these values are underestimated, and are indicated as '>'.

chosen as this was the mean periodicity of a sample of 365 modern human molars.[11] (Estimates of cusp-specific crown formation time using 7- and 9-day periodicities are given in Appendix 1.)

Results

Average and relative enamel thicknesses based on mesial 2D planes of section are shown in Table 1 for MSA and living human molars. MSA enamel thickness was generally within modern South African and mixed human population ranges. One large first molar was slightly thicker than all modern human values (EQ H5); the segmented enamel cap and coronal dentine of this tooth are shown in Fig. 2. Values of dental tissue volumes, surface areas, and thickness indices were also similar to modern human values (Table 2).

Perikymata were observed on all well-preserved molar cusps. Table 3 shows mean perikymata number and cuspal enamel thickness for each cusp, along with estimated formation times. Comparison with a large sample of modern human molars shows that estimated cusp-specific crown formation times in three MSA first molars falls within one standard deviation of a modern human sample.

Discussion

Permanent South African MSA teeth are limited in number, particularly unworn and lightly worn molars. With this limitation

Table 3. Enamel developmental variables and estimated cusp-specific crown formation time in Middle Stone Age and modern human first mandibular molars.

Tooth	Cusp	Population	*n*	Thick. (µm)	s.d.	PK/LP	s.d.	CFT (days)	s.d.
LM1	mb	MSA	2-3	1155	–	94	–	1128	–
		Modern SA	1-5	1100	–	90	9	1163	–
		Modern Mix	18-31	1093	245	94.5	14	1140	66
	ml	MSA	2-3	1240	–	80	–	965	–
		Modern SA	6-18	1075	172	75	9	983	59
		Modern Mix	27-50	1061	194	75	11	986	48
	db	MSA	2-3	1637	–	87	–	1196	–
		Modern SA	3-6	1183	126	84	6	1063	31
		Modern Mix	8-13	1485	261	82	11	1124.5	76
	dl	MSA	2-3	1473	–	80	–	1028	–
		Modern SA	2-5	1050	–	68	6	938	–
		Modern Mix	7-10	1314	219	67	9	983	56

Tooth: LM1, lower first molars. Cusp: mb, mesiobuccal cusp (protoconid); ml, mesiolingual cusp (metaconid); db, distobuccal cusp (hypoconid); dl, distolingual cusp (entoconid). Population: MSA, Middle Stone Age humans from South Africa; Modern SA, modern South Africans; Modern Mix, modern humans from four global populations.[11] *n*, sample size, which differed for each developmental variable. Thick.: cuspal enamel thickness measured from a mesial or distal plane of section (see text). s.d., standard deviation. PK/LP, number of perikymata or equivalent long-period Retzius lines counted from high-resolution casts of the fossil material or histological sections of the modern samples, respectively. CFT: cusp-specific crown formation time, estimated for the MSA cusps by adding cuspal enamel formation time (estimated from a modern human regression equation[5]) to the number of perikymata multiplied by 8, which is the mean periodicity value for a sample of 365 modern humans.[11] CFT was calculated for the modern human sample using regressed cuspal formation estimates plus Retzius line number times the known periodicity value.[11]

in mind, the results of this investigation show that relative enamel thickness, crown volumes, enamel developmental variables, and estimated cusp-specific crown formation times are similar to living human populations.[10–12] These findings are consistent with the results of other metric and morphological analyses that emphasize the similarity between living and fossil sub-Saharan MSA humans.[8,9]

Two-dimensional enamel thickness is highly variable within modern humans, with ranges encompassing values for *Australopithecus africanus* and *Paranthropus robustus*[12] (although *Paranthropus* may show greater mean values for linear and relative enamel thickness[23]). It has been suggested that the advent of tool use in *Homo erectus* may relate to a trend of declining enamel thickness up to the present,[24] although little is known about enamel thickness from controlled planes of sections in *H. erectus*. Moreover, character state changes in this aspect of morphology are difficult to assess throughout human evolutionary history, as few fossil taxa have been studied with large enough samples to make unqualified descriptions of their enamel thickness. Nonetheless, the results of this study suggest that molar enamel thickness has remained stable for at least 60 000 years. Similar work in progress on diverse samples of Neanderthals suggests that contemporaneous hominins show a slightly different enamel thickness condition, largely due to differences in the proportions of enamel and dentine.[25]

