**Title**

Enamel growth rate variation of inner, mid, and outer enamel regions between select permanent tooth types across five temporally distinct British samples

**Running Title:**

Enamel growth variation between tooth types

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**Abstract**

**Objective:** This study explored differences in the regional daily growth rates of human enamel between tooth types across a temporal transect in Britain.

**Methods:** Upper permanent central incisors (n = 81), upper permanent canines (n = 69), and upper and lower permanent first molars (n = 115) from Roman, Pre-Medieval, Medieval, and Modern day populations were analysed using histological methods. Daily secretion rates (DSRs) were collected for inner, mid, and outer regions of cuspal and lateral enamel for each tooth type and temporal sample. Variation in DSRs between the tooth types, within each population, was sought using Welch’s tests.

**Results:** Numerous significant differences were observed in DSRs between equivalent enamel regions of different tooth types. The majority of differences were observed between molars and the anterior teeth, but there were no obvious trends as to which typically grew faster/slower, nor was there any consistency across the temporal samples. In contrast, comparisons between
incisors and canines yielded minimal differences and variation, when significant, was found to be enamel area- and sample-specific.

**Conclusions:** This study presents evidence for a high level of variation in DSRs between anterior teeth and first molars of the permanent dentition. This variation appears sporadic with no clear trend outside of anterior tooth comparisons, where analyses of the Late Pre-Medieval and Modern-day populations highlight how DSRs within cuspal and lateral enamel can vary independently.

**KEYWORDS:** Dentition, permanent; Dental enamel; Amelogenesis

**1|Introduction**

Over the past two decades research into the growth of permanent human enamel through daily secretion rates (DSRs) has focused on molars from individual populations (Beynon et al., 1991b; Lacruz and Bromage, 2006; Mahoney, 2008), or pooled data from multiple population offered as a single proxy sample for the human species (Smith et al., 2007). Similar analyses of anterior teeth have been conducted, but they have been either similarly limited in analysing single tooth types (Schwartz et al., 2001), or lacking inter-population analyses when multiple populations were included in the sampling frame (Fitzgerald, 1998). More recent research has investigated multiple populations, specifically looking at British populations. These analyses, spread across molars (Aris et al., 2020b) and incisors and canines (Aris et al., 2020a) have identified significant differences in enamel growth rates over time between populations. In the latter published analysis of anterior tooth types, Aris and colleagues discuss the variation in the anterior tooth growth rates compared to their prior analysis of molars from the same populations, commenting that molars appear to have developed at a faster rate (Aris et al., 2020b).

Building on the earlier studies on single tooth types, these recent studies have begun to expand our knowledge regarding modern human enamel DSRs. However, there is a lack of direct inter-tooth type comparison regarding enamel DSRs, especially across multiple populations. This project aims to address this deficiency by investigating differences in enamel growth rates for three different permanent tooth types (first molars, canines, and incisors), using teeth from each category sampled, and five different populations from different time periods spanning the Roman period to modern-day. There is also the potential for this study to help further contextualise the findings of recent research into inter-tooth biorhythm variation (McFarlane et al., 2020)

**1.1|Amelogenesis, biorhythms, and enamel secretion rates**

The process by which enamel cells (ameloblasts) secrete and mineralize protein matrix is known as amelogenesis (Boyde, 1989). During the secretory stage of amelogenesis the secretion of matrix is altered periodically and such generates short- and long-period lines that are retained in enamel (e.g. Dean et al., 1993; Smith and Nanci, 2003). The short period lines are known as cross striations, which correspond with daily (24 hour) circadian rhythms of enamel secretion in human and non-human primates, and extinct hominin species (e.g., Antoine, 2000; Antoine et al., 2009; Boyde, 1963, 1990; Bromage, 1991; Dean, 1995; 1998; Dean and Scandrett, 1996; Fitzgerald, 1995, 1998). Alteration of amelogenesis produces cross striations that have a different refractive index to the majority volume of enamel prisms, thus make these lines observable through thin section light microscopy (e.g., Berkovitz et al., 2017; Zheng et al., 2013).

Daily secretions rates are calculated directly using the length of adjacent cross striations (e.g., Mahoney, 2008). Within a typical tooth enamel DSRs will change progressively from enamel regions near the enamel dentine junction (EDJ) (termed the inner region), to in the middle regions of enamel, through to the outer regions of enamel near the outer enamel surface – this change involves an increase in enamel DSRs and thereby growth (e.g., Beynon et al., 1991b; Beynon et al., 1998; Lacruz and Bromage, 2006; Mahoney, 2008; Reid et al., 1998). Daily secretion rates are also slower in the region with greater proximity to the dental cervix (tooth neck) than those near the dentine horn (Beynon et al., 1991b). Due to the variation in enamel DSRs across dental crowns, any comparisons of these growth rates between groups (tooth types, representative samples, populations) are done for specific regions within dental crowns (e.g., Dean, 1998). This involves dividing crowns into a pair of triadic categories: cuspal, lateral, and cervical enamel areas; and inner, mid and outer regions (e.g. Aris et al., 2020a; 2020b).

The circadian rhythm affecting the formation of cross-striations is thought to be one of a number of biorhythms which is reflected in incremental markers in enamel. Retzius lines, also known as long period lines, form within enamel and can be viewed as darker lines crossing enamel prisms at an angle (e.g. Fitzgerald, 1998; Hillson, 1996; Mahoney et al., 2017; McFarlane et al., 2020; Retzius, 1837). The periodicity of these lines is defined by the number of cross striations between each Retzius line, Retzius periodicity therefore being the number of days between their formations. In humans this has been found to follow a circaseptan (roughly seven day) cycle with the value of Retzius periodicity, while varying from 6-12 days, thought to remain consistent in individuals (e.g. Beynon 1992; Dean and Beynon, 1991; Fitzgerald, 1998). Retzius periodicity is thereby considered the reflection of an underlying circaseptan biorhythm. Due to Retzius periodicity’s relation to enamel DSRs through dependence on cross striation morphology, any variations observed between groups in regards to secretion rates has the potential to influence the wider study of enamel biorhythms.

