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Variation in modern human enamel formation times

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Abstract

Most of what we know about the timing of human enamel formation comes from radiographic studies on children of known age. Here, we present new longitudinal data derived from a histological analysis of tooth enamel. Two samples, one from southern Africa and one from northern Europe, contained all anterior and molar tooth types. Two further samples contained only one tooth type: canines from a medieval Danish sample and third molars from a modern North American sample. Data were collected on 326 molars and 352 anterior teeth. Each tooth was sectioned and prepared for polarized light microscopy. We used daily enamel cross striations to determine cuspal enamel formation time, recorded the periodicity of long-period striae in the lateral enamel, and used this value to calculate enamel formation times for each decile of crown length. We present data that reveal some of the processes whereby differences in enamel formation times arise between our samples. Mean cuspal enamel formation times were similar in southern African and northern European anterior teeth, but differed in certain molar cusps. All the southern African anterior teeth completed enamel formation earlier. The greatest difference in mean chronological age at enamel completion was 5.2 vs. 6.2 years of age in lower canines. However, enamel completion times in the molar teeth showed few differences between the samples, with mean times for the longest forming cusps all falling between 3.0 years and 3.45 years. Our data suggest fewer differences between samples and smaller ranges of variation than in many radiographic studies and present a more realistic picture of worldwide variation in enamel formation times.

Keywords: Cross striations; Striae of Retzius; Enamel formation; Tooth growth; Dental development

Introduction

Studies of dental development have a long history because of their obvious usefulness. In particular, dental development is one of the best indicators of chronological age when no record of birth exists (Garn et al., 1965). It is important both clinically and for comparative studies to have well founded standards of modern human dental development and to document the true extent of worldwide variation in dental development. In comparative studies, it is especially important to define ranges of variation in dental development within and between groups of living and fossil primates. Recording tooth development in ways that can be standardized across primate taxa makes this task easier.

A number of key variables have become especially important in comparative studies; these include the age at initiation of tooth mineralization, the time taken to complete enamel formation, and the age at gingival emergence of teeth. In this study, we concentrate on documenting enamel formation times in modern humans using a histological approach that is now widely used in primate comparative studies. Our broad aim is to increase the accuracy of the database on worldwide variation in enamel formation times; we also identify the growth processes that underlie observed differences. In order to accomplish this goal, we have recorded enamel formation times for smaller fractions of total crown formation than in many previous studies of modern humans. Our specific objectives are: (1) to document the times taken to form various fractional stages of the crown in incisors, canines, and molars; (2) to

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document these enamel formation times in an important sample of teeth of southern African origin; (3) to compare these data with those collected in an identical manner from one sample of teeth of northern European origin and two smaller samples (M3s only and canines only) of recent North American and medieval Danish origins.

Each of the many approaches to studying modern human dental development has its drawbacks, but each also provides different but equally important information. Because dental development can be observed and recorded in so many ways and for so many reasons, a comparison of the different lines of evidence they provide can either imply greater variation than actually exists or, alternatively, fail to identify important geographical variation that does exist. Three very different kinds of studies of dental development, designed to document different kinds of data, illustrate how hard it is to reach a consensus about variation in dental development. Together, they make a case for undertaking new studies, such as this one, based on the histological analysis of enamel.

Dental eruption (i.e., gingival emergence) can be observed directly in growing children, and emergence times for both deciduous and permanent teeth have mostly been documented with respect to chronological age. A large number of studies exist on deciduous and permanent tooth emergence times in many geographically diverse populations, and a significant number of these are based on direct observations of children of known age. Direct comparison of the findings of these studies suggests considerable variation in tooth emergence times worldwide. However, a recent review of the data from a representative sample of these studies, but after calculating mean age of attainment from the various data sets, suggests that the true extent of geographical variation in permanent tooth emergence times may be much less than has been assumed (Liversidge, 2003). This finding raises questions about variation in other aspects of dental development documented both within and between human populations and as to whether some of it might actually be generated by, for example, subtle differences in technique or different statistical treatment of the data.

Radiographic studies of dental development in modern humans are a second major group of studies that have documented considerable variation in dental development. Radiographic studies of the developing dentition are the source of the most widely used data on enamel formation times in modern humans. The amount of variation documented in radiographic studies of tooth development, even in closely related populations of children, is a cause for concern. For example, Gleiser and Hunt (1955) defined fractional stages of first permanent molar tooth growth (as well as its eruption and decay) and documented ages for these that compare well with clinical observations within many populations of growing children (crown completion ± 2 SD = 2.5–4.4 years). However, identical definitions of fractional stages used in a subsequent study (Moorrees et al., 1963), but with a more refined statistical analysis of the data, generated ages for some stages of first permanent molar formation that are much shorter (crown completion ± 2 SD = 1.7–2.8 years).

A brief survey of some of the classic radiographic studies (e.g., Gleiser and Hunt, 1955; Nolla, 1960; Moorrees et al., 1963; Fass, 1969; Haavikko, 1970; Demirjian et al., 1973; Gustafson and Koch, 1974; Anderson et al., 1976; Demirjian and Levesque, 1980; Demirjian, 1986; Daito et al., 1990; Harris and McKee, 1990; Simpson and Kunos, 1998) reveals a wide range of mean crown formation times for human teeth and suggests differences between populations. For example, once again, Moorrees et al. (1963; see also Harris and Buck, 2002, for a reanalysis of the data) cite mean age at crown completion for permanent mandibular canines as 3.9–4.0 years in girls and boys, respectively, which is approximately 2 years short of the mean age cited by Gustafson and Koch (1974) in their extensive review of studies on tooth formation.

It is not always clear if this variation is due to differing definitions of crucial stages of tooth growth, poor resolution of the radiographic images, different statistical treatment of the results, or to biological variation among the various populations studied (the majority of which are of European origin in the studies cited here). Furthermore, studies of recent and past archaeological populations, as well as those on early fossil hominids, can be frustrated by data that often fail to include information on the very early stages of dental development and which define stages of tooth growth that are hard to visualize on radiographs of non-human primates and may differ in appearance from those defined on teeth removed from the mouth.

While radiographic studies are able to record both the sequence of tooth mineralization (Tompkins, 1996) and the timing of the various stages of tooth mineralization of individual teeth, often with respect to chronological age, they do not have the resolution to distinguish near-microscopic changes in tooth growth (Beynon et al., 1998; Kuykendall, 2001) of the kind that are increasingly reported in comparative studies of primates. Another concern is that, in many radiographic studies, variation in the time of initiation of tooth mineralization also becomes a component of the chronological data that describes variation in crown completion. Many comparative studies report only crown formation times, and sometimes only for isolated teeth, with no knowledge of chronological age or of the age at which initial mineralization occurred. Nonetheless, the advantage of being able to include very large numbers of individuals in either cross-sectional or longitudinal radiographic growth studies often outweighs all these concerns, and radiographic studies of modern human tooth development remain an important component of many comparative studies.

Because enamel is preserved better than any other part of the skeleton, does not remodel, and grows in an incremental fashion, it is possible to estimate crown formation times more precisely and record the timing of these events on a scale of days and weeks rather than just months and years. In many cases, however, histological analyses of teeth are avoided because the methods are inherently destructive and very time consuming, and the sample sizes are usually small. A third group of studies of dental development are based on this histological approach to recording enamel formation times.

Table 1
Numbers of teeth used from each group used in the study

Tooth type	UI1	UI2	UC	LI1	LI2	LC	UM1	LM1	UM2	LM2	UM3	LM3
Northern European	19	16	39	15	13	13	15	15	16	16	15	15
Southern African	22	22	30	29	27	25	37	29	19	17	20	14
North American (Caucasian)											24	7
North American (mixed)											51	16
Medieval Danish			15			67						
Subtotals	41	38	84	44	40	105	52	44	35	33	110	52
Grand total = 678												

These studies depend on counts and measurements of incremental growth markings and can provide information about the timing of crown and root formation (Boyde, 1964; Dean, 1987; Boyde, 1989; Risnes, 1998; Shellis, 1998). Antoine (2001) carefully documented the major sources of error in histological analyses of this kind using material of known chronological age. It seems possible to achieve an accuracy of between 2% and 5% depending on the clarity of the incremental markings in enamel and, in particular, how well defined the neonatal line is in ground sections. The disadvantage of this approach is that rarely, if ever, are the sample sizes as large as those in radiographic studies. Nonetheless, the data are essentially longitudinal for each individual tooth included in a study (and can even include data for the period before birth). There is also potential for greater resolution of the various fractional stages of tooth formation that are difficult to define and see on radiographs, but which are of fundamental importance in comparative studies, and it is possible to split the variation in enamel formation times from the variation in tooth initiation times and assess each separately.