This study also provides an integrative approach to studying the dentition, taking into account not only the absolute and relative quantities of dental tissues (e.g. enamel thickness), but also the development of these molars. This approach demonstrates that it is possible to examine both gross morphological and developmental characteristics of fossil hominins simultaneously and non-destructively using modern technologies. Additional data are needed on enamel thickness and development in other fossil hominins, and mCT data are likely to provide increased samples.[15,20] The application of synchrotron mCT represents a particularly promising tool for studies of dental tissues, as it is possible to resolve dental microstructure,[15,16] which may allow for highly accurate reconstructions of both crown tissue thickness and development.

Dean and colleagues[5] recently documented rates of enamel formation and estimated molar eruption ages in early *Homo*, which showed more rapid development than modern humans. Given the relationship between dental development and life history proposed for other fossil hominins,[5,26] Middle Stone Age hominins from Die Kelders and Equus Cave may have achieved a fully modern pattern of growth and development by at least 33 000 years ago, and in the case of Die Kelders, this is likely to have occurred more than 60 000 years ago. However, additional data regarding root formation and age at molar eruption would strengthen these findings. The condition seen in aspects of *H. antecessor/H. heidelbergensis* anterior tooth development is more similar to Neanderthals than to Upper Paleolithic/Mesolithic modern humans,[6] suggesting that the current developmental condition may have appeared in synchrony with the advent of other modern craniodental morphologies. Research is under way to investigate this enamel character complex in slightly older material from Europe and northern Africa, which will provide additional insight into the question of when and where our human ancestors became fully modern.

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Appendix 1. Relative enamel thickness, enamel volume, cuspal thickness, and estimated formation times of MSA fossil hominin teeth.

Tooth code	Tooth	2D RET	Vol. (mm^3)	Cusp	Thick. (μm)	Cusp time (days)	PK	CFT – 7 (days)	CFT – 8 (days)	CFT – 9 (days)	CFT – 8 (yr)
SAM-AP 6242	RLM1	16.29	195.0	mb	1100	355	93	1006	1099	1192	3.01
				ml	800	273	80	833	913	993	2.50
				db	1350	417	86	1019	1105	1191	3.03
				dl	1200	381	80	941	1021	1101	2.80
SAM-AP 6277	LLM1	18.53	258.4	mb	1135	364	> 88				
				ml	1190	378	80	938	1018	1098	2.79
				db	1350	417	> 67				
				dl	1230	388	81	955	1036	1117	2.84
EQ H5	RLM1	23.28	361.6	mb	1230	388	96	1060	1156	1252	3.17
				ml	1730	499	> 70				
				db	2210	582	88	1198	1286	1374	3.52
				dl	1990	547	> 66				
SAM-AP 6282	RLM3*	26.35	> 169.5	mb	~1400	429	> 60				
				ml	~1350	417	> 60				
				db	~1690	491	> 60				
				dl	~1300	405	> 60				

Tooth code: given in primary references (see text). Tooth: RLM1, right lower first molar; LLM1, left lower first molar; RLM3, right lower third molar. 2D RET: relative enamel thickness, a scaled measure of enamel thickness derived from a plane across the mesial dentine horn tips; values are dimensionless. Vol.: enamel volume calculated from high-resolution mCT slices (see text). Cusp: the position on the tooth crown; mb, mesiobuccal cusp; ml, mesiolingual cusp; db, distobuccal cusp; dl, distolingual cusp. Thick.: cuspal thickness measured from mCT slices. Cusp time: cuspal formation time, calculated by entering the cuspal enamel thickness into a regression formula for modern human teeth.[5] PK: Perikymata numbers, manifestations of long-period growth lines on the enamel surface counted from casts of the original teeth. CFT – 7: cuspal time plus the total number of perikymata multiplied by 7, the most common minimum periodicity value found in a large sample of modern humans.[11] CFT – 8: cuspal time plus the total number of perikymata multiplied by 8, the mean periodicity value found in a large sample of modern humans.[11] CFT – 9: cuspal time plus the total number of perikymata multiplied by 9, the most common maximum periodicity value found in a large sample of modern humans.[11] *Grine[9] had originally identified SAM-AP 6282 as a second molar, but this was changed during the current study due to lack of a distal facet and its slightly diminutive size.