Lateral enamel growth in human incisors from Çatalhöyük in Turkey

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Abstract

Objectives

Whereas the differences in lateral enamel growth between fossil and modern populations have been well documented in recent years, few studies report on the variability in perikymata counts and distribution between modern human populations. There is a need for information on modern human populations from a wide range of geographical regions and archaeological populations to determine whether existing patterns are representative. The aim of this paper is to document enamel surface microstructures in human teeth from a previously unknown region and time period comprehensively.

Methods

Perikymata counts and distribution are assessed in a large sample of relatively unworn permanent incisors from the mid-Holocene site of Çatalhöyük in Turkey.

Results

All four incisor types exhibit total perikymata counts that are intermediate between values for modern samples from northern Europe and South Africa. The perikymata distribution followed the modern human pattern of a marked decrease in spacing in the cervical half of the crown.

Discussion

The existence of regional differences in perikymata number and distribution demonstrates the importance of documenting enamel microstructures in a wider range of modern human populations, both geographically and chronologically.

Introduction

There has been a dramatic increase over the last decade in the number of studies using enamel microstructures to address questions concerning the pattern and rate of development in human evolution. Counts of perikymata and striae of Retzius have been used to investigate possible differences in tooth crown development between modern humans and fossil species (Guatelli-Steinberg et al., 2005, 2007, 2012; Guatelli-Steinberg and Reid, 2008, 2010; Ramirez Rozzi and Bermúdez de Castro, 2004; Reid and Dean, 2000, 2006; Smith et al., 2007a, 2010).

Perikymata are incremental growth lines that appear on the surface of enamel as a series of grooves (Beynon, 1992; Hillson, 2014). They provide a particularly useful way of evaluating dental development as they can be counted and measured without involving destructive techniques. Growth chronologies for individual teeth can be constructed based upon perikymata counts in conjunction with population averages for perikymata periodicities and assumptions about ages at crown formation initiation and the duration of appositional enamel completion. This enables estimation of crown formation times in modern and fossil teeth and, in cases where tooth crowns are still developing, estimation of age at death (Beynon and Wood, 1987; Boyde 1964; Bromage and Dean, 1985; Dean et al., 1986; Dean, 1987; Dean and Smith, 2009; Lacruz, 2007; Lacruz et al., 2006; Lacruz and Ramirez-Rossi, 2010; Machiarelli et al., 2006; Smith et al., 2007a; Suwa et al., 2009).

Perikymata distribution patterns, which are based on counts of perikymata along the crown surface, can be assessed and compared between fossil and modern human teeth (Bermudez de Castro et al., 2003; Dean and Reid, 2001; Ramirez- Rozzi and Bermudez de Castro, 2004; Guatelli-Steinberg et al., 2007, 2008; Guatelli-Steinberg and Reid, 2008, 2010; Hlusko et al., 2013; Modesto Mata et al., 2015; Reid et al., 2008). A decile approach, which consists of considering the number of perikymata per one-tenth of crown height, is generally used for these comparisons. This approach has revealed that differences between modern humans and Neanderthals in crown formation are concentrated in the cervical part of the tooth and are manifested as a difference in the number of perikymata in later forming deciles (Guatelli-Steinberg et al., 2007; Guatelli-Steinberg and Reid, 2010).

Finally, a sudden change in the distance between adjacent perikymata in one tooth type, which corresponds with a change in perikymata spacing in another tooth type from the same jaw, can indicate a systemic disruption to enamel secretion (Hillson and Bond, 1997). The investigation of these disruptions (furrow-form or linear enamel hypoplastic defects) provides the opportunity to build a comprehensive picture of developmental disruptions experienced by an individual during childhood (Antoine et al., 2005; Bullion, 1987; FitzGerald and Saunders, 2005; FitzGerald et al., 2006; Guatelli−Steinberg, 2003; Guatelli−Steinberg et al., 2004; Hassett, 2011; Hillson, 1992; Hillson and Bond, 1997; King et al., 2002, 2005; Reid and Dean, 2000; Rose, 1977; Rose et al., 1978; Temple, 2010; Temple et al., 2012).

Perikymata distribution patterns are affected by daily secretion rates, enamel extension rates and long-period line (striae of Retzius) periodicities (Hillson, 2014). Daily secretion rates determine how fast a tooth crown grows in thickness ("outward growth") and are estimated using measurements of cross-striation length, with larger values indicating faster daily secretion rates (Fig. 1). Faster secretion rates in the outer enamel can change the angle at which striae of Retzius emerge on the surface as perikymata (Dean and Shellis, 1998). Shallow angles in the occlusal part of the crown cause perikymata to be situated relatively far apart, whereas sharper angles in the cervical part of the crown are linked to the progressive decrease in perikymata spacing from occlusal to cervical (Hillson and Bond, 1997). Daily secretion rates within human permanent teeth vary from the inner enamel (close to the enamel-dentine junction or EDJ) to the outer enamel (Beynon and Reid, 1987; Beynon et al., 1991; Shellis, 1984; Smith et al., 2007b). Shellis (1984) noted differences in enamel daily secretion rates between permanent and deciduous teeth. Differences in daily secretion rates within molars have been compared previously (Lacruz and Bromage, 2006; Mahoney, 2008), but differences between and within other modern human permanent tooth types or between modern human populations have not yet been systematically quantified for analogous regions.