Asper (1916) first used a histological section to calculate the crown formation time in a single upper canine as 1560 days (4.3 years). Gysi (1931) adopted this approach, but more in order to confirm that enamel cross striations had a circadian periodicity. Subsequently, Komai (1942) recorded upper central and lateral incisor crown formation times of 1800 and 1539 days (4.9 and 4.2 years), respectively, using the same technique. Boyde (1963, 1990) used this technique to age an individual at death and, in so doing, calculated the cuspal enamel formation of a lower M1 as 334 days, initiation of the upper central incisor as 22 days after birth, and the chronological age of enamel completion in an upper central incisor as 1692 days (4.64 years). One of the most comprehensive histological studies is that of Kajiyama (1965) on Japanese crown formation times in 140 teeth. Kajiyama (1965) analyzed photomicrographs of the whole enamel cap of ten teeth for each of the upper and lower permanent tooth types, except third permanent molars. Total regular long-period striae counts were made from each (mean of five total counts) and an average 8–9 day periodicity was used to calculate total enamel formation times, the mean values of which varied between 3.85 years (lower first permanent molars) and 7.5 years (upper canines). FitzGerald (1995) also calculated crown formation times using the same histological approach

Table 2
Crown length, cuspal thickness, and periodicity in the anterior teeth from each sample ±1 standard deviation
Southern African anterior teeth

	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
UI1 n = 22	12.45	10.00–14.80 ± 0.94	810	720–960 ± 62	9.60 (10)	8–12 ± 0.96
UI2 n = 22	10.79	9.40–12.40 ± 0.73	807	740–915 ± 66	9.55 (10)	7–11 ± 1.10
UC n = 30	10.83	8.40–13.50 ± 1.05	1013	820–1255 ± 100	8.90 (9)	6–12 ± 1.35
LI1 n = 29	9.93	9.10–10.60 ± 0.45	586	400–670 ± 78	8.97 (9)	8–11 ± 0.82
LI2 n = 27	10.08	9.20–11.60 ± 0.50	606	495–795 ± 66	9.26 (9)	7–12 ± 1.13
LC n = 25	11.45	9.60–12.00 ± 0.62	965	795–1155 ± 82	8.54 (8)	7–11 ± 1.14
Northern European anterior teeth						
	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
UI1 n = 19	13.63	12.45–14.4 ± 0.54	828	700–900 ± 55	8.47 (8)	7–10 ± 1.17
UI2 n = 16	11.60	11.0–12.5 ± 0.41	778	700–900 ± 55	9.13 (9)	8–11 ± 1.09
UC n = 39	11.83	9.2–15.2 ± 1.03	1068	900–1335 ± 100	9.00 (9)	8–11 ± 1.05
LI1 n = 15	10.31	10.0–11.2 ± 0.29	707	600–800 ± 73	8.71 (8)	7–9 ± 0.49
LI2 n = 13	10.06	9.6–10.8 ± 0.37	594	480–650 ± 42	8.85 (9)	7–11 ± 0.71
LC n = 13	13.41	11.2–15.2 ± 1.32	1047	850–1150 ± 107	8.69 (8)	7–10 ± 0.85
Northern European (medieval Danish) canines						
	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
LC n = 67	11.57	8.80–13.60 ± 1.00	847	700–1100 ± 93	8.49 (8)	7–11 ± 0.93
UC n = 15	11.24	9.40–12.80 ± 1.15	927	800–1150 ± 145	8.67 (9)	6–12 ± 1.72

Table 3
Crown length, cuspal thickness, and periodicity in the molar teeth from each sample ± 1 standard deviation[1]

Southern African upper molar teeth

	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
UM1 (pr) n = 37	7.78	6.4–8.8 ± 0.53	1328	1100–1600 ± 119	8.78 (8)	6–12 ± 1.25
UM1 (pa) n = 37	7.29	6.0–8.60 ± 0.64	1093	1000–1400 ± 113	8.73 (8)	6–12 ± 1.28
UM2 (pr) n = 18	7.82	6.6–9.8 ± 0.83	1719	1200–2000 ± 113	8.61 (8)	7–11 ± 1.04
UM2 (pa) n = 19	7.41	6.4–10.4 ± 0.97	1391	1100–1700 ± 165	8.58 (8)	7–11 ± 1.02
UM3 (pr) n = 20	8.09	7.2–9.6 ± 0.68	1623	1350–1900 ± 149	8.3 (8)	6–10 ± 1.13
UM3 (pa) n = 19	7.86	6.8–9.2 ± 0.65	1418	1200–1600 ± 106	8.26 (8)	6–10 ± 1.15

Northern European upper molar teeth

	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
UM1 (pa) n = 15	7.77	6.0–8.8 ± 0.72	1213	700–1550 ± 241	8.27 (8)	6–10 ± 1.10
UM1 (pr) n = 15	9.08	8.0–10.4 ± 0.64	1620	1100–2200 ± 241	8.27 (8)	6–10 ± 1.10
UM2 (pa) n = 16	8.10	6.8–9.6 ± 0.58	1388	1100–1700 ± 165	7.69 (8)	6–9 ± 0.87
UM2 (pr) n = 15	8.88	7.6–11.0 ± 0.88	1640	1400–1900 ± 148	7.73 (8)	6–9 ± 0.88
UM3 (pa) n = 15	7.70	6.6–9.2 ± 0.67	1532	1000–1900 ± 227	7.94 (8)	6–9 ± 0.77
UM3 (pr) n = 15	8.85	7.4–9.8 ± 0.60	1727	1500–2000 ± 165	7.94 (8)	6–9 ± 0.77

North American upper molar teeth

	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
UM3 (pa) (Cauc.) n = 24			1767	1280–2452 ± 291	7.75 (8)	7–9 ± 0.68
UM3 (pr) (Cauc.) n = 23			2024	1555–2400 ± 205	7.78 (8)	7–9 ± 0.67
UM3 (pa) (mixed) n = 50			1753	1267–2350 ± 256	7.86 (8)	7–9 ± 0.61
UM3 (pr) (mixed) n = 51			2041	1560–2600 ± 271	7.88 (8)	7–9 ± 0.62

Southern African lower molar teeth

	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
LM1 (prd) n = 28	8.11	7.2–9.0 ± 0.49	1184	1000–1400 ± 84	8.57 (9)	7–10 ± 0.69
LM1 (med) n = 29	7.26	6.4–8.0 ± 0.42	953	700–1100 ± 92	8.59 (9)	7–10 ± 0.68
LM2 (prd) n = 17	7.89	7.2–8.4 ± 0.32	1472	1100–1620 ± 142	9.0 (8)	7–12 ± 1.17
LM2 (med) n = 17	6.94	6.0–7.6 ± 0.49	1214	800–1380 ± 195	8.7 (8)	7–10 ± 0.90
LM3 (prd) n = 14	8.49	7.2–10 ± 0.79	1651	1500–1800 ± 80	8.14 (8)	7–9 ± 0.66
LM3 (med) n = 14	7.14	6.4–8.0 ± 0.65	1369	1200–1540 ± 94	8.21 (8)	7–9 ± 0.58

Northern European lower molar teeth

	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
LM1 (prd) n = 15	8.99	8.0–9.8 ± 0.51	1573	1200–2000 ± 84	8.47 (8)	7–11 ± 1.25
LM1 (med) n = 15	7.45	6.4–8.4 ± 0.68	1307	1050–1600 ± 170	8.47 (8)	7–11 ± 1.25
LM2 (prd) n = 16	8.65	7.6–10.4 ± 0.85	1489	1200–1800 ± 167	8.31 (8)	7–9 ± 0.60
LM2 (med) n = 16	7.25	6.0–8.8 ± 0.69	1284	1100–1550 ± 133	8.31 (8)	7–9 ± 0.60
LM3 (prd) n = 15	8.92	7.4–10.2 ± 0.91	1587	1050–2000 ± 269	7.73 (8)	6–10 ± 1.10
LM3 (med) n = 15	7.60	7.0–9.2 ± 0.60	1333	1000–1600 ± 189	7.73 (8)	6–10 ± 1.10

North American lower molar teeth

	Crown length (mm)	Range (mm) ±1 SD	Cusp thickness (μms)	Range (μms) ±1 SD	Mean periodicity (mode)	Range (days) ±1 SD
LM3 (prd) (Cauc.) n = 7			1691	1425–2043 ± 273	7.86 (8)	7–9 ± 0.69
LM3 (med) (Cauc.) n = 7			1498	1256–1734 ± 157	7.86 (8)	7–9 ± 0.69
LM3 (prd) (mixed) n = 13			1767	1241–2360 ± 289	7.92 (8)	7–9 ± 0.64
LM3 (med) (mixed) n = 16			1559	1120–2106 ± 269	8.0 (8)	7–9 ± 0.63

[1] Protocone = pr; paracone = pa; protoconid = prd; metaconid = med.

in a small but geographically and temporally diverse sample of modern human teeth. FitzGerald (1995: 213, Table 12-8), in a useful summary of crown formation times derived from radiographic data, histological data, and from direct observations of tooth germs in archaeological material of known age (Liversidge et al., 1993; Liversidge and Molleson, 1999; Liversidge, 1999, 2000), drew attention to the range of crown formation times in teeth of African and Japanese origin. By way of example, Kajiyama (1965) cited 7.0–7.9 years for the range of upper permanent canine crown completion times, whereas FitzGerald (1995) calculated these to be between 4.5 and 4.7 years for two teeth of southern African origin.

A number of recent studies of human and non-human primate fossil teeth (Reid and Dean, 2000; Dean and Reid, 2001; Ramirez Rozzi and Bermudez de Castro, 2004) have adopted this histological approach and have demonstrated that tooth enamel is one of the best sources of information that archaeologists and palaeontologists have for reconstructing primate life histories, developmental schedules, and phylogenetic relationships (Kelley, 2004). It follows that a more comprehensive histological study of modern human teeth carried out in a uniform manner is likely to be a useful contribution to future studies on comparative dental development.

Materials

Four samples of teeth were included in this study, three of which have been reported on previously. A summary of the numbers of each tooth type and their origins appear in Table 1. Reid

Table 4
Age (in days) for enamel formation at each decile of crown height for anterior teeth in each sample ±1 standard deviation

Southern African anterior tooth crown formation times

Age at	UI1 n = 22	UI2 n = 22	UC n = 30	LI1 n = 29	LI2 n = 27	LC n = 25
Initiation	128 days	383 days	274 days	90 days	146 days	200 days
Cusp completion	284 ± 18	283 ± 19	339 ± 26	214 ± 23	223 ± 20	327 ± 21
10% of crown length	344 ± 16	345 ± 17	400 ± 30	259 ± 26	275 ± 23	397 ± 25
20% of crown length	410 ± 23	416 ± 25	474 ± 35	317 ± 23	337 ± 28	480 ± 33
30% of crown length	482 ± 29	486 ± 27	556 ± 38	380 ± 26	403 ± 30	578 ± 38
40% of crown length	569 ± 33	567 ± 31	646 ± 42	444 ± 30	478 ± 30	686 ± 46
50% of crown length	670 ± 34	665 ± 34	748 ± 48	525 ± 32	559 ± 32	812 ± 55
60% of crown length	792 ± 36	781 ± 38	871 ± 49	625 ± 31	659 ± 37	961 ± 65
70% of crown length	937 ± 36	905 ± 43	1013 ± 49	748 ± 33	786 ± 43	1136 ± 71
80% of crown length	1094 ± 44	1045 ± 44	1169 ± 48	883 ± 29	932 ± 46	1326 ± 68
90% of crown length	1266 ± 42	1215 ± 31	1334 ± 46	1028 ± 29	1087 ± 42	1521 ± 57
Crown completion	1389 ± 30	1367 ± 36	1487 ± 42	1156 ± 31	1226 ± 26	1694 ± 56