**1.2|Enamel growth rates and biorhythms between populations**

As previously mentioned, studies of modern human enamel DSRs have usually been based on samples drawn from a single population (Beynon et al., 1991b; Lacruz and Bromage, 2006; Mahoney, 2008). When a number of populations have been examined these have been pooled into a single sample that serves as the basis for infra-specific studies of enamel growth (e.g., Smith et al., 2007). More recent studies have addressed the lack of inter-population analysis for human enamel DSRs. Aris and their colleagues (2020a, 2020b) have published two studies that assessed growth rates of permanent teeth and investigated differences between British populations within a temporal transect. The first found that enamel growth of first molars across both lateral and cuspal regions slowed on average between populations over time from the Roman period to modern day (Aris et al., 2020b). The second identified a similar trend in slowing enamel growth rates from the same population, using a pooled sample of anterior teeth consisting of upper first incisors and upper canines (Aris et al., 2020a). These studies provide insight into the variation in growth rates between temporally distinct samples, but are limited in their inter-tooth analyses outside of preliminary comments in the second article (Aris et al., 2020a).

Research has also been conducted in the past that presents data relating to enamel growth for multiple population samples. Reid and Dean (2006) and Reid and Ferrell (2006) conducted inter-population research into human enamel growth through the analysis of 678 dental samples. These teeth covered all tooth types sourced from five different populations across four continents. They found that crown formation times (CFT; a measure relating to the total number of days for an enamel crown to form) varied sporadically between African and European populations with both presenting significantly higher and lower rates than the other according to the tooth types analysed (Reid and Dean, 2006; Reid and Ferrell, 2006). In particular, Reid and colleagues (2008) found significant differences in the CFTs of all upper premolars and first lower premolars between their samples of Europeans and Africans. The differences showed a general trend towards longer CFTs among Europeans. While these results suggest major differences in enamel growth patterns between different populations and distinct samples, CFT only relates to the time taken for all enamel to develop, not accounting for the rate at which enamel grew via secretion at a regional level. It is therefore important to expand research into enamel DSR analyses as well as CFTs as the exact relation between the two measures is currently not fully understood.

As noted earlier, Retzius periodicity is strongly associated with enamel DSRs. This means that any research identifying significant variation between populations’ enamels DSRs could have a notable impact on assumptions regarding Retzius periodicity differences within humans. This is especially pertinent given the use of Retzius periodicity (and associated perikymata counts) to investigate inter-species difference and evolutionary trajectories via dental analysis (e.g. Bocaege & Humphrey, 2016; Dean and Reid, 2001; Guatelli-Steinberg et al., 2005, 2010, 2018; Modesto-Mata et al., 2017, 2020; Ramirez Rozzi & Bermudez de Castro, 2004). Recent research has highlighted that Retzius periodicity can vary significantly between populations. In particular McFarlane and colleagues (2020) noted differences between British and southern African populations. Past research has observed similar variations, notably between southern African and European samples (Reid and Dean, 2006), and southern African and English samples (Smith et al., 2007). These, when combined with recent findings regarding inter-population differences in human enamel DSRs, highlight the need for more extensive investigations into how these DSRs vary within the human species.

**1.3|Enamel growth rates and biorhythms between tooth types**

In the same aforementioned study by Reid and Dean (2006), all tooth types from the permanent dental arcade were analysed for growth patterns. In particular, CFTs were reported for all these tooth types for Northern European and Southern African populations, alongside data from canines of a sample of Medieval Danes and third molars of a North American sample. While data for all tooth types is presented, minimal comparisons are made as to the differences between the tooth types within either the context of inter- or intra-population analyses. Such comparisons were limited to comments as to differences between anterior and posterior tooth types, but even these suggested canines had slow growing enamel relative to other teeth. Subsequent research has published similar data, with Reid and colleagues (2008) analysing all four premolar types for CFT data. While observation of their data alludes to possible inter-premolar type differences in CFTs, Reid and colleagues’ (2008) analyses did not involve looking for potential differences between tooth types and was instead focussed on differences in CFTs between modern human and Neanderthals. Further research, dedicated to investigating for inter-tooth differences in multiple different populations, would be valuable to develop our understanding of enamel growth patterns in human permanent dentition.

Recent studies have addressed the limitation of inter-tooth enamel DSR differences. Aris and colleagues, alongside analyses of inter-population differences, made further comparisons between the enamel DSRs of molars and anterior tooth types (Aris et al., 2020a). However, the extent of these comparisons were comments made from comparing data sets collected from pooled canine and incisor teeth, to equivalent molar data published in a previous study (Aris et al., 2020b). The preliminary comparisons did however allude to differences between the enamel DSRs of the anterior and posterior tooth types, notably that molars grew faster (Aris et al., 2020a). While intriguing, these comparisons were only preliminary and lacked direct comparison or statistical approach. Furthermore, they utilised pooled anterior tooth types thereby limiting the ability to examine the true differences between tooth types beyond anteriorly and posteriorly located teeth. As a result of these factors, analysis supported by statistical testing on canines, incisors, and molars is warranted both in general and for these populations. Moreover, given the previously discussed tendency for dental research to pool tooth types (e.g. Smith et al., 2007), there is clear merit to expanding our understanding of the variation in growth rates between different tooth types to help contextualise the reliability of pooling teeth is similar future research.

The merits of investigating for variation in enamel DSRs between tooth types are not limited to our understanding of the speed of enamel growth. Until recently Retzius periodicity was thought to be similar within individuals, comparably to how enamel DSRs were once thought to be consistent within humans as a species. However, in a recent study McFarlane and colleagues (2020) observed a slowing of Retzius periodicity from posterior teeth to anterior teeth within individuals. Such variation was observed within multiple contexts, including both British and southern African populations, and male and female groups when analysed separately. Despite this wide variation however, Retzius periodicity remained consistent within tooth types, namely molars and anterior teeth as a group (McFarlane et al., 2020). Should any variation be observed in enamel DSRs within such a context, it could potentially shed light on the causality of Retzius periodicity variation due to their close relationship via cross striations.

**2|Materials and Methods**

**2.1|Dental sample**

Permanent teeth, specifically first upper and lower molars (n=115), upper central incisors (n=81), and upper canines (n=69) were selected from populations across five different time periods. The time periods and associated dates of the populations analysed include the Roman period (n=32), Early Pre-Medieval (EPM; n=62), Late Pre-Medieval (LPM; n=41), Medieval (n=91), and Modern-day (n=39). Each tooth selected came from a different individual – a condition of the conduction of destructive analysis on each collection in order to preserve as much bioarchaeological material of each set of remains as possible.

