Perikymata numbers and enamel extension rates in the incisors of three archaeological modern human populations from two caves located in Spain: Maltravieso Cave (Cáceres) and Mirador Cave (Burgos)

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Abstract
A number of authors have studied the variability of total perikymata counts on permanent incisors in different modern human populations, finding that some populations show a significantly lower number of perikymata than others. However, little is known about the overall variability of these traits in archaeological populations of modern humans. Our aim was to broaden the available data on total perikymata counts on incisors, and to further discuss enamel extension rate variability in modern human incisors. Our sample consisted of 15 incisors from three different archaeological populations belonging to the Holocene: two populations from Mirador Cave (Sierra de Atapuerca, Burgos) assigned to two different chronological periods, and a population from Maltravieso Cave (Cáceres). We refer to these populations as the MTV-MIR sample. Perikymata were counted from several images obtained using an environmental scanning electron microscope (ESEM). Our results suggest the total number of perikymata of the MTV-MIR incisors fall most comfortably within the distribution of counts reported for modern Europeans and Inuits rather than those representing southern African samples of incisors. Furthermore, the percentage of the perikymata numbers in the last five deciles into which the crowns were divided (the cervical half) did not show statistically significant differences when compared to the other modern human populations. This suggests that enamel extension rates among modern human incisors share a common pattern, which might differ from that present in other species. More data from other modern and archaeological sub-Saharan African samples are needed to test whether low perikymata counts are exclusive to the southern African group or are indeed truly representative of sub-Saharan African populations as a whole today and in the past.

Keywords: perikymata number, incisor, lateral enamel formation time, modern human variability, enamel extension rate, cervical half

1. Introduction

One method of estimating crown formation times is by adding the lateral (imbricational) and the cuspal (appositional) enamel formation times (Guatelli-Steinberg and Reid, 2008; Reid et al., 1998a, 1998b; Reid and Dean, 2006; Smith, 2008). Lateral enamel formation time has been a major focus of previous research because it is relatively easier to count long-period lines (perikymata) on a crown surface and establish lateral enamel formation times (especially when long-line periodicity is accurately known) than it is to estimate cuspal enamel formation times that are hidden within a tooth. Some authors have studied the variability of total perikymata numbers in different modern human populations, as well as enamel extension rates, by dividing the crown height into deciles and counting the perikymata within each decile (Guatelli-Steinberg et al., 2007, 2005; 2012; Guatelli-Steinberg and Reid, 2008; Ramirez Rozzi and Bermúdez de Castro, 2004; Reid and Dean, 2006). Some authors have noticed that although certain modern human populations appear to have statistically different numbers of perikymata distributed between some deciles on the same incisor-type, they share a common pattern of enamel extension rate, which has been judged to be different from that present in Neandertals (Guatelli-Steinberg et al., 2007).

Other authors have suggested that the general growth period of a hominin species is reflected in the lateral enamel formation times of their anterior teeth. Because Neandertals had lateral enamel formation times 15% shorter than prehistoric *Homo sapiens*, Neandertals would by this argument have had shorter periods of general growth (Ramirez Rozzi and Bermúdez de Castro, 2004). However, these results have been challenged on the basis that long-period stria and perikymata periodicity was unknown in this sample of Neandertal teeth and because anterior tooth formation time, on its own, is a questionable measure of general maturity. When a wide range of long period line periodicities are employed, lateral enamel formation times of Neandertal incisors would potentially fall within the known range of modern human variation (Guatelli-Steinberg et al., 2007, 2005). Some authors have defended the claim that Neandertal growth periods were shorter than in modern humans. (Smith et al., 2010). In this case, however, they extended their study to include perikymata counts, long-period line periodicities, cuspal enamel thicknesses, cuspal and lateral enamel formation times and root formation times. Their conclusions were based on the overall period of dental development being shorter in Neandertals than in modern humans. Moreover, Neandertals showed thinner cuspal enamel, lower long-period line periodicities and faster extension rates, which it was argued each contributed to shorter crown formation times and by proxy shorter general growth periods.

In order to better understand how these dental histological variables evolved, it is clear we must continue to document modern human variation more fully in both present and archaeological samples of teeth. Our aim in this study was, therefore, to add new data to a growing body of data related to total perikymata numbers, on the buccal surfaces of incisors. A further aim was to estimate enamel extension rates, from three archaeological modern human populations which were uncovered in two different caves located in Spain: Maltravieso Cave (Cáceres, Extremadura) and Mirador Cave (Sierra de Atapuerca, Burgos). Our goal overall was to identify potential variables that might be shared by all modern humans but be different from other hominin species, especially Neandertals. Because some authors have observed that the percentage of perikymata in the cervical halves of the crown is a useful variable to differentiate Neandertals from modern humans (Guatelli-Steinberg et al., 2007), we have tried to confirm this observation.