Northern European anterior tooth crown formation times

Age at	UI1 n = 19	UI2 n = 16	UC n = 39	LI1 n = 15	LI2 n = 13	LC n = 13
Initiation	128 days	383 days	274 days	90 days	146 days	200 days
Cusp completion	289 ± 16	274 ± 16	355 ± 24	256 ± 21	212 ± 21	348 ± 28
10% of crown length	361 ± 9	344 ± 165	432 ± 25	316 ± 27	268 ± 25	427 ± 26
20% of crown length	441 ± 31	419 ± 22	515 ± 31	385 ± 28	335 ± 34	524 ± 32
30% of crown length	524 ± 40	495 ± 27	605 ± 36	453 ± 32	412 ± 37	639 ± 37
40% of crown length	621 ± 53	583 ± 38	709 ± 42	528 ± 36	496 ± 45	771 ± 44
50% of crown length	747 ± 60	690 ± 42	825 ± 45	620 ± 40	603 ± 54	925 ± 39
60% of crown length	913 ± 78	816 ± 47	962 ± 53	735 ± 44	727 ± 77	1119 ± 54
70% of crown length	1095 ± 69	956 ± 53	1109 ± 63	863 ± 54	887 ± 87	1333 ± 51
80% of crown length	1293 ± 65	1119 ± 52	1243 ± 63	911 ± 51	1056 ± 85	1581 ± 46
90% of crown length	1484 ± 49	1308 ± 51	1494 ± 60	1167 ± 48	1215 ± 76	1848 ± 50
Crown completion	1708 ± 50	1478 ± 49	1672 ± 55	1309 ± 50	1376 ± 46	2066 ± 73

Northern European (medieval Danish) crown formation times

Age at	UC n = 15	LC n = 67
Initiation	274 days	200 days
Cusp completion	303 ± 39	282 ± 36
10% of crown length	373 ± 44	357 ± 28
20% of crown length	448 ± 47	449 ± 35
30% of crown length	543 ± 46	555 ± 41
40% of crown length	657 ± 55	677 ± 47
50% of crown length	785 ± 64	821 ± 57
60% of crown length	937 ± 69	996 ± 66
70% of crown length	1105 ± 69	1213 ± 70
80% of crown length	1288 ± 65	1452 ± 70
90% of crown length	1468 ± 65	1684 ± 68
Crown completion	1632 ± 53	1870 ± 60

Table 5
Age (in days) for enamel formation at each decile of crown height for molar teeth in each sample ±1 standard deviation[1]

Southern African upper molar tooth crown formation times

Age at	UM1 (pa) n = 37	UM1 (pr) n = 37	UM2 (pa) n = 19	UM2 (pr) n = 18	UM3 (pa) n = 19	UM3 (pr) n = 20
Initiation	Birth	Birth	3 years	3 years	8 years	8 years
Cusp completion	353 ± 29	411 ± 28	425 ± 38	495 ± 41	432 ± 24	476 ± 31
10% of crown length	386 ± 26	448 ± 29	459 ± 40	534 ± 45	464 ± 23	511 ± 30
20% of crown length	426 ± 27	490 ± 32	497 ± 44	578 ± 50	496 ± 28	550 ± 30
30% of crown length	467 ± 29	534 ± 35	540 ± 49	625 ± 54	533 ± 31	590 ± 33
40% of crown length	510 ± 34	583 ± 39	588 ± 54	678 ± 59	674 ± 35	636 ± 35
50% of crown length	562 ± 42	639 ± 45	564 ± 57	745 ± 63	628 ± 39	691 ± 36
60% of crown length	632 ± 54	704 ± 53	725 ± 60	820 ± 64	704 ± 43	756 ± 40
70% of crown length	718 ± 64	776 ± 59	823 ± 64	903 ± 63	794 ± 36	839 ± 44
80% of crown length	821 ± 68	860 ± 62	935 ± 65	1001 ± 63	910 ± 35	942 ± 44
90% of crown length	937 ± 74	969 ± 61	1057 ± 67	1114 ± 61	1036 ± 47	1064 ± 43
Crown completion	1047 ± 77	1096 ± 60	1174 ± 69	1235 ± 59	1157 ± 45	1199 ± 41

Southern African lower molar tooth crown formation times

Age at	LM1 (prd) n = 28	LM1 (med) n = 29	LM2 (prd) n = 17	LM2 (med) n = 17	LM3 (prd) n = 14	LM3 (med) n = 14
Initiation	Birth	Birth	3 years	3 years	8 years	8 years
Cusp completion	376 ± 21	315 ± 25	444 ± 33	382 ± 51	483 ± 16	421 ± 22
10% of crown length	411 ± 24	345 ± 25	485 ± 34	410 ± 47	526 ± 18	452 ± 26
20% of crown length	452 ± 27	381 ± 26	528 ± 32	442 ± 45	572 ± 21	490 ± 29
30% of crown length	500 ± 32	419 ± 31	577 ± 31	477 ± 44	626 ± 26	533 ± 35
40% of crown length	558 ± 40	461 ± 35	633 ± 33	518 ± 44	681 ± 31	585 ± 44
50% of crown length	627 ± 43	512 ± 39	701 ± 39	569 ± 48	742 ± 37	643 ± 50
60% of crown length	706 ± 50	573 ± 44	785 ± 44	629 ± 51	810 ± 43	706 ± 60
70% of crown length	793 ± 55	643 ± 48	873 ± 46	696 ± 53	885 ± 51	773 ± 61
80% of crown length	896 ± 56	729 ± 50	971 ± 43	772 ± 56	979 ± 49	843 ± 67
90% of crown length	1014 ± 55	838 ± 54	1078 ± 40	874 ± 53	1086 ± 42	936 ± 68
Crown completion	1117 ± 55	936 ± 55	1168 ± 37	963 ± 52	1193 ± 42	1027 ± 66

Northern European upper molar tooth crown formation times

Age at	UM1 (pa) n = 15	UM1 (pr) n = 15	UM2 (pa) n = 12	UM2 (pr) n = 11	UM3 (pa) n = 15	UM3 (pr) n = 15
Initiation	Birth	Birth	3 years	3 years	8 years	8 years
Cusp completion	381 ± 62	474 ± 50	425 ± 38	480 ± 30	426 ± 67	498 ± 28
10% of crown length	426 ± 45	515 ± 44	463 ± 36	521 ± 34	460 ± 68	533 ± 33
20% of crown length	463 ± 41	557 ± 40	498 ± 38	557 ± 33	487 ± 68	569 ± 33
30% of crown length	501 ± 43	598 ± 45	527 ± 39	602 ± 39	510 ± 67	607 ± 34
40% of crown length	537 ± 41	647 ± 50	559 ± 39	647 ± 45	538 ± 64	649 ± 34
50% of crown length	587 ± 43	706 ± 58	607 ± 38	697 ± 52	573 ± 66	689 ± 33
60% of crown length	667 ± 42	780 ± 67	674 ± 41	762 ± 58	629 ± 63	749 ± 27
70% of crown length	762 ± 48	865 ± 72	765 ± 45	846 ± 59	707 ± 51	827 ± 19
80% of crown length	866 ± 45	965 ± 72	866 ± 48	945 ± 57	805 ± 55	935 ± 10
90% of crown length	988 ± 43	1087 ± 67	982 ± 49	1067 ± 48	913 ± 79	1059 ± 26
Crown completion	1097 ± 51	1210 ± 58	1098 ± 49	1197 ± 55	1026 ± 93	1224 ± 33

Northern European lower molar tooth crown formation times

Age at	LM1 (prd) n = 15	LM1 (med) n = 15	LM2 (prd) n = 16	LM2 (med) n = 16	LM3 (prd) n = 15	LM3 (med) n = 15
Initiation	Birth	Birth	3 years	3 years	8 years	8 years
Cusp completion	464 ± 53	405 ± 41	447 ± 37	401 ± 32	458 ± 62	405 ± 51
10% of crown length	507 ± 47	440 ± 41	492 ± 37	432 ± 34	499 ± 61	438 ± 50
20% of crown length	549 ± 44	475 ± 43	529 ± 36	462 ± 35	534 ± 62	470 ± 51
30% of crown length	592 ± 44	516 ± 44	570 ± 39	494 ± 39	577 ± 59	504 ± 49
40% of crown length	641 ± 43	560 ± 46	615 ± 38	532 ± 46	623 ± 59	541 ± 51
50% of crown length	702 ± 41	614 ± 51	676 ± 37	583 ± 51	674 ± 58	585 ± 55
60% of crown length	782 ± 39	677 ± 57	745 ± 33	642 ± 57	740 ± 54	639 ± 53
70% of crown length	871 ± 42	743 ± 60	828 ± 26	712 ± 63	822 ± 61	712 ± 43
80% of crown length	975 ± 45	826 ± 58	934 ± 30	798 ± 63	926 ± 69	801 ± 47
90% of crown length	1087 ± 44	922 ± 54	1050 ± 33	897 ± 63	1045 ± 75	907 ± 51
Crown completion	1188 ± 39	1012 ± 51	1156 ± 38	994 ± 67	1159 ± 71	1009 ± 56

Table 5 (*continued*)
North American (Caucasian) third molar tooth crown formation times

Age at	UM3 (pa) n = 24	UM3 (pr) n = 23	LM3 (prd) n = 7	LM3 (med) n = 7
Initiation	8 years	8 years	8 years	8 years
Cusp completion	500 ± 59	559 ± 37	516 ± 57	472 ± 41
10% of crown length	538 ± 62	606 ± 38	551 ± 55	502 ± 42
20% of crown length	575 ± 65	650 ± 39	588 ± 54	539 ± 41
30% of crown length	613 ± 68	692 ± 40	630 ± 47	582 ± 37
40% of crown length	655 ± 72	743 ± 47	680 ± 47	632 ± 40
50% of crown length	709 ± 79	801 ± 49	748 ± 49	687 ± 43
60% of crown length	788 ± 84	870 ± 46	822 ± 57	750 ± 51
70% of crown length	887 ± 81	950 ± 46	904 ± 57	818 ± 55
80% of crown length	989 ± 86	1048 ± 59	1001 ± 57	894 ± 61
90% of crown length	1105 ± 93	1165 ± 62	1099 ± 57	981 ± 63
Crown completion	1208 ± 92	1260 ± 79	1177 ± 55	1064 ± 76