The rate at which ameloblasts differentiate along the enamel-dentine junction (EDJ) -the extension rate- determines how fast a tooth crown grows in height (Dean, 2009). Enamel extension rates can be measured at regular intervals along the EDJ by counting cross-striations following the direction of enamel prisms over a pre-defined distance (thickness) of 200µm along the direction of the path of the enamel prisms and then tracking back to a lower position on the EDJ following a line drawn along or parallel to a stria of Retzius or accentuated line. The enamel extension rate is calculated by dividing the distance between the two points on the EDJ between the number of cross striations within the pre-defined 200µm (Dean 2009, 2012; Guatelli-Steinberg et al., 2012). Shellis (1984) observed a curvilinear relationship between the inclination of the incremental lines to the EDJ and enamel extension rates, but also noted that the marked variation of extension rates associated with sharp angles prevents accurate estimations of enamel extension rates.

As enamel extension rates influence the direction of ameloblast movement (i.e. the angles the striae of Retzius make with the EDJ as well as the with the crown surface), it is expected that this rate will affect perikymata spacing (Fig. 1). Guatelli-Steinberg and colleagues (2012) have shown that the decline in enamel extension rate from the cuspal to cervical part of modern human tooth crowns is associated with a higher number of perikymata per decile. They have also shown a statistically significant association between tooth type and the pattern of change in enamel extension rates and populational differences in the rate of decline in enamel extension rate from the cuspal to the cervical part of the crown (Guatelli-Steinberg et al., 2012).

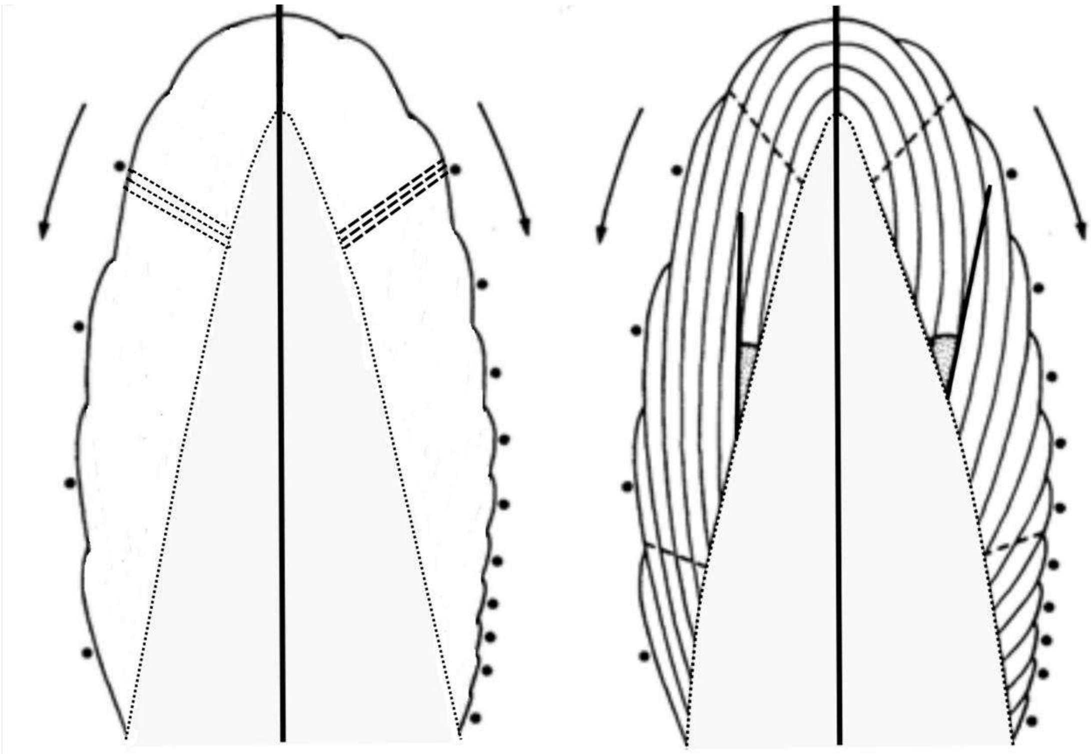

Figure 1: Left. Schematic representation of differences in daily secretion rates (DSR or 24 hours of growth) assuming all other variables remain equal. Left: small dashed line = low DSR, Right: large dashed line = high DSR (adapted from Boyde 1964 and Aiello and Dean 2006). Right. Schematic representation of differences in enamel extension rates. Left: sharp angle between enamel-dentine junction (striped line) and the striae of Retzius, faster enamel extension rate and fewer perikymata on the crown surface (marked by dots). Right: Greater angle between enamel-dentine junction and the striae of Retzius, slower enamel extension rate and more perikymata on the crown surface (adapted from Boyde 1964a and Aiello and Dean 2006)

Long-period line periodicities are estimated based on the cross-striation count between adjacent striae of Retzius (Hillson, 2014). Periodicities have been shown to stay constant within tooth crowns and between all tooth types in a single dentition, but can range from six to twelve days across modern human individuals (Reid and Dean, 2006). With regard to the influence of striae periodicities on total perikymata counts, Reid and Ferrell found that higher periodicities are associated with lower perikymata counts (Reid and Ferrell, 2006, also see Guatelli-Steinberg et al., 2012). In other words, if one individual's teeth form for the same time as another individual, but with a lower periodicity, each of the former's tooth crowns will show a higher total number of perikymata as well as a higher number of perikymata in every decile relative to the teeth of an individual with a higher periodicity.