1.1. Maltravieso Cave

Maltravieso Cave is located in the southwestern part of the Iberian Peninsula (Fig. 1). The cave consists of several rooms and corridors developed as karstic system partially filled with allochthonous sediments (Jordá Pardo, 1988). The site is known mainly due to an important group of Paleolithic rock art (Ripoll López, 1999) although the research developed in recent decades indicate a prolonged anthropic use of the cavity that can be traced back to the late Middle Pleistocene (Bañuls Cardona et al., 2012; Canals et al., 2010; Rodríguez-Hidalgo et al., 2010; Rodríguez Hidalgo et al., 2010; Rodríguez-Hidalgo et al., 2013).

The cave was accidentally discovered in 1951 in a limestone quarry. The affected area was called Sala del Descubrimiento (Discovery Room). In it were found a thousand ceramic and human remains that were part of a collective grave (Callejo Serrano, 1958). The few pottery fragments available indicate that the room was used as a burial cave at least in the half of the second millennium BC (Cerrillo Cuenca and González Cordero, 2007). In 2002, various mechanical and manual test pits were performed in the area originally occupied by the Sala del Descubrimiento, uncovering new 172 remains belonging to *Homo sapiens* and several new pottery fragments (Muñoz and Canals, 2008). All of this new remains were assigned to be part of the assemblage discovered in the 50's.

1.2. Mirador Cave

The cave of El Mirador is located on the southern side of the Sierra de Atapuerca (Burgos, Spain), at an altitude of 1.033 meters above sea level. The Edelweiss Speleological Group carried out the first archaeological work in the 1970s. In 1999, the archaeological fieldwork was restarted by the interdisciplinary Atapuerca's Research Team, and it is still ongoing (Vergès et al., 2002, 2008). Thereafter, three human samples were discovered in different areas of the site. The first human assemblage came from a 6m^2 survey in the central area of the site. There were found six individuals of different sexes and ages at death dated to the Early Bronze Age (4.400-4.100 cal BP) (Cáceres et al., 2007). These individuals were cannibalized, their remains were considered rubbish and remained exposed in the cave. The human remains were buried by other human group later in the Middle or Late Bronze Age (Cáceres et al., 2007).

On the other hand, the second human assemblage is a collective burial found in an about 14 m^2 natural chamber located in the NE corner of the cave. The fieldwork started in 2009 and it is still in progress. Although there are some individuals in their original anatomical position, the superficial remains were mixed and disturbed by the actions of the clandestine excavators in the 1980s. Up to now, there are a minimum number of 22 individuals of different sexes (Gómez-Sánchez et al., 2014). The buried individuals covered a wide range of ages from two until more than 40 years old. All of these human remains belong to the Chalcolithic period and have been dated to 4.760-4.200 years cal. BP.

Finally there is an individual burial of a young female located in the NW corner of the cave dated to 3.690 Cal BP.

2.1. Material: dental remains and comparative samples

We present here perikymata numbers of 9 incisors from Maltravieso Cave and 6 from Mirador Cave, where three incisors belong to the Chalcolithic period and three to the Bronze Age period (Table 1 and Fig. 2). We will refer to these populations from now on as the MTV-MIR sample. The MTV-MIR sample is composed of 6 upper I1s, 5 upper I2s, 1 lower I1 and 3 lower I2s (Table 1 and Fig. 2).

The modern human comparative samples for perikymata counts were obtained from previous publications (Guatelli-Steinberg et al., 2007; Guatelli-Steinberg and Reid, 2008) (Table 2). The modern human samples published by these authors are from three extant populations: Newcastle upon Tyne (UK), southern Africans and Canadian Inuits. On the other hand, we have also included data of southern Africans and northern Europeans published by Reid and Dean (2006). The latter southern African sample is composed of 13 population groups ("tribes"). Because in the previous report, information on crown formation times per decile are shown rather than perikymata counts, we transformed times into perikymata by dividing the number of days in every decile by the mean and 95% confidence interval of the incisor-type specific periodicities, which are also published in Reid and Dean (2006).

2.2. Methodology

Incisors were initially selected depending on their degree of wear, according to grades that have been previously established (Molnar, 1971). Only grades 1 and 2 were useful in our study, where the former refers to teeth with absolutely no wear degree on the enamel surface, whilst the latter refers to moderate degree without exposing the dentine horns. However, selected grade-2 incisors show a rather limited degree of wear in the incisal edges, minimizing the number of perikymata that were lost. In those few incisors that were slightly eroded, an estimation of the perikymata that were lost was not performed. All the incisors were still developing at the moment of death, since all of their roots were still open.