North American (mixed) third molar tooth crown formation times

Age at	UM3 (pa) n = 50	UM3 (pr) n = 51	LM3 (prd) n = 13	LM3 (med) n = 16
Initiation	8 years	8 years	8 years	8 years
Cusp completion	501 ± 49	549 ± 43	485 ± 52	446 ± 57
10% of crown length	533 ± 49	585 ± 44	526 ± 49	484 ± 57
20% of crown length	564 ± 50	622 ± 42	572 ± 49	525 ± 53
30% of crown length	598 ± 52	665 ± 42	621 ± 49	570 ± 50
40% of crown length	637 ± 56	714 ± 45	667 ± 54	619 ± 53
50% of crown length	692 ± 63	769 ± 50	727 ± 55	677 ± 54
60% of crown length	769 ± 67	835 ± 54	799 ± 54	744 ± 56
70% of crown length	864 ± 66	919 ± 58	878 ± 57	818 ± 59
80% of crown length	971 ± 69	1019 ± 63	964 ± 59	902 ± 57
90% of crown length	1083 ± 71	1133 ± 65	1055 ± 53	996 ± 52
Crown completion	1187 ± 72	1251 ± 69	1151 ± 51	1086 ± 53

[1] Protocone = pr; paracone = pa, protoconid = prd; metaconid = med.

and Dean (2000) described the sample of anterior teeth of northern European origin, but in this study, we included additional molar teeth from the same population. Reid et al. (2002) and Reid and Ferrell (2006) have also previously described the sample of medieval Danish teeth included here. The sample of upper and lower third permanent molar teeth of recent North American origin was originally prepared for another study of a different nature and are described in Bracha (2004). For reasons appropriate to that study (Bracha, 2004), individuals were given the opportunity to define their own genetic origins, which allowed us to combine or divide this sample of teeth into a mixed, diverse group of modern North American origin or into a subgroup self-defined as Caucasian in origin.

The teeth of southern African origin were prepared and analyzed specifically for this study and were selected from a large sample of 727 teeth from 617 individuals representing 13 population groups (''tribes''). From this sample we chose 291 (Table 1). Any tooth demonstrating more than minimal attrition or with any evidence of caries, cervical abrasion, or other hard tissue pathology was excluded from this analysis. The teeth were collected between 1986 and 1987 during clinical procedures at the Dental Hospital of the University of the Witwatersrand and were curated in the School of Anatomical Sciences (then the Department of Anatomy and Human Biology). For each tooth, the individual's sex, age, and population group had been recorded in Dental Hospital records. In many cases, several teeth from one individual were made available for study. In all cases, teeth were extracted with consent. Following fixation, cleaning, and curation, permission from the Inspector of Anatomy in South Africa was granted both for the export of these teeth and their use in this study.

Methods

All the teeth in the African sample were sorted by tooth type and marked for subsequent histological sectioning in the buccolingual plane. A 200–300 μm slice was made perpendicular to the incisal edge or cusp(s) of the canine and molars and through the last formed enamel of the buccal cervix. In the case of lower molars, the plane of section was through the metaconid and protoconid and, in upper molars, through the paracone and protocone. Each slice was lapped and polished to a 60–80 μm-thick section, then cleaned and mounted for routine polarized light microscopy. The other European and North American samples of teeth were prepared in exactly the same manner in the same laboratory. A detailed description of the histological preparation techniques used is given in Reid et al. (1998).

Each ground section was examined under polarized light with a Zeiss Universal microscope. All measurements were made using a filar optical measuring eyepiece with ×16 and ×40 objectives. Each section was analyzed to determine the following: (1) the linear thickness of cuspal enamel; (2) cuspal enamel formation time based on the distance between adjacent daily cross striations in the inner, middle, and outer portions of the cuspal enamel; (3) the number of daily enamel cross

striations between adjacent long-period striae of Retzius in lateral enamel (the periodicity of the long-period striae); (4) the number of long-period striae in each tenth (or decile) of crown length; and (5) the total enamel formation time (defined as the time to form both cuspal and lateral enamel on the buccal aspect of all teeth, and lingual/palatal aspects of molar teeth).

Measurements of linear cuspal enamel thickness were made between the dentine horn and the outer enamel surface at the point coincident with the first perikyma. Where there was evidence of minimal wear at this point, the thickness of enamel lost was estimated. These estimates were based on the sectional morphology of unworn tooth types from the same sample and the contour of preserved accentuated markings in the cuspal enamel.

Cuspal enamel formation times were estimated using the distance between daily incremental markings (cross striations) measured in the inner, middle, and outer portions of the cuspal enamel. Three average measurements were, in turn, averaged to give the final average daily secretion rate, which when divided into the enamel thickness, gave an estimate of the number of days of enamel formation along a straight line between the dentine horn and the enamel surface. A correction factor of 0.15 was then applied (Risnes, 1986) to take account of average enamel prism deviation from this straight line.

The number of days between adjacent long-period lines (periodicity) in the lateral enamel of each tooth was determined by two methods, both using a $\times 40$ objective (Reid and Dean, 2000). The first method involves direct counts of cross striations between adjacent long-period lines. The second involves dividing the distance between adjacent long-period markings by the distance between cross striations.

To calculate the length of the enamel surface for the purpose of dividing it into deciles, a filar optical measuring eyepiece with $\times 16$ objective was used. In anterior teeth, this was done on the labial surface, but in molar teeth, on the mesiobuccal and mesiolingual surfaces. Since tooth crowns have a slightly curved surface (less marked in some anterior teeth than others, but considerable in some molars), this length is usually greater than linear measurements of crown height (see discussion in Hillson and Bond, 1998; Dean and Reid, 2001). Thus, our measure of crown length over the tooth surface is not equivalent to crown height. The length of this surface was then divided into ten equal segments (deciles) between the cervix and the cusp tip or incisal edge. The number of long-period striae that emerged at the surface as perikymata was then counted within each decile and used to calculate the formation time in days for each decile of crown length. The total count of long-period striae in all ten deciles is equal to the total lateral enamel formation time. The total crown formation time is the sum of lateral enamel formation time and cuspal enamel formation time.

Estimates of the chronological age of enamel completion include an estimate of the age at initiation of each particular tooth type. Most reports of initial mineralization times of permanent teeth can be traced back to Logan and Kronfeld (1933). These authors dissected tooth germs from a small number of postmortem specimens of known age. However, Takiguchi (1966) made histological sections of each tooth from eight cadavers and used accentuated striae to cross-match the enamel forming at the same time in each individual dentition. She noted considerable variation in the initiation sequence of mineralization among the anterior teeth. Subsequently, FitzGerald (1995, 1998) and Antoine (2001) reviewed the literature and provided some new data for the age at initial mineralization of permanent teeth. Antoine (2001) noted as much as 250 days variation for estimates in some anterior teeth. In this study, essentially to be consistent, we chose to adopt the initiation times for anterior teeth given in Reid et al. (1998), Reid and Dean (2000), Dean and Reid (2001), and the rounded values given by Antoine (2001) and Reid et al. (1998) for M1s (birth) and M2s (3 years). A great deal of variation exists in the initiation time of M3, which can vary by more than 2 years between populations (Fanning and Moorrees, 1969; Tompkins, 1996; Liversidge, 2005). In this study, we used 8 years for M3 initiation, but are aware M3 may initiate closer to 7 years or 9 years in some populations.

The initiation times given in Reid and Dean (2000) and Reid et al. (1998) are 128 days in upper central incisors, 383 days in upper lateral incisors, 274 days in upper canines, 90 days in lower central incisors, 146 days in lower lateral incisors, 200 days in lower canines, and 1059 days in second permanent molars. Initiation ages for M1 were presumed to be at birth. M_2 initiation was presumed to be 3 years (Reid et al., 1998; Antoine, 2001) and M3 initiation, 8 years (Liversidge, 2005).

Results

The summary statistics for buccal crown length, cuspal enamel thickness, and cross striation periodicity for anterior teeth are given in Table 2 and, for posterior teeth, in Table 3. The calculations of enamel formation time for each decile of crown length and of the total enamel formation time for each tooth type for anterior teeth appear in Table 4 and, for posterior teeth, in Table 5. A summary of the data for each decile of crown length in the southern Africans and northern Europeans is also presented in Fig. 1 for anterior teeth and in Fig. 2 for posterior teeth. Chronological estimates of enamel formation that include initiation times are presented for southern African and northern European anterior teeth and for the longest forming cusps of molars in Figs. 3–4.