The Roman population (70–400 AD) is represented by a sample of individuals excavated from two collections excavated in Cirencester (St James’ Place and Bath Gate, see: McWhirr et al., 1982). The Early Pre-Medieval samples (500–600 AD) were excavated from Ozengell Grange, Ramsgate (Millard et al., 1969). The Late Pre-Medieval samples (800–1200 AD) were excavated from the Black Gate Cemetery, Newcastle-Upon-Tyne (Swales, 2012). The Medieval samples were excavated from two sites: St Gregory's Priory, Canterbury (1100–1500 AD) (Hicks and Hicks, 2001), and Fishergate House, York (1000–1600 AD) (Holst, 2005).

The Modern-day dental samples were sourced from a collection held in the Skeletal Biology Research Centre, University of Kent, as a part of the UCL/Kent Collection (Aris, 2022). This collection consists of teeth extracted in dental surgeries in northern England and Glasgow (southern Scotland) between 1964 and 1973. Ethical approval for destructive histology research on this collection was obtained from the UK National Health Service research ethics committee (REC reference: 16/SC/0166; project ID: 203541).

The molar samples constitute pooled samples of upper and lower permanent first molars as these have been found to not significantly vary in regards to equivalent regional DSRs for the exact sample analysed here (see Table S2 in Aris et al., 2020b). Only teeth lacking evidence of pathology and unworn or minimally worn teeth were selected. Right teeth were selected unless the left was better preserved or if the right was unavailable. It should be noted that the Pre-Medieval populations have been referred to as ‘Anglo-Saxon’ previously (Aris et al., 2020a; 2020b; Aris and Street 2021). It is due to the exclusive nature of this term, its contextual association with white supremacy, and its appropriation by associated fringe groups, that here this is amended to the more appropriate reference of ‘Pre-Medieval’ (e.g. Dockray-Miller, 2017; Schmid et al., 2020).

**2.2|Sample preparation**

One-to-one scale resin casts, followed by high resolution images, were produced before any destructive sampling was undertaken for each tooth analysed (Aris, 2020). Following this, standard thin section histological methods were used to produce a slide for each tooth, in order to implement polarised light microscopy (e.g. Aris, 2020; Mahoney, 2008; Schwartz and Dean, 2005).

The first stage of preparing histological thin sections involved embedding each tooth in a four-to-one, hardener and epoxy resin, solution (Buehler®). By embedding the teeth in such a solution the risk of enamel fracturing was minimized, as well as allowing for easier alignment of each sample within a precision vice (Buehler®), during the cutting stage. A diamond-edged wafering saw blade (Buehler® IsoMet 1000 Precision Cutter) was used to cut the embedded teeth. All cuts were made at low speeds (between 100-200 rotations per minute) in order to control the risk of subsequent abrasion error. The cuts were made as to align with a straight line drawn along longitudinal axis of each tooth, passing through a cusp apex and its associated dentine horn. The cusps selected were the single cusp apex of the anterior teeth and the apexes of the distal cusps of the molars (see *Figure 3* in: Aris, 2022). Cuts were made in a labial-lingual direction for the anterior teeth, and buccal-lingual direction for the molars. In making cuts with this alignment and direction they were guaranteed to be made along the length of enamel prisms making the final sections suitable for analysis of DSRs (see below).

Once cut, each sample was then mounted on a glass microscope slide. The mounted sample was then lapped using fine grinding pads (Buehler®) until between 100–120μm thick. Lapped sections were then polished using 0.3μm aluminium oxide powder (Buehler®), which served to remove evidence of the lapping step. Polished sections were then placed in an ultrasonic bath for two-minute periods with the vibrations removing the remaining debris from the remaining sample’s surface. In the final step, each slide was dehydrated using 90%, and then 100%, concentrations of ethanol solution (Fisher scientific®) before being finally dip-cleaned (using Histoclear®). To protect sections from future contamination and surface damage, the exposed surface of the sectioned tooth was covered with a glass cover slip using mounting medium (DPX®). Once cover-slipped, the samples were checked for their original cut alignment. Correctly aligned cuts, as described previously, were identified through a sharp “V-shape” of the dentine horn, whereas misaligned cuts presented a rounded dentine horn (see *Figure 4* in: Aris, 2022). Only in correctly aligned sections had the cut been made through the length of enamel prisms. Only those sections made with correctly aligned cuts were analysed under polarized light with a BX53 upright microscope (Olympus®) and micro imaging software (cellSens; see below for detail).

**2.3|Daily secretion rates**

The DSRs for the incisors, canines, and molars were calculated for the inner, mid, and outer areas of the lateral and cuspal enamel regions using standard methods (e.g., Beynon, Dean, and Reid, 1991a; Mahoney, 2008; Schwartz et al., 2001). All enamel areas were determined within the labial enamel of the incisors and canines, and for the mesial-buccal enamel of the molars. Each of these areas within the cuspal and lateral regions were determined by dividing the length of the enamel regions into three equidistant sections, located along the longitudinal axis of local enamel prisms (see Figure 1). Regions of the cuspal enamel area were determined within the appositional enamel located in near proximity the dentine horn. The lateral enamel areas were determined within the section of imbricational enamel located equidistant between the dentine horn apex and the dental cervix, measured along the enamel dentine junction. Within each enamel region (inner, mid, outer) a measurement was made of five adjacent and consecutive cross striations along the length of a local enamel prism. This measurement was then divided by five to give a mean daily rate of secretion (μm/day). This process was repeated six times, with the batches of adjacent cross striations selected according to clarity and dispersal in order to get as representative a sample as possible to account for any variation present within each region. The sum of these six results were then divided to give a grand mean and standard deviation. All measurements of cross striations were taken between ×20 and ×40 magnification (see Figure 2).

INSERT FIGURE 1 HERE

INSERT FIGURE 2 HERE

**2.4|Statistical analysis**

Due to the variance in samples sizes between samples by tooth type and population (total range: n=6-46; mode range: n=10-12; where n = number of teeth) for statistical analysis Welch’s tests were selected in order to accommodate and adjust for the homogeneity of variance between groups. A series of tests were then run in order to identify any differences between the mean DSRs of equivalent regions between each pair of tooth types for each different British sample. Paired comparisons of tooth types between individuals were impossible to conduct due to the selection criteria of the teeth sampled. Due to the number of multiple comparisons being made through statistical analysis all the *p* value outputs for all tests were adjusted, before reporting, according to Dunn-Bonferroni corrections – in this way all results were individually adjusted to ensure statistical biases were addressed, while a threshold of significance of *p*<0.05 could be kept consistent between tables as to ensure accessibility. All statistical analyses were performed using the SPSS 26.0.