Perikymata numbers of the incisors were counted by using an environmental scanning electron microscope (ESEM) (FEI Quanta 600, located at the CENIEH, Burgos). We worked on it in low vacuum (60-80 Pa), between 15-16 kV, with a spot of 3.5-3.6 and around 60 µA. The incisor crowns were positioned obliquely to the electron beam in order to maximize the distance of their crown heights. Several images at maximum resolution were obtained at 70x for each incisor on its buccal aspect, attempting to capture as much dental surface as possible in order to be able to resolve the count of continuous perikymata when some part of the surface is eroded or they are not clearly visible for any reason. A single orthogonal image capturing the whole crown surface of each incisor was also obtained on which the crown height was measured and upon which the decile divisions were superimposed. The method we followed to measure crown height and the method of dividing the crown height into ten deciles is visually depicted in Fig. 5 from Guatelli-Steinberg et al. (2007). We acknowledge that other non-linear measures of crown height have also been described (Reid and Dean, 2006). These authors measured the length of the enamel by following the profile of the physical histological section of the incisors, from the cervix until the incisal edge, with the aim of dividing that length by ten in order to count the number of perikymata in each decile. This is a relatively easy task since histological sections are ideal for this; however, in non-sectioned teeth this is a much harder to achieve since it is difficult to accurately establish the number of perikymata in each decile.

The images were then merged using GIMP 2.8 and perikymata were counted on it twice in different days by the same person (M-M). Both counts were then compared and in any regions where the perikymata count did not match, a detailed revision was done in order to select the real incremental lines and delete those that were over- or under-counted. In order to increase the ease of counting the incremental lines in some pictures where they are not clearly identifiable, a highpass filter was used by handling the software Darktable 1.4 and increasing the contrast boost up to 100%.

Because we were unable to make histological sections of the samples, we could not estimate or observe the periodicity that exists between two long-period striae or perikymata. Thus, we used the most frequent values observed in modern humans that are between 7 and 9 days (Reid and Dean, 2006) although we acknowledge that a wider range of variation does exist across all modern humans when very large samples are available. For this reason we are cautious when inferring lateral enamel formation times from our data.

The distribution of perikymata on the enamel surface is correlated with the pattern of change of the enamel extension rate (EER) along the crown height (Guatelli-Steinberg et al., 2012). Moreover, the decline of the EERs in the most cervical portion of the tooth is associated with an increase in perikymata density. On the other hand, initial EERs and the pattern of decline along the crown height are related to the length of the enamel-dentine junction Guatelli-Steinberg et al., 2012). In our case, a straight line was drawn across the crown height in the midpart of each labial incisor. This line ideally divides the crown in two symmetrical parts. The distance along this line, measured from the cervix to the incisal edge was divided in ten parts (deciles) and perikymata counts were registered in each. The place where perikymata counts were recorded was on the line or nearby it.

2.3. Statistical methods

To plot these comparative samples alongside the Maltravieso and Mirador incisor data, we used the statistical programming language R by using its graphical user interface R Commander. As only mean and standard deviations were available for these populations, we calculated their normal distributions by using the R functions *dnorm*, which returns the height of the probability density function, and *plot*, which represents graphically the normal distributions. Otherwise, the modern human comparison samples for perikymata number per deciles were obtained from Guatelli-Steinberg et al. (2007).

3. Results

Perikymata counts of each incisor and their lateral enamel formation times appear in Table 1. An example of the buccal aspect of the lower first incisor (R1429) under ESEM can be seen in Fig. 3.

The total number of perikymata of the MTV-MIR sample compared to other modern human populations can be seen in Fig. 4. The number of perikymata of the upper I1s falls within 1 standard deviation (SD) of modern human populations (Newcastle, UK and Canadian Inuit) with the exception of the incisors R1404 and R1412, which belong to the same specimen (being antimeres) and fall beyond +1SD of these modern samples. The MTV-MIR I1s don't overlap within the 1SD with the southern African sample. The upper I2 of the MTV-MIR incisors fall beyond 1SD of the southern African sample. In this case, the degree of overlap among all the populations is higher in the upper I2s. Excepting R1435, all the MTV-MIR incisors fall within the Newcastle 1SD, but most of them also fit within Inuit 1SDs. On the other hand, lower incisors show a much greater difference compared to upper incisors. None of them, on their own (lower central or lateral incisors), are within 1SD of the modern human samples. Moreover, the unique lower I1 (R1429) is by far the most distant tooth with respect to the averages and 1SD of the other populations. This fact also applies to the lower I2 R1422. What is clear is that MTV-MIR sample does not fit within 1SD of the southern African sample in any of the incisors types considered. Upper incisors, however, with just a few exceptions overlap with 1SD of the Newcastle and Inuit samples, whilst lower incisors are clearly beyond 1SD of the modern humans distributions.