Stria periodicities

Stria periodicities show a remarkable consistency across all of the samples and all of the tooth types. The highest mean values occur in southern African anterior teeth, in which the grand mean for all tooth types is 9.1. This appears to be due to a larger number of high periodicities of 11 or 12 days than in other samples. The lowest periodicities occur in the North American sample of molars, in which the grand mean for upper M3s is 7.8. In the North American sample, there are no periodicities above 9 days. Since long period stria periodicity is always a whole number of days, modal values can be

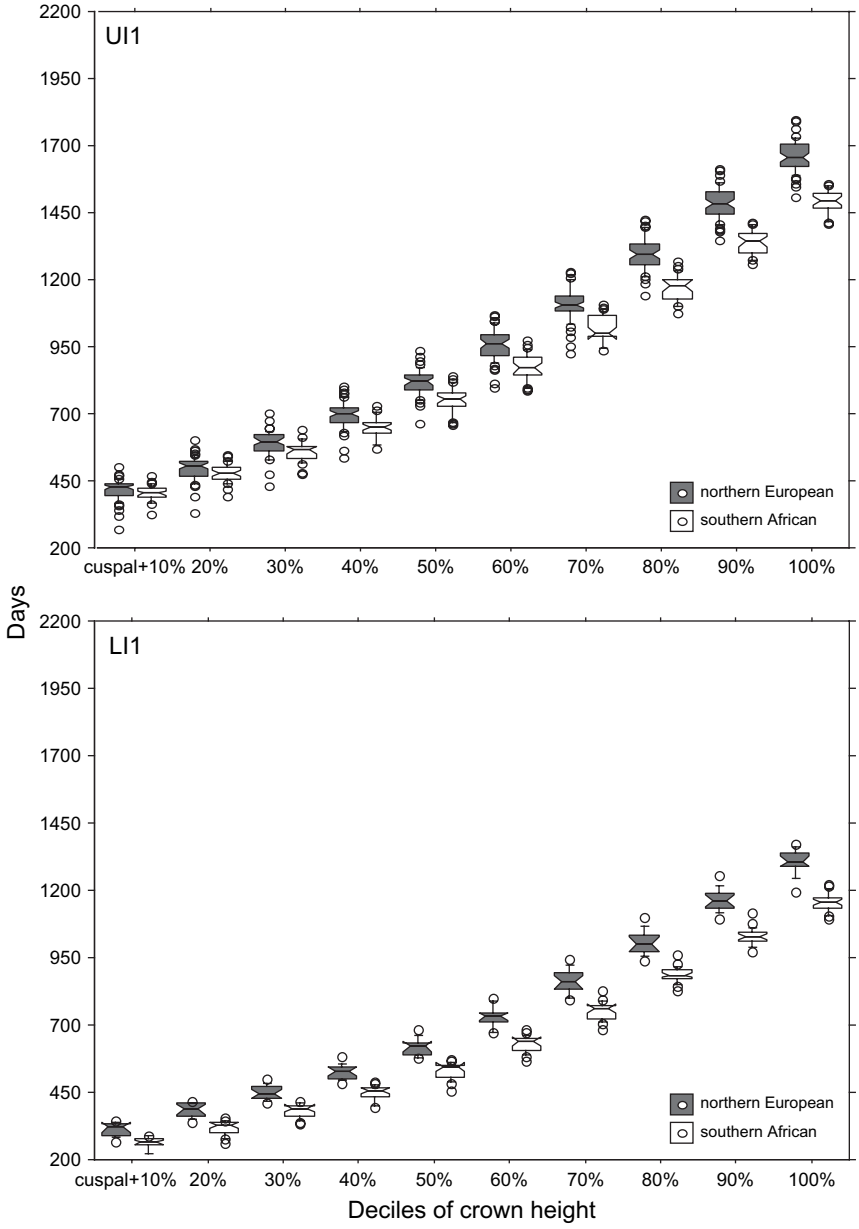


Fig. 1. Box plots showing the time taken (days) to form each decile of crown length (mm) for each anterior tooth type. Cuspal enamel formation times, but not the initiation times, are included in the times for each decile. The five horizontal lines indicate the 10th, 25th, 50th, 75th, and 90th percentiles and the notches represent a 95% confidence interval around the median. Outliers are plotted as open circles.

more useful than mean values when sample sizes are large. The modal periodicity is 8 in all molar tooth types except two, in which it is 9 (southern African LM1 and LM2). However, it is 8 in only three anterior tooth types (northern European LC, LI1, and southern African LC). Each of the remaining anterior tooth types has a modal periodicity of 9, or in two cases (southern African UI1 and UI2), a higher modal periodicity of 10 days. When all posterior teeth from all samples are combined, the modal value is 8 days, and when all anterior teeth are combined the modal value is 9. FitzGerald (1995) previously noted high periodicities among a sample of South African anterior teeth and commented on the strong association between high periodicities and low stria numbers, as well as the high degree of negative correlation between these variables, particularly among canines and lateral incisors. These and other issues relating to stria periodicities and lateral enamel formation times are discussed further in forthcoming papers (Guatelli-Steinberg et al., 2005; Reid and Ferrell, 2006; Smith et al., in press).

Cuspal and lateral enamel formation times

Cuspal enamel formation times in the present sample of southern African anterior teeth are almost identical to those reported previously for northern Europeans (Reid and Dean, 2000). Only the formation times of lower central incisors are shorter in the southern African sample (Fig. 1; Table 2). This result contrasts with lateral enamel formation times in

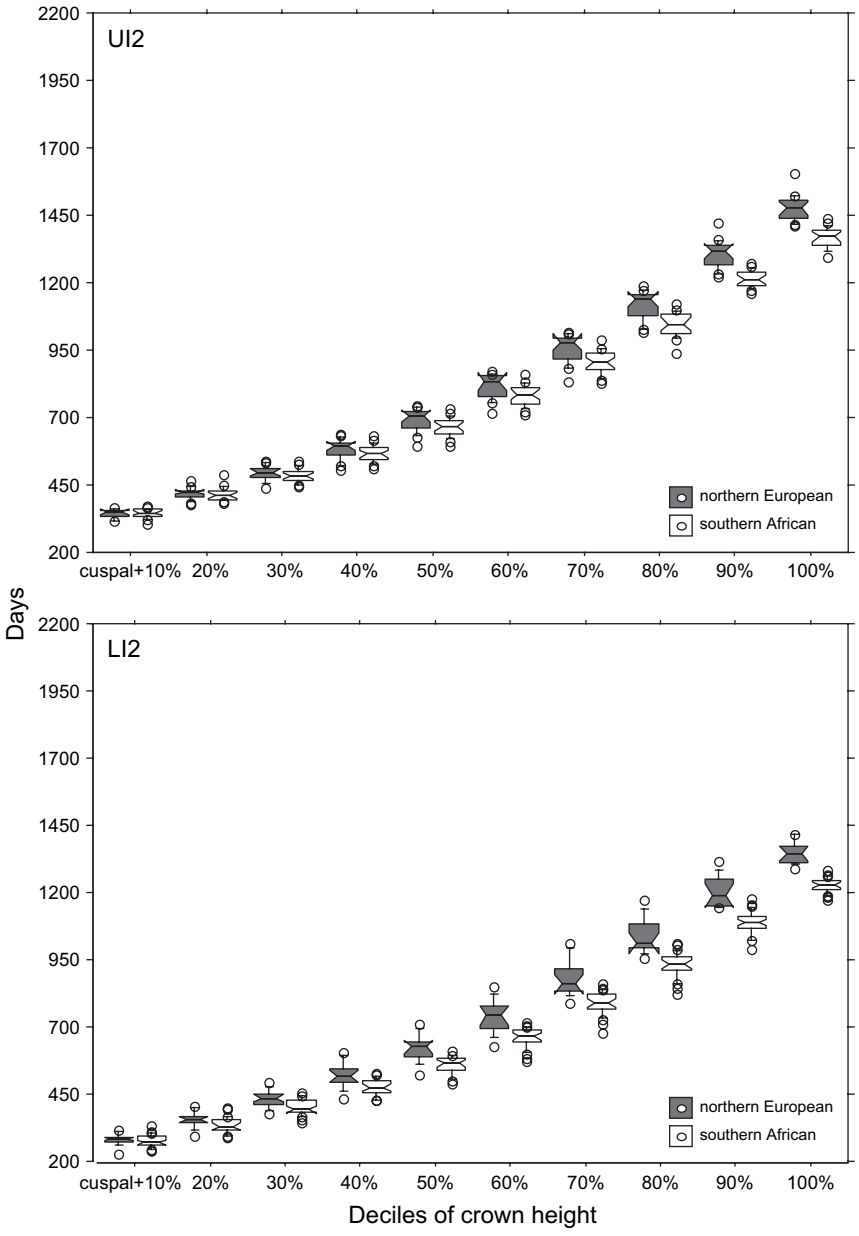


Fig. 1 (*continued*)

anterior teeth, which become increasingly shorter in the southern African sample from the first to last decile compared to northern Europeans (Fig. 1; Table 4).

In posterior teeth, the similarities and differences between the two populations are more complex. Cuspal enamel in the southern African lower M1s have cuspal enamel that forms in less time (in both the metaconid and protoconid) than in the northern European sample (Fig. 2; Table 3). These differences in cuspal enamel formation times are less marked in the upper M1s. A gradual trend toward longer enamel formation times through the deciles of crown length exists in both the northern European and southern African samples, but is more marked in the former, which results in slightly longer enamel formation times in the northern European sample than in the southern African sample. However, to put this into perspective, there is only a 71-day difference in mean M1 protoconid and 114-day difference in M1 protocone total enamel formation times between the two samples.

When both mesial cusps of the sample of M2s and M3s are compared, few differences emerge between the samples (Fig. 2). In both samples, the lower M2 metaconid cuspal enamel takes less time to form than the protoconid cuspal enamel, but the difference is less marked than in the lower M1. This difference in formation time between the cusps does, however, become more marked as the deciles of crown length cumulate to crown completion, but homologous cusps in both samples take nearly identical times to complete enamel formation. The M3 protocone shows the least difference between the two samples in cuspal enamel formation time of