**3|Results**

**3.1|Upper central incisors versus upper canines**

Table 1 reports the results of comparing the regional mean lateral DSRs between the incisor and canine samples of each population. Two significant differences were observed, and both involve the Late Pre-Medieval sample. Here, the incisors presented significantly faster mean DSRs than canines for the inner and outer regions (*p*=0.01 in both cases). Although statistically insignificant, the mean difference between the incisors and the canines of the same population was still notable for the mid region, with a difference of 0.14µm/day.

Table 2 reports the results of comparing the regional mean cuspal DSRs. Similar to the lateral area comparisons, two significant differences were observed for a single population. In this case the incisors presented significantly faster mean DSRs than canines, in the Modern-day sample, for the inner and mid regions (*p*=0.02 and *p*<0.01, respectively). Also similar to the comparisons of lateral areas, though statistically insignificant, the DSR among the incisors was still faster than the canines in the Modern-day sample with a notable difference of 0.32µm/day in the outer region.

INSERT TABLE 1 HERE

INSERT TABLE 2 HERE

**3.2|Upper canines versus upper and lower first molars**

The results of comparing regional DSRs between the canines and molars were more sporadic than among canines to incisors. Table 3 reports the results of these comparisons for the lateral DSRs of each population sample. Four significant differences were observed across the three temporal samples. For the inner region comparisons mean DSRs were found to be significantly faster in molars within the Medieval sample (*p*<0.01); conversely canine DSRs were found to be faster in the Modern-day sample (*p*=0.01). For the mid and outer regions canine DSRs were found to be faster in the Late Pre-Medieval sample (*p*=0.01 and *p*=0.03 respectively).

 Table 4 reports the results of the same comparisons for cuspal DSRs. An increased number of significant differences (n=7) were observed across four temporal samples. For the inner region mean DSRs were found to be significantly faster in molars within the Early Pre-Medieval sample (*p*<0.01); conversely canine DSRs were found to be faster in the Modern-day population (*p*=0.03). For the mid region comparisons DSRs were significantly faster in molars in the Modern-day sample (*p*<0.01); conversely canine DSRs were found to be faster in the Late Pre-Medieval sample (*p*<0.01). For the outer region comparisons, mean DSRs were significantly faster in molars within the Modern-day population (*p*=0.02); conversely canine DSRs were significantly faster in the Late-Pre-Medieval and Medieval samples (*p*<0.01 and *p*=0.03, respectively).

INSERT TABLE 3 HERE

INSERT TABLE 4 HERE

**3.3|Upper and lower molars versus upper central incisors**

Results obtained from comparing the regional DSRs between the incisors and molars were similar to those described for the comparison of canines to molars. Table 5 reports these comparisons for the lateral DSRs of each temporal sample. Four significant differences were observed across two samples. For the inner region mean DSRs were significantly faster in molars within the Medieval sample (*p*<0.01); conversely incisor DSRs were faster in the Late Pre-Medieval sample (*p*=0.01). For the mid and outer regions canine DSRs were faster in the Late Pre-Medieval sample (*p*<0.01 in both cases).

 Table 6 reports the results of the same comparisons for the cuspal DSRs. An increased number of six significant differences were observed across four populations. For the inner region comparisons mean DSRs were found to be significantly faster in molars within the Roman and Early Pre-Medieval populations (*p*=0.03 and *p*<0.01, respectively). For the mid region comparisons DSRs were found to be significantly faster in incisors in the Late Pre-Medieval and Medieval populations (*p*<0.01 and *p*=0.02, respectively). For the outer region comparisons mean DSRs were found to be significantly faster in incisors within the Roman and Late Pre-Medieval populations (*p*=0.03 and *p*<0.01, respectively).

INSERT TABLE 5 HERE

INSERT TABLE 6 HERE

**4|Discussion**

**4.1|Inter-tooth differences**

In the limited cases where researchers have compared enamel growth rates between tooth types within human dentition, faster rates have typically been observed for molars. In particular, faster CFTs have been observed when compared to canines (Reid and Dean, 2006; Reid and Ferrell, 2006; Reid et al., 2008) and faster DSRs when compared to pooled anterior tooth samples (Aris et al., 2020a). In addition, decreased Retzius periodicity, an enamel feature dependent on cross-striation morphology and thereby associated with DSRs, has also been found to vary between anterior and posterior teeth – notably with a decrease from anterior to posterior seen in both British and southern African samples (McFarlane et al., 2020). The findings presented here partially corroborate these past findings of variation in enamel growth features with tooth position. Across lateral and cuspal enamel regions, molars regularly presented faster mean DSRs both when compared to incisors and canines. Cuspal enamel region comparisons displayed the greatest number of such differences, particularly in comparisons of molars to canines. Moreover, the relative similarity, and lack of wide significant differences between canine and incisors DSRs, agrees with findings of past research which has yet to note significant differences between anterior tooth DSRs (e.g. Aris et al., 2020a). At a preliminary glance then, the findings of this project appear to support the limited comments as to growth rate variation across the tooth row in permanent human teeth.

However, alongside the differences where molars grew significantly faster than the anterior teeth, there were in fact more cases where incisors and/or canines presented faster mean DSRs than molars. This stands in direct opposition to the theory that molars consistently grow and develop at faster rates than their anterior counterparts in permanent human dental arcades. This is not necessarily unexpected given the dearth of research dedicated to studying the differences in growth rates between human tooth types. Furthermore, recent research into human DSRs have found them to vary to a far wider degree than previously thought between human populations (Aris et al., 2020a; 2020b; Aris and Street, 2021). Consequently, the authors of these articles have noted the potential for variation in DSRs to exist between differently defined groups. The findings of inconsistent and sporadic differences between anterior teeth and molars is thereby not to be entirely unexpected, and supports the claims advanced in other recent research that caution must be taken when pooling human dental data with regard to growth rates when forming representative samples, either within single populations, or when pooling multiple populations.

In addition to the sporadic variation between molars and the anterior teeth, the general inconsistency between where significant differences were observed with regard to enamel area and region is also a notable finding. Specifically, the fact that there was no obvious pattern observed across lateral and cuspal DSR comparisons between any two tooth types, indicates that DSRs of different enamel regions can vary independently between different teeth and potentially between different populations. One example of this occurs in the comparisons of the molars to the incisors and canines of the Medieval sample, where lateral enamel tended to grow faster in molars, but cuspal enamel grew faster in the anterior teeth. This is particularly interesting as past research has found DSR variation to be relatively consistent across equivalent lateral and cuspal comparisons (Aris et al., 2020a; 2020b). However, this consistency is likely due – at least in part – to the fact that observations were of either single tooth (Aris et al., 2020b) or pooled tooth types (Aris et al., 2020a), and in both of these were only analysed for differences between populations. Thus it appears that although DSRs tend to be consistent in their differences across the enamel cap for single teeth between populations, the reverse is true when different tooth types are compared within both within single and across multiple populations.