Concerning 95% confident limits (CL) and 2SD of the total number of perikymata (Fig. 4), there are some observations that must be pointed out when MTV-MIR incisors are compared to the other modern human populations. None of the MTV-MIR incisors individually falls within 95%CL of southern African. MTV-MIR 95%CL of the upper I1s overlaps with Inuits and Newcastle sample.

Upper I2s overall fall within 95%CL of Inuits and Newcastle sample, with the exception of the incisor R1435. Interestingly, none of the lower I2s fall within modern human 95%CL. The unique lower I1 incisor, R1429, is clearly beyond all already known human variation for this tooth-type. Compared to the other modern human populations, MTV-MIR 95%CLs of the upper incisors are wider due to their relatively low number of incisors included per tooth-type. In spite of this matter, MTV-MIR upper I1s broadly overlap with non-African populations. On the other hand, MTV-MIR upper I2s slightly overlap with southern African, which might be caused by a wider 95%CL, as was stated before. Concerning the 2SD of the upper incisors, the degree of overlap is undoubtedly higher. In upper I1s, non-African populations, where MTV-MIR sample is included, show a much higher degree of overlap among themselves than any of them independently with southern Africans. The situation in the upper I2s is slightly different, since there is a gradual transition between southern Africans and the group comprised by the MTV-MIR and Inuit population. In this case, Newcastle sample is placed between these two groups.

The inferred enamel extension rates of the incisors of the MTV-MIR sample, compared to modern human samples taken from southern Africans, Inuits and Europeans, are represented in Fig. 5. Interestingly, both southern African population perikymata counts from two independent studies (Guatelli-Steinberg et al., 2008; Reid and Dean, 2008) widely overlap. The same occurs with the two northern European populations. Six upper I1s from the MTV-MIR sample seem to fall within the ranges observed for the Inuit and Newcastle samples, although some of their individual deciles display values of perikymata counts that are above or below the observed variation in these modern human populations. This is the case of the R1406, R1412, R1404 and MIR201 P37 163 incisors. There is a tendency towards increasing variability closer to the cervix. This tendency can also be discerned in the upper I2, in some teeth, as with R1435, being clearly beyond the modern range of variation in the last three deciles: the R1435 incisor displays perikymata counts in the 4th and 5th deciles that are beyond that seen in any other population sample. The other teeth of this type fall within Inuit or Newcastle populations. With respect to lower incisors, both central and lateral incisors present perikymata counts in their last three deciles that are remarkably greater than those observed in other populations. One exception is incisor R1419. It is also interesting to point out that the second and third deciles in both lower incisor tooth-types also show perikymata counts that fall beyond those observed in the other populations, although this high number is not as large as that one present in the last three deciles. So, considering all the incisors as a whole, the main difference with respect to modern human population samples lies in the greater number of perikymata present in the last three deciles. It is this region where the population differences can principally be best differentiated.

Since the MTV-MIR sample consists of more than three incisor teeth each, statistical analysis have been performed between our sample and three different modern human population samples published by Guatelly-Steinberg et al. (2007): southern Africans, Inuits and Newcastle sample. Significant statistical differences ($p < 0.05$) are present when we consider the total number of perikymata on both upper incisors between MIR-MTV and southern Africans (Table 4). The percentages of the perikymata counts in the cervical halves of these teeth with respect to the total number on the whole crown are not significantly different ($p > 0.05$) between MIR-MTV and the other three modern human populations (Table 5). All the modern human population samples considered, including MTV-MIR sample, show a unique overall pattern of enamel extension rate, which might be different from that present in other species, such as Neandertals. So, although in absolute terms there are differences, because some modern human populations display lower number of perikymata than the others, these differences disappear when we consider the estimates of enamel extension rates in relative terms.

4. Discussion

Total perikymata counts on permanent incisors have been relatively well studied in the past few years (Guatelli-Steinberg et al., 2007, 2005; 2012; Guatelli-Steinberg and Reid, 2008; Ramirez Rozzi and Bermúdez de Castro, 2004). While some authors have suggested that perikymata number in incisors may be an useful variable to establish differences between Neandertals and modern humans (Ramirez Rozzi and Bermúdez de Castro, 2004), others believe that it is not useful, primarily because they regard Neandertal counts as falling within the known modern human range. Therefore, Neandertals do not appear to be distinguished in this way as was previously argued (Guatelli-Steinberg et al., 2007). So, enamel extension rates and perikymata counts in Neandertals remains unresolved. Furthermore, data published by Guatelli-Steinberg and colleagues concerning this matter have been criticized as having combined data for several samples together and as having other methodological problems, and so recommending these data should not be used in future studies (Ramírez Rozzi and Sardi, 2007).