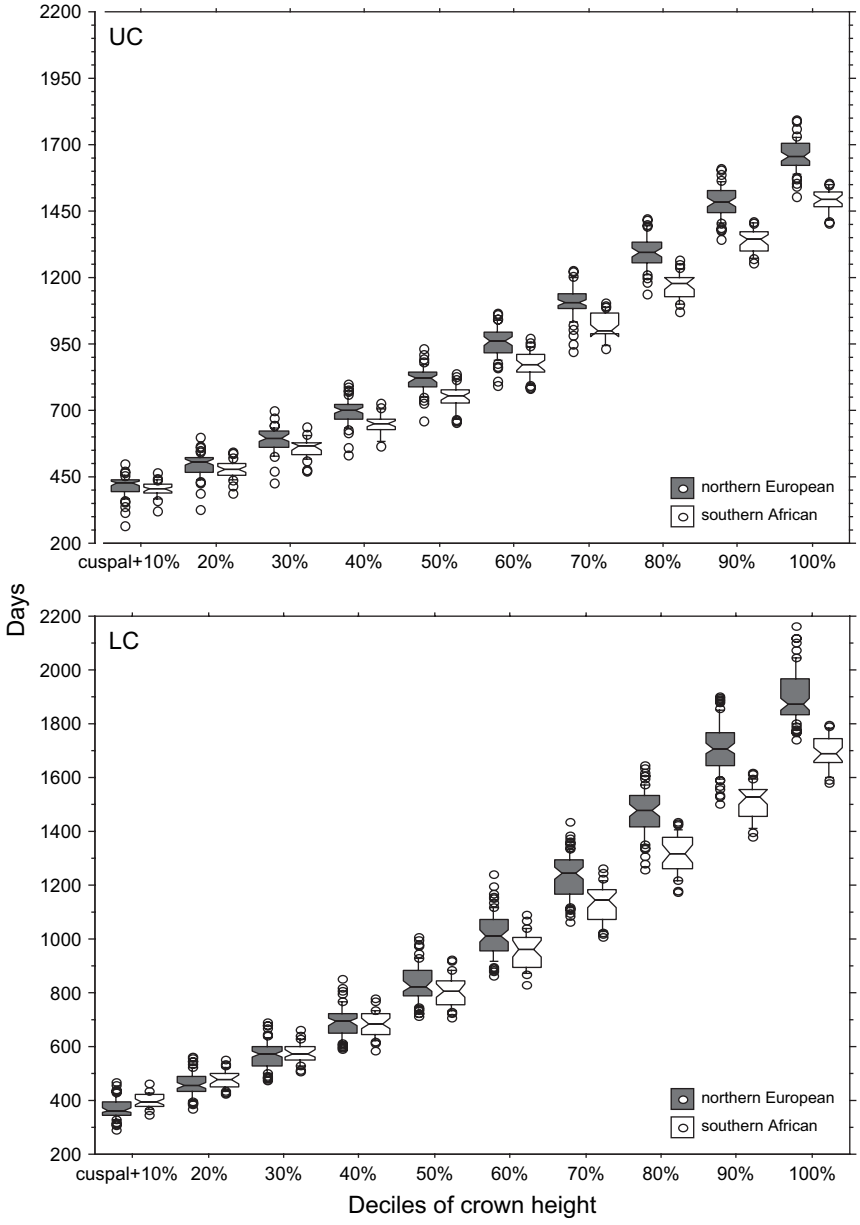


Fig. 1 (*continued*)

all the molars. However, one further difference between the two samples is the total time taken to form the paracone. This cusp forms more quickly in the northern Europeans than in the southern Africans, in whom it tends to be more equal to the formation time of the protocone. This is most marked in the M3 paracone. It would be interesting to know if any differences in cuspal area, of the kind measured by Wood and Engleman (1988), Macho and Moggi-Cecchi (1992) and Dinh and Harris (2005) mirror this difference in formation time. Apart from this difference, the two longest-forming M3 cusps (protocone and protoconid) in the southern African and northern European samples are nearly identical in their total enamel formation times. Cuspal enamel formation times in the modern North American sample of upper M3s (but not lowers) stand out as being greater (see Table 3). This difference remains unchanged when the sample is taken as a whole or when the Caucasians are split from the total sample and examined independently. This difference appears to be established by the first decile of crown length and it is cuspal enamel—not the subsequent lateral enamel growth—that underlies this.

Crown formation times

Within the anterior dentition, lower canines take longest to form enamel in all three populations (Fig. 3). The greatest difference in the mean total enamel formation time between populations is about 12 months—5.2 years in southern Africans vs. 6.2 years in northern Europeans. However, the larger sample of medieval Danish lower canines fall midway between these samples, taking an average of 6.5 months less time to complete enamel formation than the Newcastle sample. In lower central incisors, which complete crown formation

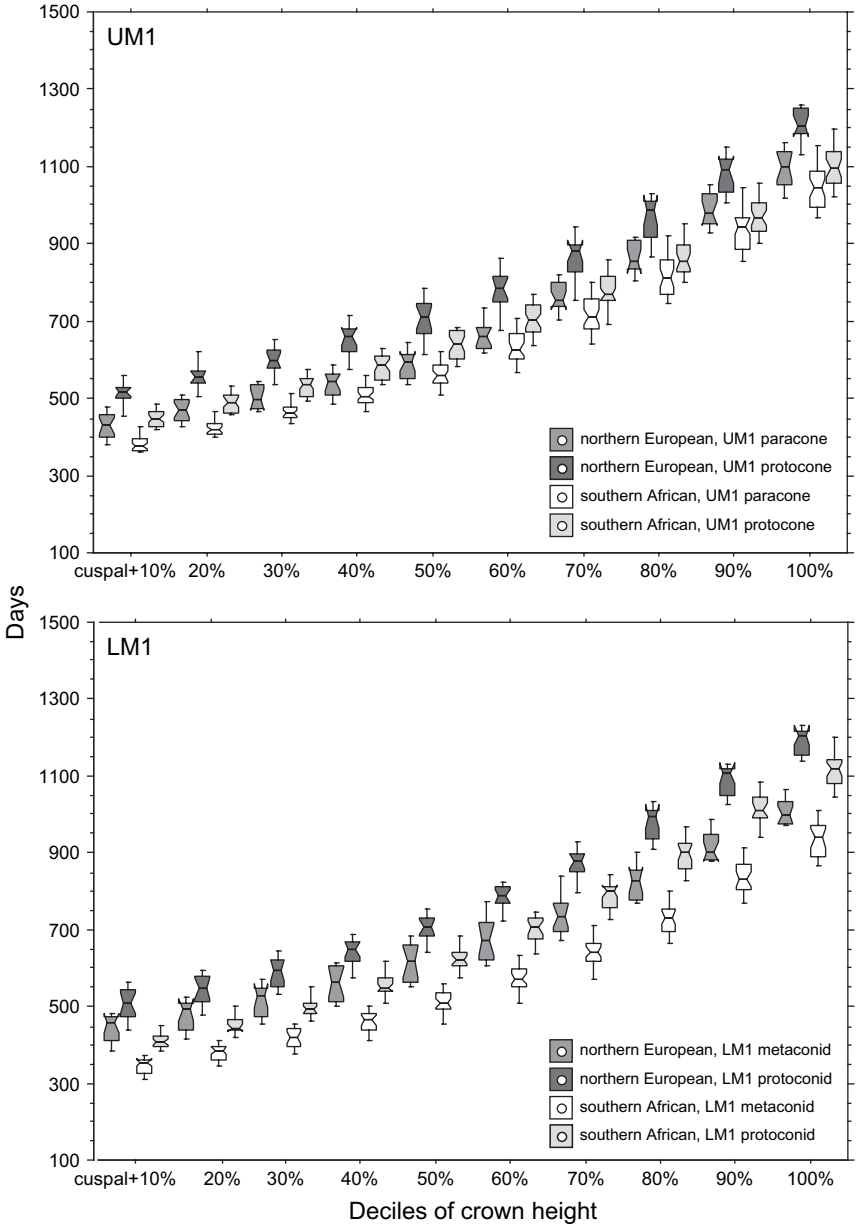


Fig. 2. Box plots showing the time taken (days) to form each decile of crown length (mm) for both anterior cusps of each posterior tooth type. Cuspal enamel formation times, but not initiation times, are included in the times for each decile. The five horizontal lines indicate the 10th, 25th, 50th, 75th, and 90th percentiles and the notches represent a 95% confidence interval around the median. Outliers are not plotted for molar tooth types to avoid confusion.

first, the difference is less marked. Mean times for total crown formation are 3.4 years and 3.8 years, respectively. In all anterior tooth types, however, the difference between populations accrues gradually from the cusp to the cervix as lateral enamel formation proceeds. A clear pattern emerges when the northern European and southern African populations are compared. Total enamel formation times are shorter in each of the southern African anterior teeth. Mann et al. (1991) previously reported low perikymata counts on African anterior teeth, which may contribute to their shorter crown formation times.

Much less difference in total enamel formation time exists between the molar cusps of all groups than between the anterior teeth (Fig. 4). However, total cuspal enamel formation times are not equivalent to total crown formation times since the greatest total molar enamel formation times presented here for individual cusps may still not span the whole period of time between earliest initiation and the last formed enamel of each molar tooth type. Usually, the paracone and protoconid initiate first, with the protocone and metaconid next, often almost immediately (Dean and Beynon, 1991; Reid et al., 1998). The mean times for protoconid formation in the lower molars are 3.25 years (M1) and 3.17 years (M2 and M3) in the northern European sample and 3.06 years (M1), 3.2 years (M2), and 3.27 years (M3) in the southern African sample. These differences are negligible compared to those reported in many radiographic studies and remarkable because they are so similar between molar tooth types. The mean times for protocone formation in molars are 3.32 years (UM1),