The primary focus of recent studies of lateral enamel growth has been differences between fossil and modern populations rather than the variability between modern human groups. Relatively few modern human samples are available for comparison and the reported variation in perikymata numbers is very large (Table 1). Few studies report on the variation in perikyma characteristics between and within tooth types and as far as we know, no study has compared the variation between or within tooth types using matching teeth. The aim of this paper is to further our knowledge about the variation in modern human perikyma characteristics. Total perikymata numbers and perikymata distribution patterns are compared between individuals and individual teeth using published literature and new data on a population sample from Southwest Asia.

MATERIAL

Tooth wear can reduce the visibility of incremental structures or remove them altogether, thereby introducing error into the identification of the number and spacing of perikymata (Guatelli−Steinberg et al., 2004; King et al., 2002). One way to address this issue is to reconstruct crown heights and estimate the number of perikymata in the first two deciles based on those counted in the corresponding unworn deciles in other crowns of the same sample (Guatelli−Steinberg et al., 2007). An alternative is to limit these detailed studies to the relatively unworn dentitions of immature individuals (Hillson, 1992, Modesto Mata et al., 2015). Here we determine perikymata characteristics for a sample of 83 permanent incisors with minimal cuspal wear, defined as grade 1 using Smith's (1984) attrition scoring system. The sample includes 18 upper central incisors, 26 upper lateral incisors, 15 lower central incisors and 24 lower lateral incisors. The sample included teeth from 43 individuals, and, of these, 27 individuals were represented by more than one incisor. No antimeres were included in the study (Table 1).

The sample originates from the Neolithic site of Çatalhöyük located in the Konya plain, Turkey, dated between 7400-7100 BC to 6200-5900 BC (Hodder, 2013). Impressions of the tooth crowns were made during the 2008−2009 field season. The sample includes material from the Mellaart excavations as well as the 1993 to 2008 field seasons (Mellaart, 1998).

Data from modern human comparative samples were obtained from the published literature. Data on perikymata counts (including sample sizes, mean perikyma counts, standard deviation and confidence intervals) for extant human populations (Tables 2, 3) are available for Canadian Inuit, British (Newcastle upon Tyne, extracted during routine oral surgery) and South African (13 "tribes") samples (Guatelli-Steinberg and Reid, 2008; Modesto-Mata et al., 2015). Data on perikymata distribution are only available for the Newcastle and South African samples (Reid and Dean, 2000; 2006). A published dataset on cervical percentages was available for Canadian Inuit, British (Newcastle upon Tyne, extracted during routine oral surgery) and South African (13 "tribes") samples (Guatelli-Steinberg et al., 2007).

Table 1 : Incisors from Çatalhöyük

ID	Upper central incisor	Upper lateral incisor	Lower central incisor	Lower lateral incisor
10529		x		x
11608.1		x		
11982		x		
12528	x	x		
12876	x			
12935		x		
1425		x		
1484			x	x
15467		x		
15748	x	x		x
16125			x	x
16168	x	x		
16196	x	x	x	x
16601		x		x
16638		x		
16641	x		x	
16698	x	x	x	x
1884	x	x		x
1885	x		x	
19022		x		

19039		x		x
1913	x	x	x	x
1923	x			x
1925	x			x
1939/1922	x	x		x
1959			x	x
1960	x			x
2119		x	x	x
3529		x		
5608		x		
6681		x	x	x
6682	x	x	x	x
7541		x		
7576	x		x	
7579			x	
8113			x	x
8114		x		
8423		x		x
8729				x
8841			x	x
CH7k40	x			x
CH7k40(3)				x
CHEVI8(7l)		x		

Table 1: Details of the Çatalhöyük incisor sample

METHOD

A three−dimensional technique using the Alicona 3D Infinite Focus imaging microscope and software was used to record developmental features on the incisor enamel surfaces. The technique, using high−resolution casts of tooth crowns, allows for a direct on−screen comparison to be made between measurements and images. Using this new technique, perikymata can be counted and measured down the crown and perikyma spacing profiles constructed (Bocaege et al., 2010). A profile line was drawn on microscopic images of the tooth crowns, down the vertical axis of the tooth crown, from the first visible perikyma near the occlusal margin to the cemento−enamel junction at the cervical base of the crown. Positions (horizontal and vertical coordinates) of the perikyma grooves along this profile line were identified and recorded.

Mean perikymata counts, standard deviations and confidence intervals were determined for each incisor type for the Çatalhöyük sample. Visual comparisons were made with published ranges for Canadian Inuit, British and South African samples. Spearman Rank correlations were used to compare perikymata counts between matched pairs of incisors (i.e. different incisor types from the same dentition) from the Çatalhöyük sample. Comparisons were made between all six possible permutations of incisor pairs.

The spacing between pairs of perikyma grooves was calculated in a spreadsheet using the Pythagoras formula. Cumulative spacing was calculated by continuously adding the pair−by−pair spacing between perikyma grooves, from the first occlusal to the last cervical spacings. Perikymata distribution was assessed based on cumulative perikymata spacings calculated from the first perikyma in the occlusal part of the crown to the last perikyma in the cervical part of the crown. The total cumulative distance was divided into ten equal parts (deciles) and the sequence of perikymata counts was partitioned into these deciles. As the cumulative lengths follow the tooth surface, these results are comparable to the data on modern human populations (South African and Northern European) published by Reid and Dean (2000, 2006). Data in Reid and Dean (2000, 2006) are reported in terms of days per decile rather than number of perikymata per decile. Crown formation times were transformed into perikymata by dividing the number of days in every decile by the mean and 95% confidence interval of the incisor type-specific periodicities published by these authors (as per Modesto-Mata et al., 2015).