With the exception of upper I2s, it is known that modern southern African samples show low mean incisor perikymata counts compared with European samples (Guatelli-Steinberg and Reid, 2008; Smith et al., 2010) and Inuit samples (Guatelli-Steinberg et al., 2007; Guatelli-Steinberg and Reid, 2008). Looking at Fig. 4 we see that none of our specimens fall neither within 1SD nor within the 95% confidence interval of the southern African sample represented in this study. Concerning 2SD, only some upper I2s of the MTV-MIR sample fall within southern African population. Otherwise, the MTV-MIR sample overall falls within the variation of non-African samples, depending on the tooth we consider. Moreover, some teeth seem to fall at the extreme end of the normal distributions, such as R1435 (upper I2), R1412-R1404 (upper I1) and R1429 (lower I1).

Although little is known about total perikymata counts and patterns of distribution across the crown in incisors of other modern human populations (e.g. Reid et al., 1998; Smith et al., 2010), some data has been published in the last few years concerning comparisons of fossil and modern human teeth (e.g. Guatelli-Steinberg and Reid, 2010; Smith et al., 2010). A lower I2 belonging to an early *Homo sapiens* from Morocco (Jebel Irhoud 3) had 167 perikymata on its buccal surface, suggesting 1670 days of lateral formation time since it has a 10 day long-period stria periodicity (Smith et al., 2007). In spite of the temporal distance with our sample, the perikymata counts of this specimen falls perfectly in the MTV-MIR sample, since it has an average of 171 perikymata for this incisor, which is at the same time far away from southern Africans. Other important sample of fossil humans, that include several incisors and which are attributed to early *Homo sapiens*, have been uncovered in Qafzeh Cave (Israel). The minimum and maximum perikymata counts described for the Qafzeh sample range from 106 to 150 perikymata in lower I1s, from 127 to 144 in the upper I1s, from 115 to 148 in the lower I2s and from 125 to 127 in the upper I2s (Guatelli-Steinberg and Reid, 2010; Monge et al., 2006). Compared to MTV-MIR, Qafzeh specimens display lower perikymata counts for all the incisor types, although they broadly overlap other modern non-African populations. Four recent humans, specifically from the Medieval Age of Picardie (France), were used to study dental histological variables including total perikymata counts (Reid et al., 1998a). Their adjusted total perikymata counts ranged from 110 to 127 perikymata in the lower I1s, from 119 to 170 in the upper I1s, from 148 to 172 in the lower I2s and from 104 to 150 in the upper I2s. These four individuals widely overlap the MTV-MIR sample, although some teeth of this sample aren't within their range of variation. However, other samples of modern humans, of both African and European origin, were also published recently (Smith et al., 2010). These two population samples have broadly similar origins as the ones that were used in Fig. 4, which come from data published by Guatelli-Steinberg and Reid (2008), and show the same degree of overlap in their distribution of total perikymata counts.

The Jebel Irhoud 3 incisor and the early *Homo sapiens* from the Near East of Qafzeh show perikymata counts that clearly falls above the other modern human populations (but remarkably within the variation of our MTV-MIR sample). This suggests sub-Saharan Africans today may be recently derived with respect to earlier modern humans living in the Iberian peninsula and modern non-African populations today. Nonetheless, much larger modern and archaeological samples are required to test this hypothesis and document the true worldwide variation in total perikymata counts and distribution pattern before this can be clarified further. It should be emphasized that having a lower than average perikymata count does not necessarily mean that lateral enamel formation times were also lower than average, as has been pointed out previously (Guatelli-Steinberg et al., 2007; Reid and Dean, 2006).

With respect to whether incisor crown height may or may not be a possible variable that influences total perikymata counts on the buccal side, we note that Reid and Dean (2006) measured crown length of the incisors, which is not exactly the same as the crown height in an attempt to answer this question. Here we note that in our MTV-MIR sample the higher the crown height, the higher the total perikymata count is also. It has also been suggested that variation in crown height results directly from variation in crown formation time and/or from variation in enamel extension rates, where the length of the enamel-dentine junction (EDJ) plays an important role (Guatelli-Steinberg et al., 2012). Hence, the long-period stria and perikymata periodicity emerges as a key variable, since the sample of southern African incisors have on average higher periodicities than the European population samples reported in the literature so far (Reid and Dean, 2006).

With respect to the percentages of perikymata in the last five deciles of crown height (i.e. the cervical half of the crown) the MTV-MIR sample distribute exactly as the other *Homo sapiens* population samples do. Although in some teeth from our sample the number of perikymata in the cervical half is markedly elevated over other modern human populations, this pattern of perikymata distribution, with respect to the total number, fits unequivocally within the range of modern human variation.