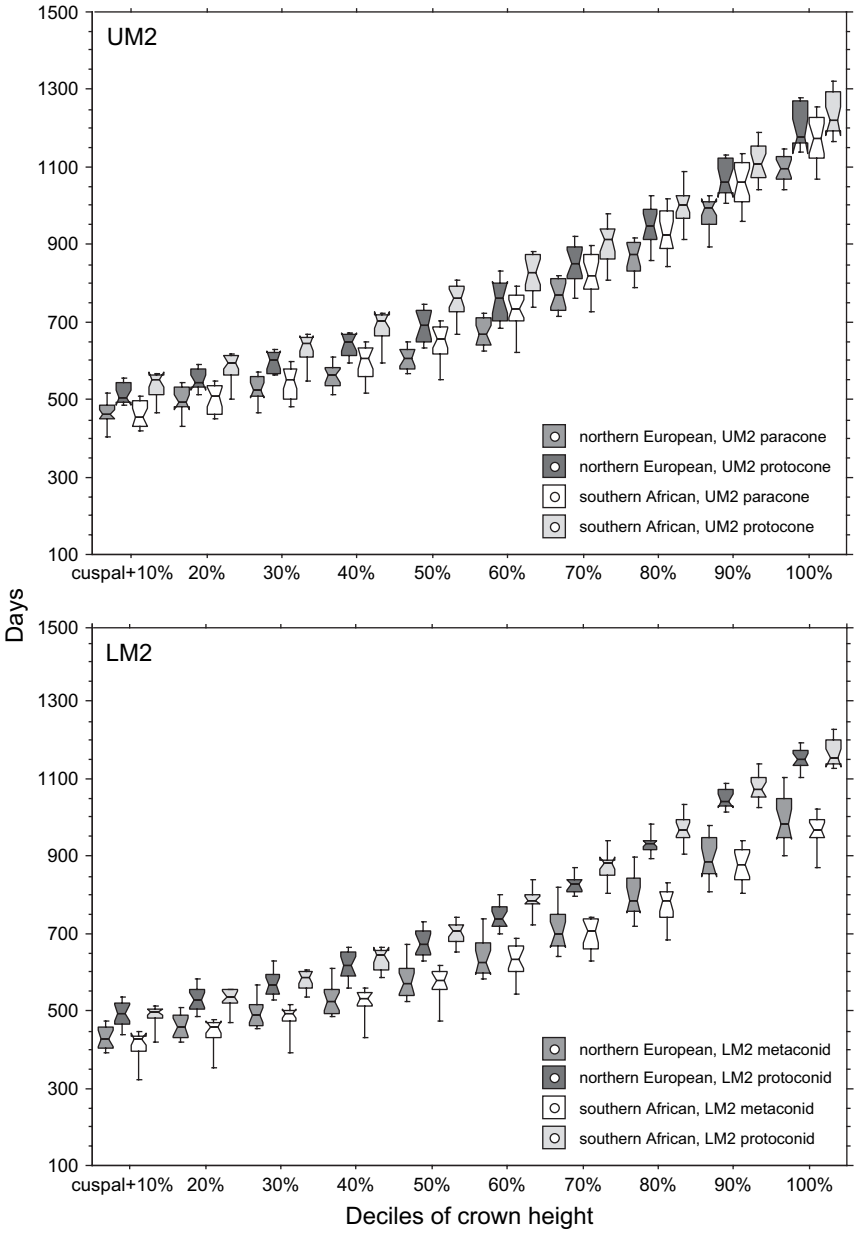
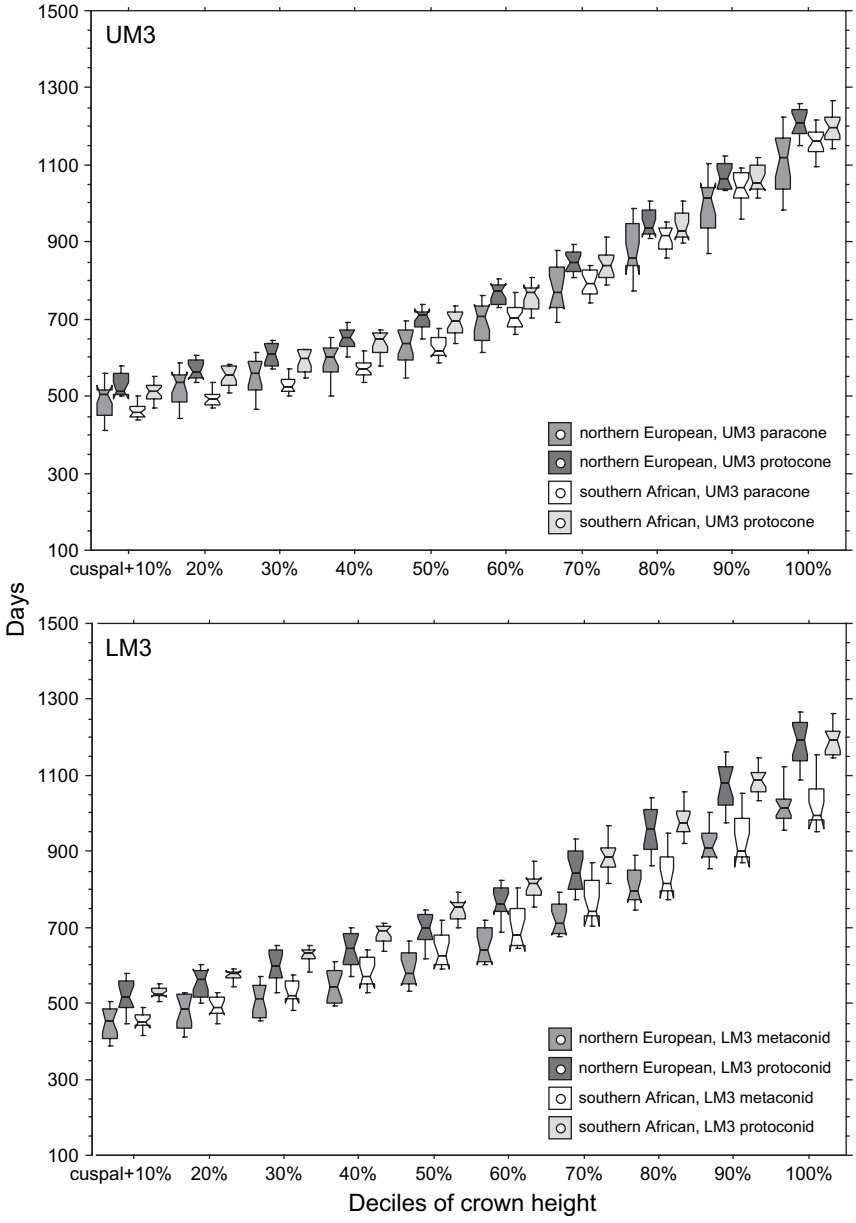


Fig. 2 (*continued*)

3.38 years (M2), and 3.35 years (M3) in the northern Europeans and 3.0 years (M1), 3.38 years (M2), and 3.28 years (M3) in the southern African sample (Fig. 4; Table 5). Again, these differences are negligible and suggest little gradient between M1 and M3. In our sample of modern North Americans, the mean times for M3 metaconid and protocone enamel formation are, respectively, 3.22 years and 3.45 years (Table 5).

Discussion

FitzGerald (1995) noted that, with the exception of the canine crown formation times (7.0–7.9 years) given by Kajiyama (1965), all those estimated from histological studies fell within the ranges documented by radiographic studies. Our results provide further support for that observation, despite the tendency in this study and in Reid and Dean (2000) for greater estimates of mean crown formation times than in some radiographic studies. Even though we have identified differences in enamel formation times between the samples studied here, a key finding is how small these differences are. Another is how much less variation there appears to be in total crown formation times between the samples compared with most data derived from radiographic studies. For example, in the northern European and southern African samples, the range (± 2 SD) of values for lower M1 crown formation times are only 0.43 and 0.6 years, respectively, compared with 1.9 years (Gleiser and Hunt, 1955) and 1.1 years (Moorrees et al., 1963; Harris and Buck, 2002). In their review of the literature, Simpson and Kunos (1998) identified considerable variation in the mean chronological age of mandibular canine crown



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formation times among radiographic studies. These ranged, in females and males, between 2.9 and 3.3 years, respectively, in the study of Demirjian and Levesque (1980), to between 5.7 and 6.0 years, respectively, in the study of Nolla (1960). Moorrees et al. (1963), in their radiographic study, reported a range (± 2 SD) of ages for lower permanent canine crown completion as 1.8 years. In our study, chronological estimates of mean lower canine crown formation times fell within a much tighter range: 5.2 years (southern Africans), 5.7 years (Danish sample), and 6.2 years (Newcastle sample), with small ranges of variation (± 2 SD) of 0.6 years (African sample), 0.65 years (Danish sample), and 0.8 years (Newcastle sample). There are two potential explanations for these findings.

In most histological studies, the definition of the end of enamel formation is different to that in radiographic studies. Enamel on the buccal and lingual aspects of lateral radiographic images is not usually visible and the end of enamel formation can only be recorded mesially and/or distally in these studies (Beynon et al., 1998; Simpson and Kunos, 1998). Defining enamel completion on the buccal or lingual aspect of teeth probably contributes to the greater mean enamel formation times reported here than in many radiographic studies. However, it is also likely that histological studies are able to define the end of enamel formation more accurately than radiographic studies, which is probably the reason radiographic studies report greater variation. Initial mineralization of a tooth is hard to detect on radiographs, but is also a very variable event (FitzGerald, 1995; Reid et al., 1998; Antoine, 2001), especially in M2s and M3s (Liversidge, 2005). Longitudinal radiographic studies that

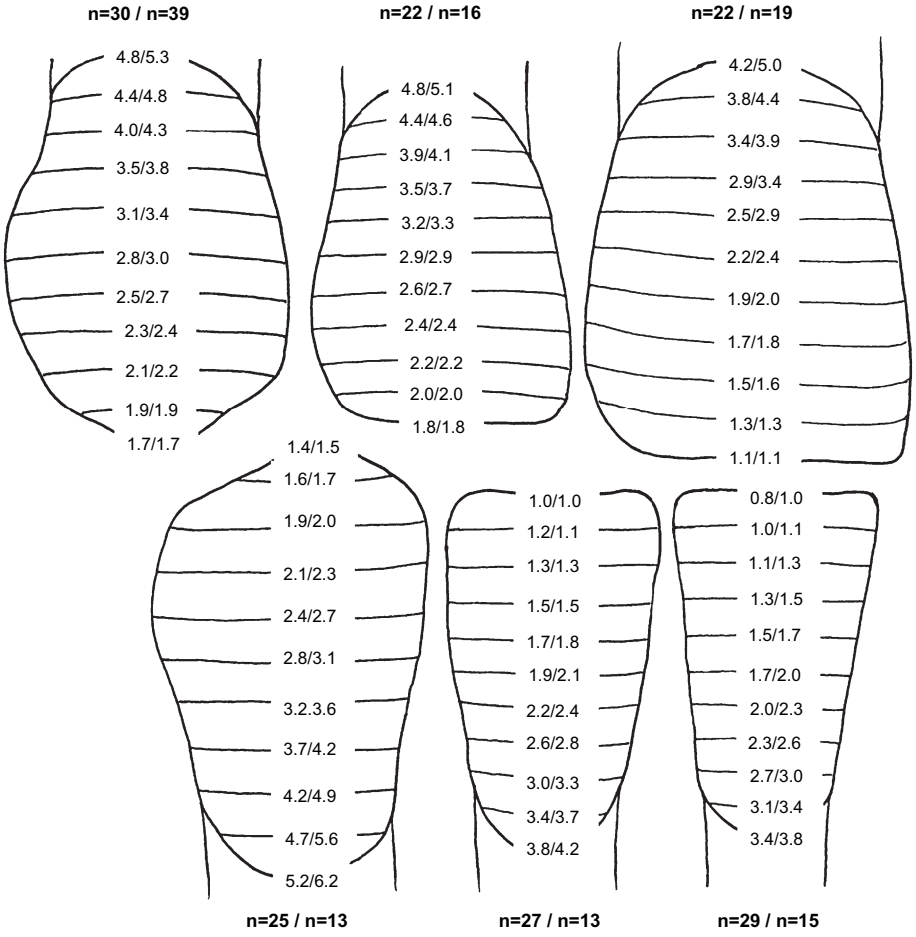

Fig. 3. Mean estimates for chronological ages of enamel formation in anterior teeth for each decile of crown length rounded up or down to 0.1 year for the southern African sample vs. the northern European sample. Both cuspal enamel formation times and initiation times are included in these estimates.

record the chronological age of crown completion inevitably incorporate variation in initial mineralization into the estimates of age at crown completion. Antoine (2001) reported a range of initiation times for anterior teeth that would easily account for the increased variation in crown formation times recorded in many radiographic studies. By being able to exclude initiation times we may now have a clearer idea about variation in enamel formation times in each tooth type. This is especially useful for comparative studies in which only isolated teeth are available and no record of chronological age exists.