The percentage of perikymata in the lower (cervical half) of the crown of each tooth type was calculated as the sum of the perikymata numbers in the sixth to tenth deciles divided by the total number of perikymata (as per Guatelli-Steinberg et al., 2007). All percentages were arcsine transformed before running independent t-tests. A paired samples t-test was undertaken to compare the number of perikymata between adjacent deciles in incisors from the Çatalhöyük sample.

An error study for perikyma counts was carried out by drawing a profile line (1mm) along the vertical axis of the crown from the occlusal extremity of towards the cervical base. Perikymata were counted down this line for 20 cases (two teeth per randomly chosen individual) on two separate occasions. Similarly to Guatelli-Steinberg (2003), percent error was calculated by expressing difference in measurement pairs as a proportion of the first measurement. The total of these values are then divided by the number of cases (20) and multiplied by 100 to give the percent error. In this error study, the sum of values amounts to 0.39, corresponding to a percent error of 1.96%. As such, the results from this quantitative analysis indicate an intra-observer error of less than 2% for perikymata counts, which is comparable to the previously reported error rates of the authors of the published samples used in this study (Dean et al., 2001; Guatelli-Steinberg 2003).

RESULTS

Perikymata number: variation between populations

The range of perikymata counts recorded for each of the Çatalhöyük incisors overlaps with published ranges for other modern human populations (Table 2). Mean perikymata counts for Çatalhöyük are higher than South African means for all four incisor types but variable in relation to the Newcastle and Inuit sample means. When limiting the counts to the 95% confidence intervals, the perikymata counts on the Çatalhöyük upper central incisors do not overlap with counts for any of the other modern human samples, and are higher than those for the South African sample and lower than those for the Newcastle and Inuit samples. In contrast, the Çatalhöyük upper lateral incisors overlap with the Newcastle and South African samples and both lower incisors overlap with the Newcastle and Inuit samples (Fig. 2).

Table 2: Perikymata counts (Pk) with standard deviations (sd) and ranges of the permanent incisors in four modern human populations.

(Inuit, Newcastle and South African samples from Guatelli-Steinberg and Reid, 2008; 95% confidence limits reported in Modesto-Mata et al., 2015)

Tooth type	Sample	N of teeth	Mean pkg count	Sd Pk	Range Pk	95% CI
UI1	Çatalhöyük	18	133	17	107-167	126-141
UI1	Inuit	10	170	20	140-197	156-184
UI1	Newcastle	19	165	21	135-197	155-173
UI1	South Africa	20	117	13	87-148	111-123
UI2	Çatalhöyük	26	124	13	102-143	119-129
UI2	Inuit	10	151	19	124-175	137-165
UI2	Newcastle	16	134	16	107-154	125-143
UI2	South Africa	21	115	15	88-152	108-122
LI1	Çatalhöyük	15	133	16	108-165	125-142
LI1	Inuit	12	130	14	129-159	121-139
LI1	Newcastle	15	132	12	113-154	125-139
LI1	South Africa	20	105	10	86-121	100-110
LI2	Çatalhöyük	24	137	15	112-169	131-143
LI2	Inuit	14	140	11	119-157	134-146
LI2	Newcastle	13	130	19	99-177	119-141
LI2	South Africa	23	110	13	85-143	104-116

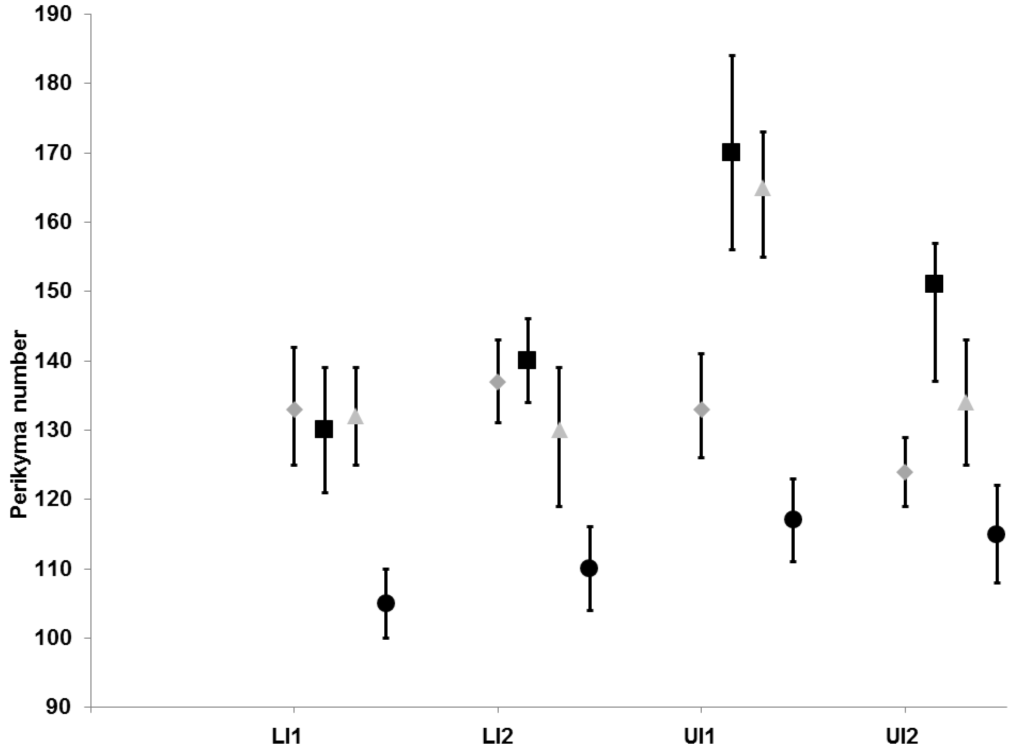

Figure 2: Mean number of perikymata and confidence interval for each population. Grey diamond = Çatalhöyük, Black square = Inuit, Grey triangle = Newcastle, Black circle = South Africa