**4.2|Inter-group differences**

While the expected trend of faster growing molar teeth relative to anterior tooth types was not fully observed, the relative consistency between the incisors and canines was noted for the majority of enamel regions and across multiple temporal samples. Such a finding matches the growth patterns as observed through CFTs and DSRs in past works, which have noted significant differences between the enamel growth of anterior teeth to faster developing molars (Reid and Dean, 2006; Reid and Ferrell, 2006; Reid et al., 2008; Aris et al., 2020a). One finding of the current research is that the trend of human molars growing at different rates to their anterior counterparts holds true generally, and while variations do exist these are limited and highly specific to individual samples and are thereby potentially unique to different populations.

Such variations can be seen in the significant differences isolated within individual enamel areas of the Late Pre-Medieval and Modern-day samples. Incisal mean DSRs were
consistently faster compared to canines in all lateral enamel areas (significantly so in the inner and outer areas) among Late Pre-Medieval individuals. The incisors also displayed consistently faster mean DSRs in all cuspal enamel areas (significantly so in the inner and mid areas) in the Modern-day sample. While it may be the case that the faster incisor DSRs are a product of coincidence given the number of teeth and different population samples being analysed, the consistency across the length of the enamel in each case indicates otherwise. Instead, these differences within the generally consistent trend of similar growth velocities of canines and incisors further highlight the level of inter-sample variability that can occur in the dentition of humans, alluding towards the exitance or marked inter-population difference. While it is important to note that due to varying sample sizes presented here that the samples should not be assumed to be truly representative of the populations they were sampled, this finding does concur with past research regarding DSRs. These have found they can vary greatly between different populations over relatively short periods of time in multiple tooth types (Aris et al., 2020a; 2020b).

Further to the differences observed between incisors and canines, the variation between the posterior and anterior tooth DSRs further highlights the high level of variability potentially existing between the British population samples from the last 2000 years. In the majority of cases the significantly different regional mean DSRs were observed sporadically across all five population samples analysed and, as previously discussed, were variable between showing faster growing molars of faster growth anterior teeth. However, in the case of the Late Pre-Medieval sample, a high degree of consistency was observed with significantly faster mean DSRs compared to molars seen in: 1) canine mid and outer lateral regions, 2) canine mid and outer cuspal regions, 3) incisor inner, mid, and outer lateral regions, and 4) incisor mid and outer cuspal regions. These consistent inter-tooth type trends show how trends in inter-tooth differences can vary drastically between populations when the Late Pre-Medieval sample was compared with the other four population samples analysed here. Past research into human DSRs has observed similar differences between populations during intra-tooth-type analyses and have subsequently warned against future research pooling populations when analysing human DSRs (Aris et al., 2020a; 2020b). The findings presented here support the call for caution to be taken when pooling human populations’ DSRs, as well as avoiding pooling tooth types even within the categories of anterior and/or posterior classifications. Moreover, if/when future research identifies trends in differences in enamel development within any transect using a single human population, caution should be taken before assuming the trend is true of another human population.

**5|Conclusion**

Results presented here found considerable variation between the DSRs of different teeth across five temporally distinct British samples. The comparisons found the majority of significant differences to be between molars and incisors/canines, but with no obvious trend to indicate if the posterior or anterior teeth were those which grew faster or slower in general. The sporadic nature of the significant differences was also notable when observing comparisons of lateral and cuspal enamel, with again no apparent trend between them alluding to DSRs being able to vary across the enamel cap within populations in regards to differences between tooth types. Overall these findings consist with other recent studies of human DSRs, showing them to be highly plastic and able to vary significantly both within and between populations within relatively small temporal and geographic contexts. Future research would benefit from investigating the growth rates of enamel from human populations of considerably different geographic origins in order to expand our understanding of the plasticity of human DSRs.

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**Tables List**

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| **Table 1.** *Results of the Welch’s tests for variation in* ***lateral*** *regional mean DSRs (µm/day*) *compared between* ***incisors and canines*** *for each population. Significant results are marked in bold.* |
| Lateral DSR comparisons |
| Region | Population | Tooth | N | Mean | SD | Min | Max | Sig. |
| Inner | Roman | Canine | 11 | 3.46 | 0.21 | 3.12 | 3.91 | 0.14 |
| Incisor | 9 | 3.57 | 0.11 | 3.36 | 3.70 |
| Early Pre-Medieval | Canine | 20 | 3.26 | 0.19 | 2.98 | 3.62 | 0.94 |
| Incisor | 22 | 3.26 | 0.21 | 2.89 | 3.77 |
| Late Pre-Medieval | Canine | 10 | 3.40 | 0.18 | 3.14 | 3.80 | **0.01** |
| Incisor | 10 | 3.58 | 0.11 | 3.42 | 3.80 |
| Medieval | Canine | 14 | 3.11 | 0.26 | 2.70 | 3.75 | 0.87 |
| Incisor | 25 | 3.13 | 0.22 | 2.69 | 3.54 |
| Modern-day | Canine | 12 | 2.85 | 0.25 | 2.45 | 3.17 | 0.07 |
| Incisor | 12 | 3.04 | 0.21 | 2.56 | 3.32 |
| Mid | Roman | Canine | 11 | 3.97 | 0.20 | 3.67 | 4.28 | 0.16 |
| Incisor | 10 | 4.08 | 0.13 | 3.91 | 4.29 |
| Early Pre-Medieval | Canine | 20 | 3.83 | 0.20 | 3.47 | 4.17 | 0.42 |
| Incisor | 22 | 3.77 | 0.26 | 3.32 | 4.42 |
| Late Pre-Medieval | Canine | 10 | 3.86 | 0.19 | 3.55 | 4.12 | 0.17 |
| Incisor | 10 | 4.00 | 0.25 | 3.66 | 4.35 |
| Medieval | Canine | 15 | 3.53 | 0.27 | 3.04 | 4.05 | 0.88 |
| Incisor | 25 | 3.54 | 0.27 | 2.92 | 4.03 |
| Modern-day | Canine | 12 | 3.30 | 0.21 | 2.99 | 3.65 | 0.14 |
| Incisor | 12 | 3.45 | 0.27 | 2.86 | 3.80 |
| Outer | Roman | Canine | 11 | 4.41 | 0.24 | 3.88 | 4.82 | 0.33 |
| Incisor | 10 | 4.50 | 0.16 | 4.27 | 4.81 |
| Early Pre-Medieval | Canine | 19 | 4.28 | 0.21 | 3.93 | 4.76 | 0.88 |
| Incisor | 20 | 4.29 | 0.28 | 3.81 | 4.75 |
| Late Pre-Medieval | Canine | 10 | 4.12 | 0.15 | 3.93 | 4.41 | **0.01** |
| Incisor | 10 | 4.36 | 0.23 | 4.04 | 4.91 |
| Medieval | Canine | 15 | 3.91 | 0.24 | 3.38 | 4.35 | 0.71 |
| Incisor | 25 | 3.88 | 0.24 | 3.50 | 4.49 |
| Modern-day | Canine | 11 | 3.60 | 0.23 | 3.03 | 3.82 | 0.24 |
| Incisor | 12 | 3.72 | 0.25 | 3.14 | 4.06 |