To establish lateral enamel formation time (i.e. the total number of perikymata multiplied by the periodicity of the individual), it would have been necessary to know the long-period stria and perikymata periodicity. Unfortunately, we could not determine this variable in any tooth. On the other hand, it is known that the highest mean values of periodicity occur in southern African anterior teeth where a large number of high periodicities of 11 and 12 days have been reported (Reid and Dean, 2006). European samples show a modal value of periodicity for anterior teeth of between 8 and 9 days (Reid and Dean, 2006). Importantly, a negative correlation exists between periodicities and total perikymata counts, that is, higher periodicities are associated with lower perikymata counts (FitzGerald, 1995; Guatelli-Steinberg et al., 2005; Reid and Ferrell, 2006). The fact that different modern human populations exhibit different total perikymata counts means that lateral enamel formation times may be no different or may overlap extensively. It has been described in anterior teeth that lateral enamel formation times become increasingly shorter in the southern African sample from the first to the last decile compared to northern Europeans (Reid and Dean, 2006). This feature, as well as that cuspal enamel formation times between these two populations remains practically identical (Reid and Dean, 2006), makes that the difference in total crown formation times lies in lateral enamel and not cuspal enamel. Because periodicity modal values in modern humans are 8 and 9 days (Reid and Dean, 2006), we can assume that these values might be the most probably to occur in our sample, although we acknowledge that others located in the tails of the normal distribution might also possibly be present. Were this the case, then lateral enamel formation times would be no different than in southern Africans, Europeans or Inuits. The fact that we have several incisors in this present archaeological sample that fall at the extreme right tail of the normal modern human perikymata distribution might suggest either lower periodicities of i.e. 7 days in these teeth or alternatively higher lateral enamel formation times. If this last option is the case, this would mean that what we know about variation in lateral enamel formation times and in total perikymata counts among and between modern human populations has so far been underestimated.

5. Conclusions

Total perikymata counts in the incisors of three Spanish archaeological modern human populations (Maltravieso Cave in Cáceres and Mirador Cave in Burgos, referred as MTV-MIR sample) show closer affiliations with modern European and Inuit population samples than with modern southern African population samples. Statistically, upper incisors from this modern archaeological sample show significant differences from a southern African sample ($p<0.05$). Some incisors from Maltravieso Cave have total perikymata counts that fall at the extreme right tails of the normal modern human distributions. This suggests either that they had lower modal long-period stria and perikymata periodicities than are typical for modern humans (i.e. 7 days rather than 8 or 9 days), or that they had greater lateral enamel formation times than is typical of modern populations today (having periodicity values over 9 days, which would increase lateral enamel formation time). Whatever the underlying cause it is clear that modern human perikymata counts and perikymata distribution patterns on incisor crowns remain under-represented in the literature today and that it is especially important to gather more data on archaeological and early fossil modern human samples to provide a clearer picture of worldwide variation both today and in the past.

Despite considerable variation in total perikymata counts it is remarkable that the percentage of the total perikymata on the cervical half of incisor crowns remains a distinguishing feature of all modern human incisor tooth types.

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Site	Specimen (antimere)	Tooth	Position	Side	Individual	CrH	WD	MOO	Pk	LEFT (days)		
										7	8	9
MTV	R1429	I1	L	L	II	9.68	1	R1/2	175	1225	1400	1575
MTV	R1419	I2	L	R		10.51	1	Rc	162	1134	1296	1458
MTV	R1422	I2	L	R		9.52	1	R1/2	180	1260	1440	1620
MIR-B	MIR3A P20 387	I2	L	L	I	9.87	2	Rc	>159	>1113	>1272	>1431
MTV	R1404 (R1412)	I1	U	L	II	11.95	1	R1/4	202	1414	1616	1818
MTV	R1406	I1	U	L		11.86	1	R3/4	188	1316	1504	1692
MTV	R1412 (R1404)	I1	U	R	II	11.85	1	R1/4	210	1470	1680	1890
MIR-C	MIR201 P37 163	I1	U	R		11.26	1	R1/4	165	1155	1320	1485
MIR-C	MIR203 R36 395	I1	U	L		11.35	1	R1/2	152	1064	1216	1368
MIR-B	MIR2 Q22 s/c	I1	U	R	I	11.34	2	Rc	>159	>1113	>1272	1431
MTV	R1418 (R1428)	I2	U	L	II	9.95	1	R1/2	147	1029	1176	1323
MTV	R1428 (R1418)	I2	U	R	II	9.61	1	R1/2	144	1008	1152	1296
MTV	R1435	I2	U	L		10.30	1	R1/4	187	1309	1496	1683
MIR-C	MIR201 REM 255	I2	U	L	IV	9.72	1	R1/4	131	917	1048	1179
MIR-B	MIR4 P22 164	I2	U	L	I	9.92	1	R3/4	143	1001	1144	1287

Table 1. Incisors from Maltravieso Cave (MTV) and two populations from Mirador Cave (MIR-C = Chalcolithic; MIR-B = Bronze Age) with their wear degree (WD) (Molnar, 1971) and their formation stages (MOO) (Moorrees et al., 1963). Their position (L = lower; U = upper), side (L = left; R = right) and crown heights (CrH, in mm) are also presented. The total perikymata count (Pk) on the buccal aspect is shown, as well as their lateral enamel formation times (LEFT) depending on the periodicity (7, 8 or 9 days).