Perikymata number: variation between tooth types

There was a significant and positive correlation between the number of perikymata in upper and lower central incisors (r_s = 0.7748 , p= 0.0408), upper central and lower lateral incisors (r_s = 0.6150 , p= 0.0440) and lower central and lower lateral incisors (r_s = 0.9133 , p= 0.0001). The number of perikymata in upper lateral incisors did not correlate significantly with any other incisor type. The number of perikymata did not differ consistently between upper and lower central incisors in seven individuals (Fig. 3).

Perikymata distribution

The variation in perikymata numbers from the first (occlusal) to the tenth (cervical) decile allows the quantification of changes in perikymata distribution patterns along the crown surface (Bermudez de Castro et al., 2003). When plotting the number of perikymata within deciles of crown height or crown length measured as cumulative distance along the surface, all modern human populations exhibit a consistent increase from occlusal to cervical deciles (Fig. 4).

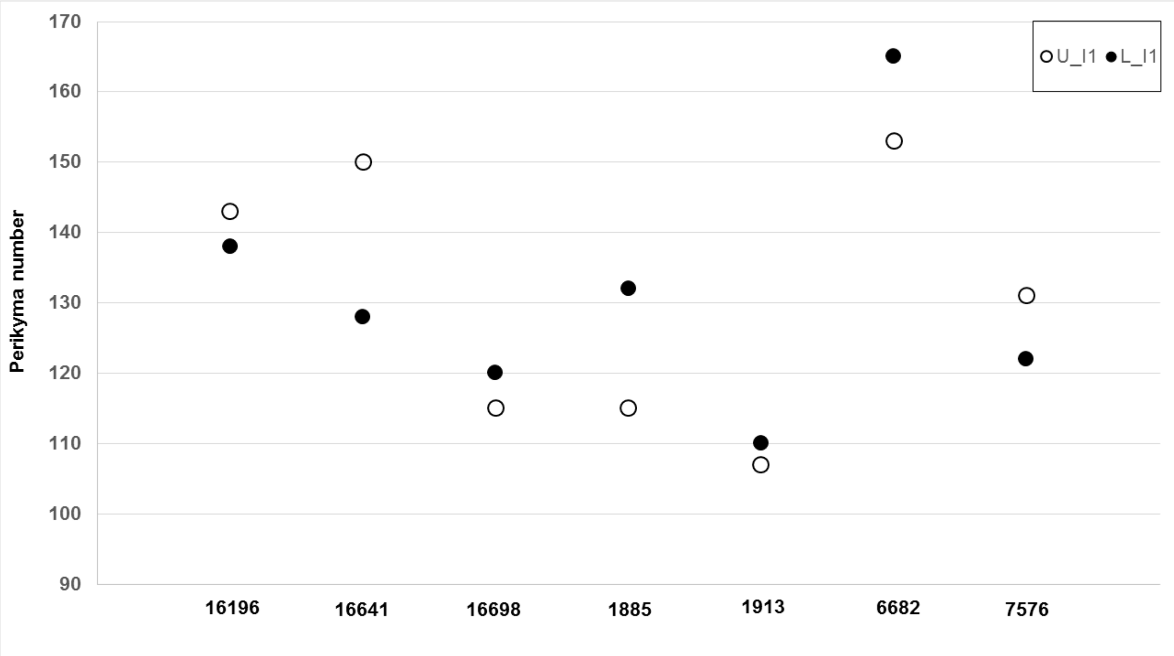

Figure 3: Perikyma counts of matching upper (open circle) and lower (closed circle) central incisors

Within the Çatalhöyük sample, the number of perikymata between all successive deciles in all four incisors increases. The increase in perikymata numbers from the first (most occlusal) decile to the tenth (most cervical) decile varies between 176% (for upper central incisors) and 298% (for upper lateral incisors). The percentage increase in perikymata numbers varies between successive deciles, ranging from 0.83% from deciles 3 to 4 in the lower central incisor to 28.39% from deciles 4 to 5 in the upper central incisors.

Previous research (Guatelli-Steinberg et al., 2012) has reported a more marked increase in perikymata numbers between successive deciles from the 6th decile onwards in South African and Newcastle samples. To assess whether statistically significant increases can be detected between deciles in the Çatalhöyük sample, a paired samples t-test was performed to quantify the differences in perikymata numbers between each successive pair of deciles. The differences in perikymata numbers between the 1st and 2nd, 3rd and 4th, 5th and 6th and 7th and 8th deciles were consistently statistically significant for all four incisor types ($p<0.05$). In contrast, the difference between the 9th and 10th deciles was consistently not statistically significant for all tooth types and the differences between the 2nd and 3rd and 4th and 5th deciles were not statistically significant for the upper and lower central incisors ($p>0.05$).