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| **Table 2.** *Results of the Welch’s tests for variation in* ***cuspal*** *regional mean DSRs (µm/day*) *compared between* ***incisors and canines*** *for each population. Significant results are marked in bold.* |
| Cuspal DSR comparisons |
| Region | Population | Tooth | N | Mean | SD | Min | Max | Sig. |
| Inner | Roman | Canine | 9 | 3.52 | 0.20 | 3.22 | 3.86 | 0.64 |
| Incisor | 9 | 3.48 | 0.15 | 3.28 | 3.68 |
| Early Pre-Medieval | Canine | 16 | 3.27 | 0.14 | 2.93 | 3.49 | 0.54 |
| Incisor | 9 | 3.31 | 0.20 | 2.85 | 3.51 |
| Late Pre-Medieval | Canine | 8 | 3.34 | 0.17 | 3.16 | 3.69 | 0.08 |
| Incisor | 9 | 3.51 | 0.21 | 3.04 | 3.70 |
| Medieval | Canine | 11 | 3.12 | 0.16 | 2.92 | 3.45 | 0.93 |
| Incisor | 16 | 3.13 | 0.18 | 2.80 | 3.46 |
| Modern-day | Canine | 10 | 2.90 | 0.29 | 2.41 | 3.20 | **0.02** |
| Incisor | 8 | 3.20 | 0.23 | 2.84 | 3.43 |
| Mid | Roman | Canine | 9 | 4.17 | 0.26 | 3.67 | 4.58 | 0.61 |
| Incisor | 10 | 4.12 | 0.11 | 3.96 | 4.31 |
| Early Pre-Medieval | Canine | 15 | 3.86 | 0.25 | 3.46 | 4.29 | 0.79 |
| Incisor | 9 | 3.89 | 0.26 | 3.38 | 4.35 |
| Late Pre-Medieval | Canine | 8 | 3.94 | 0.15 | 3.81 | 4.28 | 0.23 |
| Incisor | 9 | 4.07 | 0.26 | 3.69 | 4.68 |
| Medieval | Canine | 12 | 3.70 | 0.20 | 3.24 | 4.04 | 0.68 |
| Incisor | 20 | 3.73 | 0.22 | 3.27 | 4.18 |
| Modern-day | Canine | 10 | 3.18 | 0.22 | 2.81 | 3.57 | **0.00\*** |
| Incisor | 8 | 3.54 | 0.22 | 3.16 | 3.86 |
| Outer | Roman | Canine | 9 | 4.65 | 0.26 | 4.16 | 4.98 | 0.16 |
| Incisor | 10 | 4.79 | 0.12 | 4.69 | 5.06 |
| Early Pre-Medieval | Canine | 13 | 4.46 | 0.38 | 3.99 | 5.37 | 0.94 |
| Incisor | 8 | 4.47 | 0.22 | 4.25 | 4.93 |
| Late Pre-Medieval | Canine | 6 | 4.35 | 0.16 | 4.06 | 4.50 | 0.21 |
| Incisor | 7 | 4.49 | 0.22 | 4.26 | 4.96 |
| Medieval | Canine | 9 | 4.10 | 0.25 | 3.71 | 4.47 | 0.43 |
| Incisor | 19 | 4.01 | 0.28 | 3.57 | 4.97 |
| Modern-day | Canine | 10 | 3.57 | 0.19 | 3.16 | 3.79 | 3.79 |
| Incisor | 8 | 3.89 | 0.23 | 3.36 | 3.89 |

\**p*<0.01

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| **Table 3.** *Results of the Welch’s tests for variation in* ***lateral*** *regional mean DSRs (µm/day*) *compared between* ***molars and canines*** *for each population. Significant results are marked in bold.* |
| Lateral DSR comparisons |
| Region | Population | Tooth | N | Mean | SD | Min | Max | Sig. |
| Inner | Roman | Molar | 11 | 3.66 | 0.28 | 3.30 | 4.36 | 0.07 |
| Canine | 11 | 3.46 | 0.21 | 3.12 | 3.91 |
| Early Pre-Medieval | Molar | 20 | 3.39 | 0.22 | 3.10 | 4.03 | 0.06 |
| Canine | 20 | 3.26 | 0.19 | 2.98 | 3.62 |
| Late Pre-Medieval | Molar | 17 | 3.33 | 0.26 | 2.87 | 3.87 | 0.38 |
| Canine | 10 | 3.40 | 0.18 | 3.14 | 3.80 |
| Medieval | Molar | 25 | 3.37 | 0.25 | 2.88 | 3.81 | **0.00\*** |
| Canine | 14 | 3.11 | 0.26 | 2.70 | 3.75 |
| Modern-day | Molar | 20 | 3.08 | 0.19 | 2.61 | 3.38 | **0.01** |
| Canine | 12 | 3.27 | 0.14 | 2.93 | 3.49 |
| Mid | Roman | Molar | 11 | 4.19 | 0.33 | 3.67 | 4.78 | 0.07 |
| Canine | 11 | 3.97 | 0.20 | 3.67 | 4.28 |
| Early Pre-Medieval | Molar | 20 | 3.87 | 0.18 | 3.54 | 4.21 | 0.52 |
| Canine | 20 | 3.83 | 0.20 | 3.47 | 4.17 |
| Late Pre-Medieval | Molar | 17 | 3.56 | 0.35 | 2.85 | 4.12 | **0.01** |
| Canine | 10 | 3.86 | 0.19 | 3.55 | 4.12 |
| Medieval | Molar | 25 | 3.65 | 0.28 | 3.12 | 4.29 | 0.17 |
| Canine | 15 | 3.53 | 0.27 | 3.04 | 4.05 |
| Modern-day | Molar | 20 | 3.37 | 0.27 | 2.82 | 3.86 | 0.45 |
| Canine | 12 | 3.30 | 0.21 | 2.99 | 3.65 |
| Outer | Roman | Molar | 11 | 4.57 | 0.34 | 3.97 | 5.13 | 0.22 |
| Canine | 11 | 4.41 | 0.24 | 3.88 | 4.82 |
| Early Pre-Medieval | Molar | 20 | 4.29 | 0.24 | 3.85 | 4.78 | 0.85 |
| Canine | 19 | 4.28 | 0.21 | 3.93 | 4.76 |
| Late Pre-Medieval | Molar | 17 | 3.80 | 0.42 | 2.89 | 4.60 | **0.03** |
| Canine | 10 | 4.12 | 0.15 | 3.93 | 4.41 |
| Medieval | Molar | 25 | 3.87 | 0.24 | 3.47 | 4.49 | 0.59 |
| Canine | 15 | 3.91 | 0.24 | 3.38 | 4.35 |
| Modern-day | Molar | 20 | 3.69 | 0.25 | 3.13 | 4.06 | 0.34 |
| Canine | 11 | 3.60 | 0.23 | 3.03 | 3.82 |