The sample sizes for each tooth type included in this study are large enough to identify differences in the way enamel forms over time between populations. Crown formation time is the sum of cuspal enamel formation time and lateral enamel formation time. Enamel formation is a continuous and seamless process, but defining an imaginary junction between these two zones, or regions, makes it easier to collect and compare data from the tooth sections. Estimates of cuspal enamel formation time depend entirely upon how cuspal enamel thickness is defined. The definition used in this study is a linear distance between the dentine horn and the point at which the first perikyma emerges at the cusp tip (or central mamelon of incisors). However, surface enamel morphology can vary greatly over the cuspal region, and other measurements designed to record enamel thickness in different positions are not necessarily comparable with the one made here. For these reasons, any apparent differences in cuspal enamel formation times between populations need to be viewed with some caution, even though two potentially significant differences stand out. The M1 and the lower I1 in southern Africans appear to take less time to form cuspal enamel than northern Europeans. However, the small amounts of wear, or polish, tolerated in this study suggest that these differences might not stand up to more rigorous investigation. Another observation that may account for the slightly thinner cuspal enamel and reduced cuspal enamel formation times recorded here is a high frequency of cuspal dimples or depressions. These run deep into the buccal cuspal enamel in many southern African M1s and reduce enamel thickness over the dentine horn. In so doing, they result in a greater number of perikymata extending into the base of the dimple than would otherwise be the case, and they reduce the linear measurement we have used to calculate cuspal formation time. Thus, while the sum of cuspal and lateral enamel formation times remains unaffected, cuspal formation times are reduced and the time taken to form the first decile of crown length increased by a few perikymata. Similar dimples have also been observed in samples of Japanese molars (Kono et al., 2002; Suwa and Kono, 2005); these influence enamel

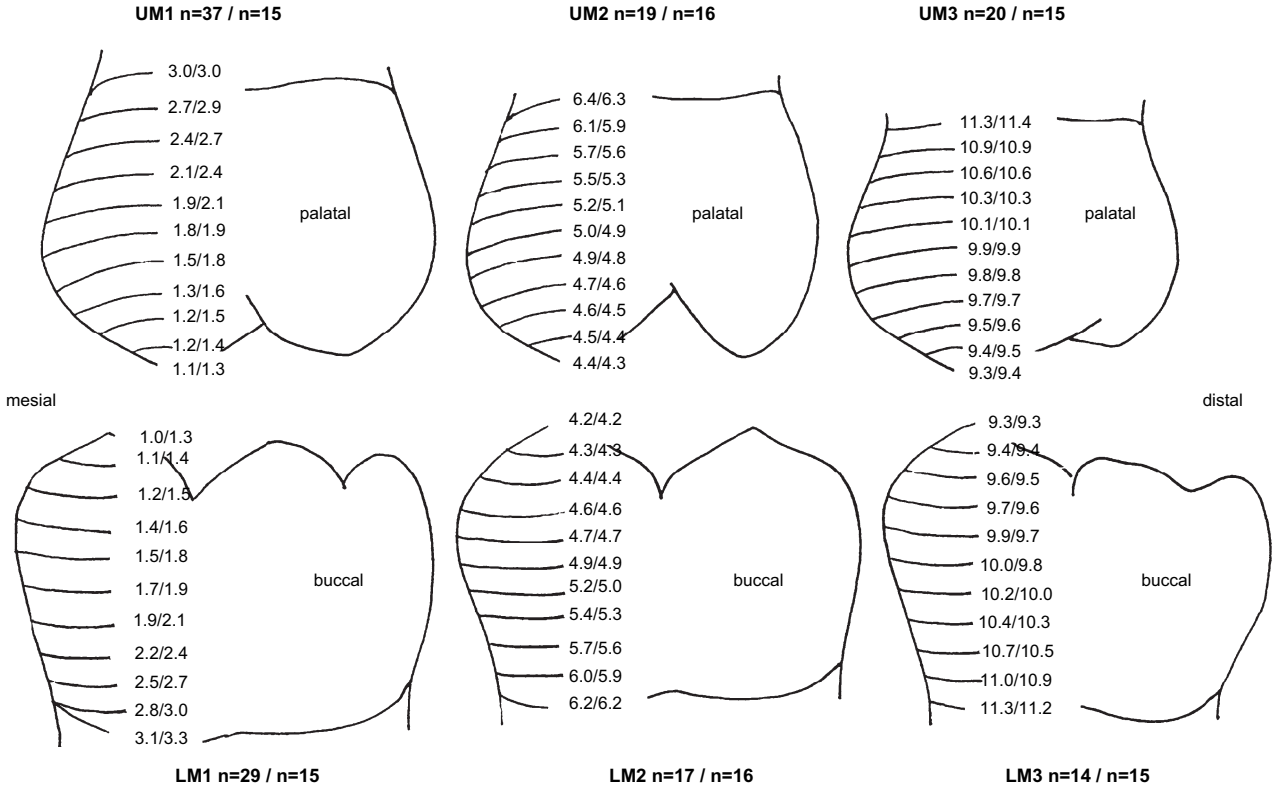

Fig. 4. Mean estimates for chronological ages of enamel formation in molars for each decile of crown height, rounded up or down to 0.1 year, for the southern African sample vs. the northern European sample. Only data for the longest forming cusps in upper and lower molars (protocone and protoconid) are shown. Both cuspal enamel formation times and initiation times are included in these estimates.

thickness measurements in the cusp. Suwa and Kono (2005) have discussed cuspal enamel development in molars in more detail.

Each of the anterior crown formation times is consistently shorter in southern Africans than northern Europeans. This difference seems to arise gradually through tooth growth and cumulates as each decile of crown length forms. Figure 1 combines data for both the Danish and Newcastle samples of canines, but the mean values for crown formation times in these two samples are, in fact, as different from each other as the Danish sample is from the southern African sample (Table 4). Mean Danish crown formation time is 0.48 years greater than in the southern African sample, and mean Newcastle crown formation time is 0.54 years greater than that of the Danish sample. While these data for lower canines show the greatest differences in crown formation times between the populations, they highlight how small these differences actually are in reality.

Molar enamel formation times seem even less different from one another than anterior crown formation times. Once again, the differences are remarkably small. The greatest differences are found in M1s and M3s. The mean M1 protoconid formation times of southern Africans are shorter than in northern Europeans at the last decile of enamel formation by 71 days. Interestingly, this is slightly less than the difference of 96 days at the end of the first decile of enamel formation, suggesting that the difference lies entirely in the shorter cuspal enamel formation time. Southern Africans, however, have greater M3 paracone formation times than the northern European sample (by 131 days). However, both of these are exceeded by the North American sample, in which total mean paracone formation time is 51 days and 182 days greater than in the southern African and northern European samples, respectively. It follows that differences in mean enamel formation times for individual cusps within samples of molar teeth sharing a comparatively close genetic origin (modern North American and northern European M3s) are as great as those differences between samples of molar teeth with more diverse genetic origins (southern African and northern European M3s).

These findings suggest that it would seem reasonable to expect similar variation among other past and present populations of modern humans. The data presented here do, however, give a clearer idea of the range of variation that we might expect to occur worldwide, and they do describe some of the growth processes that underlie this variation. From this point of view, the combined data set presented here provides a sound basis with which to explore growth processes involved in enamel formation among non-human primates and among fossil hominids including, for example, Neandertals (Ramirez Rozzi and Bermudez de Castro, 2004).

Conclusions

Previous studies on tooth development have documented considerable variation in enamel formation times. In most cases these have been radiographic studies where enamel

completion was recorded on the mesial and distal aspects of developing teeth and where variation in tooth initiation times were inevitably incorporated into the data that describe enamel formation times. The histological data presented here for modern humans were collected using methods that are repeatable on both living and fossil primate teeth. Fractional stages of enamel formation were recorded on the longest forming aspects (buccal or lingual) of incisors, canines, and molars in large samples of isolated teeth of southern African, northern European, and North American origin. Cuspal enamel formation times in anterior teeth were very similar for all tooth types. Southern African first molars took less time to form cuspal enamel but had proportionally greater paracone formation times in third molars than the first molars of northern Europeans. Total crown formation times in anterior teeth were consistently shorter in southern Africans but by small amounts. Mean crown formation times were 3.4 years vs. 3.8 years in the shortest forming lower central incisors, and 5.2 years vs. 6.2 years in the longest forming lower canines. Among molars, there was surprisingly little variation in mean crown formation times, with all molars from all samples completing enamel formation between 3.0 years and 3.4 years. For all molars and all anterior tooth types in our samples, ± 1 SD at crown completion was never more than 100 days and often less than 50 days. The crown formation times reported here fall among the higher estimates made from radiographic studies, but show less variation both within and between populations than previously reported.

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