In terms of the differences between samples, the perikymata numbers per decile are higher in the Newcastle and Çatalhöyük samples relative to the South African sample. Perikymata distribution is relatively similar for the Newcastle and Çatalhöyük samples until the 4th decile, after which differences increase. The mean number of perikyata per decile in the Newcastle sample is higher than that of the Çatalhöyük sample until the 8th decile but variable thereafter.

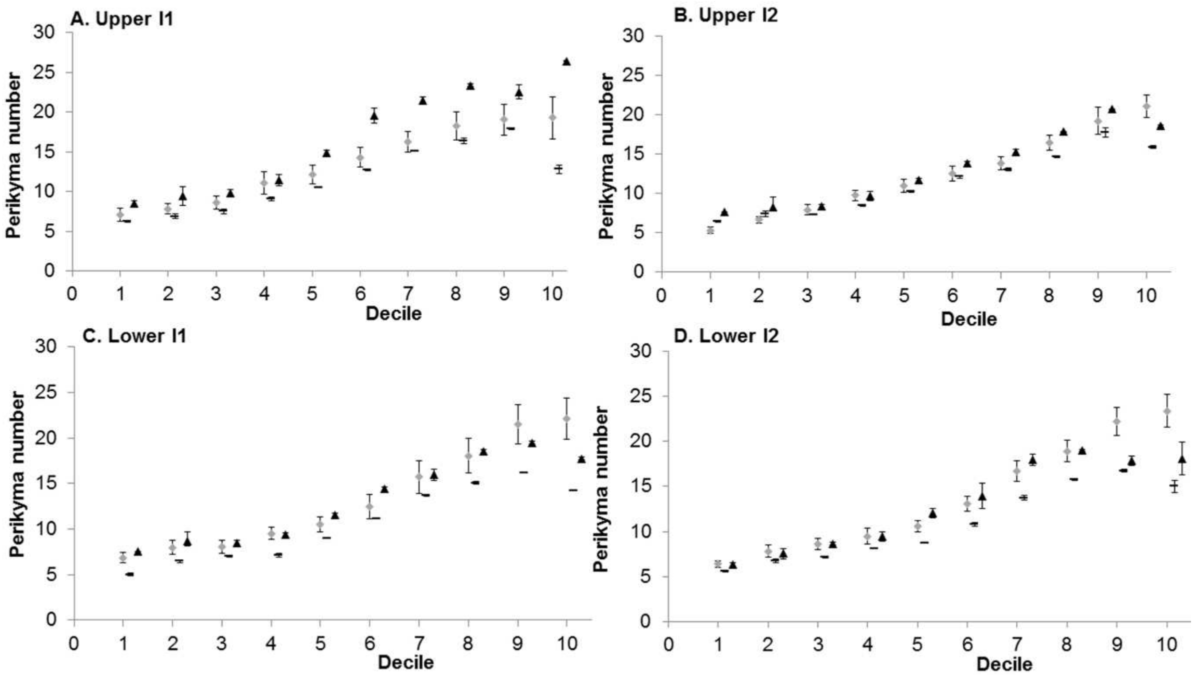

Figure 4: Mean number of perikymata per decile of crown height and confidence interval for each population. Grey diamond = Çatalhöyük, Black triangle = Newcastle, Black line= South Africa

Comparison of the percentage of perikymata on the cervical halves of each incisor (deciles 6 to 10) between the Çatalhöyük, Inuit, Newcastle and South African samples reveals that mean values differ between groups but the confidence intervals largely overlap (Fig. 5). For the upper central incisor, the pattern of population differences in mean percentages is similar to the pattern of total perikymata counts (Fig. 2), with larger means in the Inuit and Newcastle samples, lower means in the South African sample and intermediate means in the Çatalhöyük sample. Similarly, for the upper lateral incisor, there are also larger means in the Inuit sample and lower means in the South African sample, but the Çatalhöyük sample means are higher than the Newcastle sample means. For the lower (central and lateral) incisors, the Çatalhöyük mean percentage is higher than the other modern human samples. The difference between Çatalhöyük and other samples in the mean percentage of perikymata on the cervical half of the crown (cervical percentages) is not statistically significant for any of the incisor types (Table 3).