\**p*<0.01

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| **Table 4.** *Results of the Welch’s tests for variation in* ***cuspal*** *regional mean DSRs (µm/day*) *compared between* ***molars and canines*** *for each population. Significant results are marked in bold.* |
| Cuspal DSR comparisons |
| Region | Population | Tooth | N | Mean | SD | Min | Max | Sig. |
| Inner | Roman | Molar | 7 | 3.72 | 0.26 | 3.23 | 4.02 | 0.13 |
| Canine | 9 | 3.52 | 0.20 | 3.22 | 3.86 |
| Early Pre-Medieval | Molar | 13 | 3.67 | 0.36 | 3.21 | 4.67 | **0.00\*** |
| Canine | 16 | 3.27 | 0.20 | 2.85 | 3.51 |
| Late Pre-Medieval | Molar | 18 | 3.34 | 0.26 | 3.02 | 4.20 | 0.99 |
| Canine | 8 | 3.34 | 0.17 | 3.16 | 3.69 |
| Medieval | Molar | 38 | 3.23 | 0.25 | 2.77 | 3.84 | 0.11 |
| Canine | 11 | 3.12 | 0.16 | 2.92 | 3.45 |
| Modern-day | Molar | 20 | 3.17 | 0.33 | 2.54 | 3.99 | **0.03** |
| Canine | 10 | 2.90 | 0.29 | 2.41 | 3.20 |
| Mid | Roman | Molar | 8 | 4.21 | 0.17 | 4.07 | 4.58 | 0.76 |
| Canine | 9 | 4.17 | 0.26 | 3.67 | 4.58 |
| Early Pre-Medieval | Molar | 14 | 3.92 | 0.20 | 3.68 | 4.40 | 0.51 |
| Canine | 15 | 3.86 | 0.25 | 3.46 | 4.29 |
| Late Pre-Medieval | Molar | 20 | 3.65 | 0.26 | 3.39 | 4.27 | **0.00\*** |
| Canine | 8 | 3.94 | 0.15 | 3.81 | 4.28 |
| Medieval | Molar | 42 | 3.58 | 0.26 | 2.91 | 4.13 | 0.12 |
| Canine | 12 | 3.70 | 0.20 | 3.24 | 4.04 |
| Modern-day | Molar | 21 | 3.51 | 0.34 | 2.96 | 4.18 | **0.00\*** |
| Canine | 10 | 3.18 | 0.22 | 2.81 | 3.57 |
| Outer | Roman | Molar | 7 | 4.56 | 0.22 | 4.12 | 4.76 | 0.48 |
| Canine | 9 | 4.65 | 0.26 | 4.16 | 4.98 |
| Early Pre-Medieval | Molar | 12 | 4.33 | 0.24 | 4.10 | 4.81 | 0.34 |
| Canine | 13 | 4.46 | 0.38 | 3.99 | 5.37 |
| Late Pre-Medieval | Molar | 20 | 3.99 | 0.30 | 3.41 | 4.66 | **0.00\*** |
| Canine | 6 | 4.35 | 0.16 | 4.06 | 4.50 |
| Medieval | Molar | 41 | 3.87 | 0.23 | 3.13 | 4.38 | **0.03** |
| Canine | 9 | 4.10 | 0.25 | 3.71 | 4.47 |
| Modern-day | Molar | 21 | 3.81 | 0.34 | 3.15 | 4.58 | **0.02** |
| Canine | 10 | 3.57 | 0.19 | 3.16 | 3.79 |