Species (Population)	**Tooth**	**Position**	**n**	**Pk**	**sd**	**Range**	**95% CL**
Homo sapiens (Inuit)	I1	L	12	130	14	129–159	121-139
Homo sapiens (Newcastle)	I1	L	15	132	12	113–154	125-139
Homo sapiens (southern African)	I1	L	20	105	10	86–121	100-110
Homo sapiens (MTV-MIR)	I1	L	1	175	-	-	-
Homo sapiens (mixed)	I1	L	48	121	11	113-175	-
Homo sapiens (Inuit)	I2	L	14	140	11	119–157	134-146
Homo sapiens (Newcastle)	I2	L	13	130	19	99–177	119-141
Homo sapiens (southern African)	I2	L	23	110	13	85–143	104-116
Homo sapiens (MTV-MIR)	I2	L	2	171	-	162-180	-
Homo sapiens (mixed)	I2	L	52	125	14	85-180	-
Homo sapiens (Inuit)	I1	U	10	170	20	140–197	156-184
Homo sapiens (Newcastle)	I1	U	19	165	21	135–197	155-175
Homo sapiens (southern African)	I1	U	20	117	13	87–148	111-123
Homo sapiens (MTV-MIR)	I1	U	5	183	24	152-210	153-213
Homo sapiens (mixed)	I1	U	54	150	18	87-210	-
Homo sapiens (Inuit)	I2	U	10	151	19	124–175	137-165
Homo sapiens (Newcastle)	I2	U	16	134	16	107–154	125-143
Homo sapiens (southern African)	I2	U	21	115	15	88–152	108-122
Homo sapiens (MTV-MIR)	I2	U	5	150	21	143-187	124-176
Homo sapiens (mixed)	I2	U	52	131	17	88-187	-

Table 2. Perikymata counts (Pk) with their standard deviations (sd) and ranges of the incisors in Neandertals and three modern human population published by Guatelli-Steinberg and Reid (2008). 95% confidence limits (CL) have been calculated . Data for Maltravieso and Mirador Caves are in the rows labelled as Homo sapiens *(MTV-MIR). Notice that worn incisors have not been included whilst antimeres have been.*

Site	Specimen (antimere)	Tooth	Position	Deciles 1	2	3	4	5	6	7	8	9	10	Halves CeH	InH	CeH%	InH%
MTV	R1429	I1	L	10	13	11	11	11	15	17	28	21	38	119	56	68	32
MTV	R1419	I2	L	9	13	13	12	14	15	20	21	22	23	101	61	62	38
MTV	R1422	I2	L	9	12	12	11	11	14	20	32	29	30	125	55	69	31
MIR-B	MIR3A P20 387	I2	L	?	11	8	12	14	9	13	29	26	30	107	?	?	?
MTV	R1404 (R1412)	I1	U	13	15	11	13	19	20	29	33	31	18	131	71	65	35
MTV	R1406	I1	U	10	13	12	14	15	16	24	23	26	35	124	64	66	34
MTV	R1412 (R1404)	I1	U	15	13	11	14	17	23	24	30	30	33	140	70	67	33
MIR-C	MIR201 P37 163	I1	U	11	8	10	12	16	14	20	20	20	34	108	57	65	35
MIR-C	MIR203 R36 395	I1	U	11	10	11	11	13	16	20	20	16	24	96	56	63	37
MIR-B	MIR2 Q22 s/c	I1	U	?	12	10	12	16	16	16	23	25	29	109	?	?	?
MTV	R1418 (R1428)	I2	U	7	8	12	11	12	14	13	19	24	27	97	50	66	34
MTV	R1428 (R1418)	I2	U	6	7	11	13	14	15	15	16	22	25	93	51	65	35
MTV	R1435	I2	U	9	9	10	14	16	14	19	27	33	36	129	58	69	31
MIR-C	MIR201 REM 255	I2	U	7	11	9	10	10	11	12	21	20	20	84	47	64	36
MIR-B	MIR4 P22 164	I2	U	6	8	8	9	12	11	20	15	23	31	100	43	70	30

Table 3. Perikymata numbers (Pk) in each decile out of the ten deciles in which each crown height can be divided. The number of perikymata in the first five deciles (1-5) forms the incisal half of the crown (InH) whilst the number of perikymata in the last five deciles (6-19) forms the cervical half of the crown (CeH). Both halves are represented as percentages (CeH% and InH%).