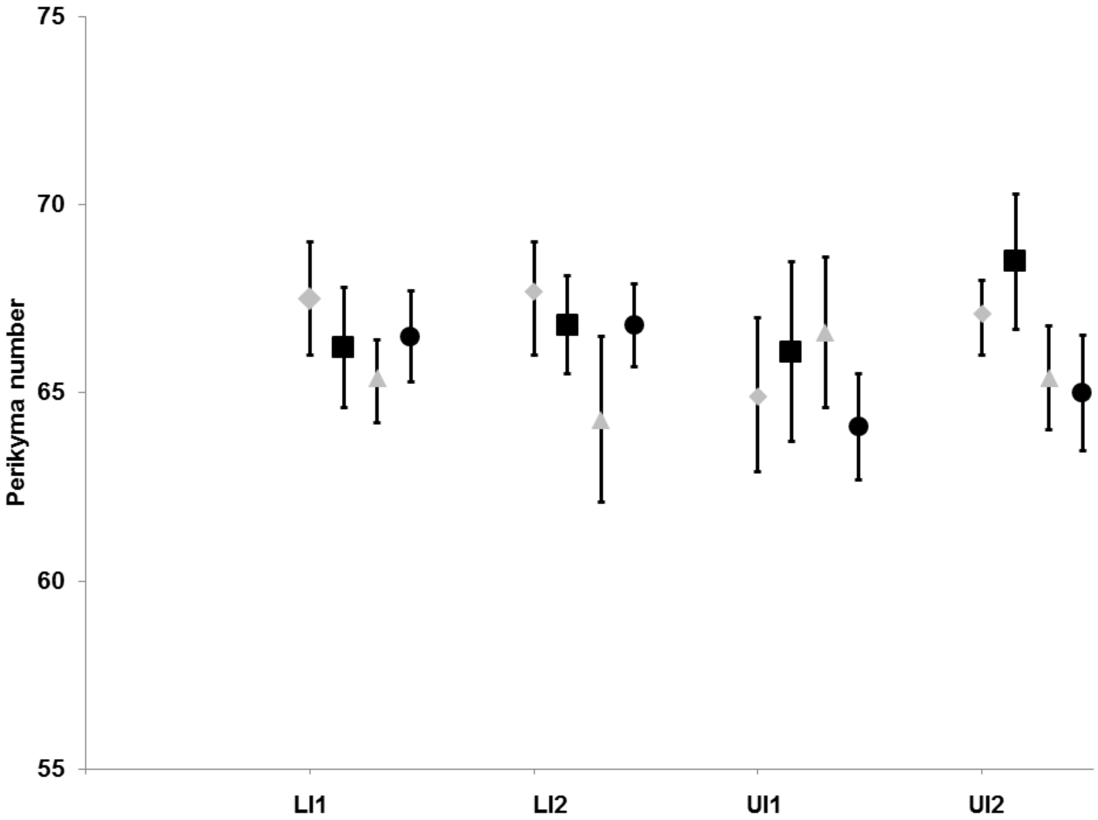

Figure 5: Mean percentage of perikymata in cervical halves and confidence interval for each population. Grey diamond = Çatalhöyük, Black square = Inuit, Grey triangle = Newcastle, Black circle = South Africa

Table 3: P-values for t-tests comparing the means of the percentages of total perikymata present in the cervical halves of teeth (deciles 6-10) between the Çatalhöyük sample against Inuit, Newcastle and southern African samples

		Inuit	Newcastle	South Africa
Çatalhöyük UI1	t	-0.009	-0.021	0.030
	p	0.993	0.984	0.977
Çatalhöyük UI2	t	-0.033	0.029	0.026
	p	0.975	0.978	0.980
Çatalhöyük LI1	t	0.036	0.068	0.033
	p	0.972	0.947	0.974
Çatalhöyük LI2	t	0.016	0.045	0.018
	p	0.988	0.965	0.986

DISCUSSION

Perikymata number: variation between populations

The large dataset on modern human perikymata characteristics in South African, Inuit and British (Newcastle) samples facilitates comparison with the Neolithic dataset from Turkey presented here (Guatelli-Steinberg and Reid, 2008; Reid and Dean, 2000; 2006). In addition to this, some data has been published concerning smaller samples of individual teeth (Bullion, 1987; Guatelli-Steinberg and Reid, 2010; King et al., 2002; Modesto-Mata et al., 2015; Monge et al., 2006; Smith et al., 2007a). Perikymata numbers for the South African sample are consistently low relative to the Çatalhöyük, Inuit, Newcastle and smaller published ranges (Table 4). Published ranges of perikymata counts for the (albeit small) sample of early modern human teeth from Qafzeh, overlap with the lower ranges for all Çatalhöyük incisors (Table 4).

For the upper incisors, the Çatalhöyük mean perikymata counts take on an intermediate position, with markedly lower counts relative to the Inuit and Newcastle samples, but for the lower incisors, differences between the Çatalhöyük, Inuit and Newcastle samples are very much reduced (Table 2). Similarly, the range of counts for the lower lateral incisors for the Çatalhöyük sample overlaps with the smaller modern European samples (Spitalfields, St Helen-on-the-Walls and Maltraviesa/Mirador), but the count on the Çatalhöyük upper central incisors is markedly lower than the Spitalfields, Abingdon and Maltraviesa/Mirador upper incisors (Table 4).

Perikymata number: variation between tooth types

The analysis of perikymata counts between tooth types using matched incisors revealed a significant correlation between the total perikymata numbers of all incisor types in the Çatalhöyük sample. This positive correlation could reflect the fact that periodicity is the same throughout each dentition. In other words, an individual with a low periodicity is likely to have more perikymata on all of his or her teeth than an individual with high periodicity (Fig. 1). In contrast, the lack of consistent differences between perikymata counts on a small sample of upper and lower central incisors suggests that the slightly thicker enamel of upper incisors (which has been demonstrated by Smith et al. 2008) may not be achieved by an increase in the total number of long-period lines in the lateral enamel. Differences in enamel thickness may depend on a faster daily secretion rate or a faster extension rate, or may be achieved by extending the duration of appositional enamel formation. A larger study of the interdependency within and between tooth types, using a larger sample and including teeth of different tooth classes would enable a more detailed examination of the influence of these factors.

We can observe the variation in the magnitude of differences between total perikymata counts on upper and lower incisors at a population level, with similar total perikymata counts for the lower incisors in the Çatalhöyük, Inuit and Newcastle samples, but with much lower perikymata counts for the upper incisors in the Çatalhöyük sample relative to the Inuit and Newcastle samples. This pattern of variation in total perikymata numbers may be related to differences in average daily secretion rates or in enamel extension rates (Fig. 1). The demonstrated variation in incisor perikymata counts between different populations indicates a need for further studies to be undertaken across the dentition. Variation in perikymata counts between all tooth types should be systematically assessed before making inferences about differences between modern human populations or between modern and fossil species.