\**p*<0.01

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| **Table 5.** *Results of the Welch’s tests for variation in* ***lateral*** *regional mean DSRs (µm/day*) *compared between* ***incisors and molars*** *for each population. Significant results are marked in bold.* |
| Lateral DSR comparisons |
| Region | Population | Tooth | N | Mean | SD | Min | Max | Sig. |
| Inner | Roman | Molar | 11 | 3.66 | 0.28 | 3.30 | 4.36 | 0.35 |
| Incisor | 9 | 3.57 | 0.11 | 3.36 | 3.70 |
| Early Pre-Medieval | Molar | 20 | 3.39 | 0.22 | 3.10 | 4.03 | 0.08 |
| Incisor | 22 | 3.26 | 0.21 | 2.89 | 3.77 |
| Late Pre-Medieval | Molar | 17 | 3.33 | 0.26 | 2.87 | 3.87 | **0.00\*** |
| Incisor | 10 | 3.58 | 0.11 | 3.42 | 3.80 |
| Medieval | Molar | 25 | 3.37 | 0.25 | 2.88 | 3.81 | **0.00\*** |
| Incisor | 25 | 3.13 | 0.22 | 2.69 | 3.54 |
| Modern-day | Molar | 20 | 3.08 | 0.19 | 2.61 | 3.38 | 0.60 |
| Incisor | 12 | 3.04 | 0.21 | 2.56 | 3.32 |
| Mid | Roman | Molar | 11 | 4.19 | 0.33 | 3.67 | 4.78 | 0.33 |
| Incisor | 10 | 4.08 | 0.13 | 3.91 | 4.29 |
| Early Pre-Medieval | Molar | 20 | 3.87 | 0.18 | 3.54 | 4.21 | 0.17 |
| Incisor | 22 | 3.77 | 0.26 | 3.32 | 4.42 |
| Late Pre-Medieval | Molar | 17 | 3.56 | 0.35 | 2.85 | 4.12 | **0.00\*** |
| Incisor | 10 | 4.00 | 0.25 | 3.66 | 4.35 |
| Medieval | Molar | 25 | 3.65 | 0.28 | 3.12 | 4.29 | 0.15 |
| Incisor | 25 | 3.54 | 0.27 | 2.92 | 4.03 |
| Modern-day | Molar | 20 | 3.37 | 0.27 | 2.82 | 3.86 | 0.42 |
| Incisor | 12 | 3.45 | 0.27 | 2.86 | 3.80 |
| Outer | Roman | Molar | 11 | 4.57 | 0.34 | 3.97 | 5.13 | 0.55 |
| Incisor | 10 | 4.50 | 0.16 | 4.27 | 4.81 |
| Early Pre-Medieval | Molar | 20 | 4.29 | 0.24 | 3.85 | 4.78 | 0.98 |
| Incisor | 20 | 4.29 | 0.28 | 3.81 | 4.75 |
| Late Pre-Medieval | Molar | 17 | 3.80 | 0.42 | 2.89 | 4.60 | **0.00\*** |
| Incisor | 10 | 4.36 | 0.23 | 4.04 | 4.91 |
| Medieval | Molar | 25 | 3.87 | 0.24 | 3.47 | 4.49 | 0.85 |
| Incisor | 25 | 3.88 | 0.24 | 3.50 | 4.49 |
| Modern-day | Molar | 20 | 3.69 | 0.25 | 3.13 | 4.06 | 0.71 |
| Incisor | 12 | 3.72 | 0.25 | 3.14 | 4.06 |

\**p*<0.01

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| **Table 6.** *Results of the Welch’s tests for variation in* ***cuspal*** *regional mean DSRs (µm/day*) *compared between* ***incisors and molars*** *for each population. Significant results are marked in bold.* |
| Cuspal DSR comparisons |
| Region | Population | Tooth | N | Mean | SD | Min | Max | Sig. |
| Inner | Roman | Molar | 7 | 3.72 | 0.26 | 3.23 | 4.02 | **0.03** |
| Incisor | 9 | 3.48 | 0.15 | 3.28 | 3.68 |
| Early Pre-Medieval | Molar | 13 | 3.67 | 0.36 | 3.21 | 4.67 | **0.00\*** |
| Incisor | 9 | 3.31 | 0.20 | 2.85 | 3.51 |
| Late Pre-Medieval | Molar | 18 | 3.34 | 0.26 | 3.02 | 4.20 | 0.08 |
| Incisor | 9 | 3.51 | 0.21 | 3.04 | 3.70 |
| Medieval | Molar | 38 | 3.23 | 0.25 | 2.77 | 3.84 | 0.12 |
| Incisor | 16 | 3.13 | 0.18 | 2.80 | 3.46 |
| Modern-day | Molar | 20 | 3.17 | 0.33 | 2.54 | 3.99 | 0.81 |
| Incisor | 8 | 3.20 | 0.23 | 2.84 | 3.43 |
| Mid | Roman | Molar | 8 | 4.21 | 0.17 | 4.07 | 4.58 | 0.27 |
| Incisor | 10 | 4.12 | 0.11 | 3.96 | 4.31 |
| Early Pre-Medieval | Molar | 14 | 3.92 | 0.20 | 3.68 | 4.40 | 0.79 |
| Incisor | 9 | 3.89 | 0.26 | 3.38 | 4.35 |
| Late Pre-Medieval | Molar | 20 | 3.65 | 0.26 | 3.39 | 4.27 | **0.00\*** |
| Incisor | 9 | 4.07 | 0.26 | 3.69 | 4.68 |
| Medieval | Molar | 42 | 3.58 | 0.26 | 2.91 | 4.13 | **0.02** |
| Incisor | 20 | 3.73 | 0.22 | 3.27 | 4.18 |
| Modern-day | Molar | 21 | 3.51 | 0.34 | 2.96 | 4.18 | 0.80 |
| Incisor | 8 | 3.54 | 0.22 | 3.16 | 3.86 |
| Outer | Roman | Molar | 7 | 4.56 | 0.22 | 4.12 | 4.76 | **0.03** |
| Incisor | 10 | 4.79 | 0.12 | 4.69 | 5.06 |
| Early Pre-Medieval | Molar | 12 | 4.33 | 0.24 | 4.10 | 4.81 | 0.23 |
| Incisor | 8 | 4.47 | 0.22 | 4.25 | 4.93 |
| Late Pre-Medieval | Molar | 20 | 3.99 | 0.30 | 3.41 | 4.66 | **0.00\*** |
| Incisor | 7 | 4.49 | 0.22 | 4.26 | 4.96 |
| Medieval | Molar | 41 | 3.87 | 0.23 | 3.13 | 4.38 | 0.07 |
| Incisor | 19 | 4.01 | 0.28 | 3.57 | 4.97 |
| Modern-day | Molar | 21 | 3.81 | 0.34 | 3.15 | 4.58 | 0.48 |
| Incisor | 8 | 3.89 | 0.23 | 3.36 | 3.89 |

\**p*<0.01

**Figure captions:**

**Figure 1.** Digital images of a first molar and canine from the Medieval population. T**he left four rectangles** show the location of the cuspal and lateral enamel areas within the dental cross sections. **The right two rectangles** display representative superimpositions of how these areas were subdivided into inner, mid, and outer regions. **Red squares (A)** display the cuspal enamel area. **Green squares (B)** display the lateral enamel areas. These regions were used for DSR calculations.

**Figure 2.** Digital image of an incisor from the Medieval population. The superimposed square shows a ×40 magnified superimposition, of a mid region of enamel, between the cuspal and lateral areas. White arrows indicate individual cross striations, with arrow clusters highlighting how adjacent cross striations were identified for DSR calculations based on clarity and dispersal within each region. Data was not collected from the exact cross-striations highlighted due to location being between the cuspal and lateral areas; however they are an ideal representation of the clarity required for cross striations to be counted.