<table>
<tr><td></td><td></td><td></td><td>IN</td><td>NW</td><td>SA</td></tr>
<tr><td rowspan="4">MIR-MTV</td><td rowspan="2">Upper I1</td><td>t</td><td>-0.5527</td><td>-1.0067</td><td>-7.4431</td></tr>
<tr><td>p</td><td>0.5906</td><td>0.3255</td><td>0.0000</td></tr>
<tr><td rowspan="2">Upper I2</td><td>t</td><td>-0.0206</td><td>-1.7420</td><td>-4.0123</td></tr>
<tr><td>p</td><td>0.9839</td><td>0.0986</td><td>0.0005</td></tr>
</table>

Table 4. T-student statistical analysis performed to seek for differences in the total perikymata number between the MIR-MTV sample against Inuits (IN), Newcastle (NW) and southern African (SA). Statistical differences are highlighted in bold. The sample size in both Upper I1 and I2 for the MIR-MTV sample is 4, as a result of deleting the R1412 and R1418 teeth, which are the antimeres of the R1404 and R1428 respectively. The sample sizes of the comparison populations are in Table 2.

<table>
<tr><td></td><td></td><td></td><td>IN</td><td>NW</td><td>SA</td></tr>
<tr><td rowspan="4">MIR-MTV</td><td rowspan="2">Upper I1</td><td>t</td><td>0.8458</td><td>0.9593</td><td>-0.4682</td></tr>
<tr><td>p</td><td>0.4130</td><td>0.3478</td><td>0.6441</td></tr>
<tr><td rowspan="2">Upper I2</td><td>t</td><td>1.0169</td><td>-0.9054</td><td>-0.9468</td></tr>
<tr><td>p</td><td>0.3293</td><td>0.3772</td><td>0.3536</td></tr>
</table>

Table 5. T-student statistical analysis performed to seek for differences in the percentages of perikymata number of the cervical halves (deciles 6-10) between the MIR-MTV sample against Inuits (IN), Newcastle (NW) and southern African (SA). No statistical differences were observed. The sample size in Upper I1 is 5 (the R1412 incisor was not included for being the antimere of the R1404 one), while in the Upper I2 is 4 (the R1418 incisor was not included for being the antimere of the R1428 one). The sample sizes of the comparison populations are in Table 2.

Fig. captions

Fig. 1. *Geographical map of Spain with the locations of the Maltravieso and Mirador Cave.*

Fig. 2. *Photographs of the buccal aspects of all the incisors included in this study. From left to right and top to bottom: MIR Q22 s/c, MIR203 R26 395, MIR201 P37 163, R1412, R1404, R1406, R1418, R1428, R1435, MIR4 P22 164, MIR201 REM 255, R1429, R1422, R1419, MIR3A P20 387. (*) = incisors from Mirador Cave. Vertical red scale = 2 cm.*

Fig. 3. *Image at the buccal aspect of lower first incisor (R1429) from Maltravieso Cave obtained by using the environmental scanning electron microscope FEI Quanta 600. Perikymata are clearly visible across the entire crown.*

Fig. 4. *Normal distributions of perikymata number obtained for every incisor type and every species and population from means and standard deviations published by Guatelli-Steinberg and Reid (2008) (Table 2). The normal distributions were obtained by using* dnorm *functions in R. Standard deviations are represented for every single normal distribution by their limits in ± 1,96 SD, coloring the area below the curve. Maltravieso and Mirador lower incisors (MTV-MIR) are represented as vertical dark dashed lines with their respective specimen names beside them. In upper incisors, MTV-MIR has been plotted as normal distributions due to their sample sizes, which is 4 in each. In upper I1s, R1412 and MIR2 Q22 s/c were removed to plot the normal distribution because they were an antimere and slightly eroded respectively. In the case that the incisors had wear degree of 2, there is a small dark arrow below the specimen name marking that the perikymata number would be slightly higher. 95% confidence intervals are represented below every single normal distribution, following the same color patterns as normal distributions. 95%CL of the comparison samples have been calculated from original values of means, standard deviations and sample sizes. See the text for further details.*

Fig. 5. *Distribution of perikymata number per deciles of the crown height of all the MTV-MIR incisors. Comparative samples are represented by their means and 95% confidence limits. Inuits are represented by yellow bars, Europeans by green bars and southern Africans by red bars. Every single MTV-MIR incisor is represented by an independent color.*