Table 4: Perikymata counts and ranges for comparative modern human samples

Site	**origin**	**Nr teeth**	**Pk nr**	**Reference**
Qafzeh UI1	Early Homo sapiens	4	127-144	Monge et al., 2006; Guatelli-Steinberg and Reid, 2010
Maltraviesa/Mirador UI1	Chalcolithic-Bronze age	6	152-210	Modesto-Mata et al., 2015
Christ Church, Spitalfields UI1	18th-19th century	1	177	King et al., 2002
Abingdon UI1	Medieval	1	159	Bocaege et al., 2010
Qafzeh UI2	Early Homo sapiens	2	125-128	Guatelli-Steinberg and Reid, 2010
Maltraviesa/Mirador UI2	Chalcolithic-Bronze age	5	131-187	Modesto-Mata et al., 2015
Abingdon UI2	Medieval	1	135	Bocaege et al., 2010
Qafzeh LI1	Early Homo sapiens	3	106-150	Guatelli-Steinberg and Reid, 2010
Maltraviesa/Mirador LI1	Chalcolithic-Bronze age	1	175	Modesto-Mata et al., 2015
Abingdon LI1	Medieval	1	168	Bocaege et al., 2010

Qafzeh LI2	Early Homo sapiens	3	115-148	Guatelli-Steinberg and Reid, 2010
Christ Church, Spitalfields LI2	18th-19th century	1	127	King et al., 2002
St Helen-on-the-Walls, York LI2	Medieval	4	109-127	Bullion, 1987
Maltraviesa/Mirador LI2	Chalcolithic-Bronze age	3	162-180	Modesto-Mata et al., 2015

Perikymata distribution

A key finding in this study is the increase in perikymata per decile from the occlusal to the cervical part of all tooth crowns. This confirms results reported in other large-scale studies (Guatelli-Steinberg and Reid, 2008; Reid and Dean, 2000, 2006). Additionally, this study has demonstrated a statistically significant trend of increasing number of perikymata from the occlusal to the cervical deciles in a mid-Holocene sample of human teeth from Turkey. This reflects the pattern observed in all other modern human teeth studied thus far and has been shown to be related to the decline in enamel extension rates in the cervical relative to the occlusal half of the tooth (Guatelli-Steinberg et al. 2012).

The slight (non-significant) differences in the mean percentages in the cervical half of the crown (deciles 6-10) between the different modern human samples could be interpreted as evidence for regional differences in perikymata distribution patterns. Interestingly, Modesto-Mata and colleagues (2015) also noted that the largest differences between their Spanish sample and comparative Northern European (Newcastle) and South African samples are located in the cervical region. The mechanism behind this variation could be related to population differences in daily secretion rates, enamel extension rates and/or long-period line periodicities (Hillson, 2014).

Periodicities could not be assessed for the Çatalhöyük sample, but given that perikymata numbers per decile are consistently higher than in the South African sample, it is possible that the average periodicity for the Çatalhöyük sample is lower than that of the South African sample. However, the difference between the Newcastle and Çatalhöyük samples seems more complex due to to the variation in perikymata counts for the 9th and 10th deciles between tooth types (higher than the Newcastle samples in the lower incisors and lower than the Newcastle sample in the upper central incisors). It is unlikely that a difference in periodicities is the mechanism behind this variation, because periodicities are known to remain constant between tooth types within a single dentition (FitzGerald 1998). In this case we can hypothesise that variations in average daily secretion rates are responsible for the pattern of variation in perikymata numbers in the most cervical part of these different incisors.

Other human species (Neanderthals, Homo rudolfensis, Homo erectus) display a more homogenous distribution of perikymata with a more gradual increase in number of perikymata per decile towards the cervical part of the crown (Dean and Read, 2001; Guatelli-Steinberg et al., 2007; Xing et al., 2015). Intriguingly, however, the Sima de los Huesos hominins, which have shown a close relationship to the Neanderthals based on nuclear DNA (Meyer et al., 2016) also show a significant difference in numbers between the 4th and the 8th deciles in the upper central incisors (Bermudez de Castro et al., 2003).

The pattern of increase in perikymata numbers per decile towards the cervix represents a deceleration in tooth formation (Ramirez-Rozzi and Bermudez de Castro, 2004; Guatelli-Steinberg et al., 2007, 2012; Modesto-Mata et al., 2015; Reid and Dean, 2000, 2006). However, the causal mechanisms behind the differences in perikymata numbers across deciles between and within species remain unclear. More data on modern human (archaeological and recent) permanent tooth crowns and their supporting structures is needed to test whether these differences are influenced by environmental (climatic or latitudinal) or genetic factors or if there are developmental constraints (reduction of the dental arch) behind this variation in dental development in the cervical region between different populations.

CONCLUSION

The aim of this paper was to detail variation perikymata numbers and distribution using a large sample of relatively unworn matching modern human permanent incisors from the mid-Holocene site of Çatalhöyük in Turkey. Total perikymata numbers were within the range of previously reported modern human perikymata numbers, with all four incisors exhibiting counts that are intermediate between values for samples from Newcastle and South Africa. The perikymata distribution followed the modern human pattern of a marked increase in perikymata numbers in the cervical deciles. These new data support existing evidence for regional differences in perikymata counts and distribution among modern humans.

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