Chronology of Linear Enamel Hypoplasia Formation in the Krapina Neanderthals

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ABSTRACT

During childhood, systemic physiological stresses such as illness, disease, and malnutrition can disrupt the growth of dental enamel. These disruptions are often recorded in the form of linear enamel hypoplasia (LEH). Many researchers have analyzed the frequency and timing of LEH formation in Neanderthal populations as they relate to ideas about Neanderthal living conditions, nutrition, and foraging efficiency. Previous age estimates for Neanderthal LEH were largely based upon modern human dental growth standards. However, recent studies provide a more complete picture of Neanderthal tooth formation. We use data from these studies to create enamel growth charts for four Neanderthal anterior tooth types (upper central and lateral incisors, upper and lower canines) analogous to those created for modern humans by Reid and Dean (2000). The Neanderthal charts differ from those of modern humans especially in initiation ages and in the duration of enamel formation within equivalent divisions of crown height. Based on these new charts, we estimate ages at formation for a series of Krapina Neanderthal defects. We also compare estimated ages at defect formation in the Krapina sample with estimated ages of defect formation in a sample of modern humans from Point Hope, Alaska. The median ages at defect formation across different anterior tooth types range from 2.3–2.5 (based on a seven-day perikymata periodicity) and 2.6–2.8 years (based on an eight-day perikymata periodicity), suggesting that Neanderthals experienced physiological stress earlier in life than indicated by previous estimates that were derived from modern human standards. By contrast, median ages at defect formation in the Point Hope sample are later than those of the Krapina Neanderthals, which may result from differences in crown growth geometry between Neanderthals and modern humans, differences between the two populations in the ages at which they experienced episodes of stress, or both.

Enamel hypoplasias are developmental defects that reflect periods of disrupted enamel growth most commonly caused by periods of malnutrition, undernutrition, or illness (Goodman and Rose 1990; Hillson 2014). Because these defects are markers of such systemic physiological stresses, they have figured promineny in the Neanderthal literature (Brennan 1991; Guatelli-Steinberg et al. 2004; Hutchinson et al. 1997; Molnar and Molnar 1985; Ogilvie et al. 1989; Skinner 1996). Enamel hypoplasias in Neanderthals are of particular interest because they provide evidence that can yield insight into whether Neanderthals lived under conditions of nutritional stress (Jelinek 1994) and/or were inefficient foragers (Binford 1989; Soffer, 1994; Trinkaus 1986, 1989; but see Sorensen and Leonard 2001).

With one exception (Brennan 1991), studies of enamel hypoplasias in Neanderthals focus on the Krapina remains

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(Hutchinson et al. 1997; Molnar and Molnar 1985) or include a large proportion of them (Guatelli-Steinberg et al. 2004; Ogilvie et al. 1989; Skinner 1996) because these fossils constitute the largest number of Neanderthal individuals from a single site (Radovčić et al. 1988). By incorporating or focusing on the Krapina dental remains, these enamel hypoplasia studies provide a glimpse into population-level stress in Neanderthals, at least in one especially well-studied setting in Central Europe. While these studies generally find high frequencies of enamel hypoplasia in the Krapina Neanderthals (using various measures and analyzing different types of enamel hypoplasia), these frequencies do not appear to differ from the high frequencies of enamel hypoplasias observed among some modern foraging groups (Guatelli-Steinberg et al. 2004; Hutchinson et al. 1997). Thus, while the enamel hypoplasia evidence is consistent with the hypothesis that the Krapina Neanderthals experienced nutritional stress, it does not lend support to the contention that they were more nutritionally stressed than were (or are) some foraging populations of anatomically modern humans.

Linear enamel hypoplasia (LEH) is the most common form of the different types of enamel hypoplasia (Hillson and Bond 1997). LEHs appear as horizontal lines, grooves, furrows, or linear arrays of pits on the enamel surface (FDI DDE Index 1982, 1992; Goodman and Rose 1990; Hillson and Bond 1997). Unlike other enamel hypoplasias, LEHs are informative about the duration or chronology of the stress episodes they represent (Hillson and Bond 1997). They can yield this information because, unlike other forms of enamel hypoplasia, LEHs are directly associated with enamel growth increments that manifest on the enamel surface as perikymata. Within the teeth of an individual, these layers take a constant number of days to form, although across modern human individuals, perikymata represent a range of six to 12 days of growth (Reid and Dean 2006). A study of 11 Neanderthals revealed a range of six to nine days across individuals (Smith et al. 2010). With the exception of linear arrays of pits, linear enamel hypoplasias are composed of one to several perikymata (Hillson and Bond 1997). Consequently, the time span represented by LEH defects, as well as the ages at which they were formed, can be determined. Unfortunately, the number of days represented by perikymata (their periodicity) and the initiation at which crown formation began are not apparent from the tooth surface. Thus, barring physical or virtual sectioning (Tafforeau and Smith 2008), the duration and timing of the stress episodes that LEH defects represent are usually estimated from previously published data.

These estimates, however, provide greater detail about physiological stress experience than do LEH frequency data alone. For example, Guatelli-Steinberg et al. (2004) found LEH frequencies to be similar in their Neanderthal and Inupiaq samples. However, they also found that the average number of perikymata in seven Inupiaq defects (13.4 perikymata) was statistically significantly greater than that found for 15 Krapina defects (7.3 perikymata). Although these sample sizes are small such that inferences must be drawn with caution, this finding suggests that Krapina Neanderthals did not experience stress episodes of longer duration than did the Inupiaq, especially if Neanderthals had slightly lower periodicities than modern humans (Smith et al. 2010).

The comparison of stress episode duration between the Krapina Neanderthals and the Point Hope Inupiaq is meaningful because both groups were foragers, with some similarities in the environments they inhabited. The Krapina Neanderthals appear to have inhabited a deciduous woodland environment (Fiorenza et al. 2011) at a time of "rapidly changing climates and oscillating landscapes" (Hutchinson et al. 1997: 912), while the Point Hope Inupiaq occupied a marginal arctic habitat. These are clearly not identical habitats, but each presents environmental challenges to a foraging way of life. If, as has been claimed (Binford 1989; Soffer 1994; Trinkaus 1986, 1989; but see Sorensen and Leonard 2001), Neanderthals were inefficient foragers relative to modern humans, then they might have been expected to have recorded in their enamel evidence of more prolonged stress episodes than did the Inupiaq. The perikymata evidence, however, does not support this view.

Here, we extend the comparison between LEH defects in the Krapina Neanderthals and the Point Hope Inupiaq to examine the chronology of stress episode occurrence. We also investigate whether there are differences between the two groups in the ages at which stress episodes, as represented by LEHs, occurred. To accomplish this comparison, we make use of recent studies on Neanderthal dental development (Guatelli-Steinberg et al. 2005, 2007; Smith et al. 2007b, 2010) to provide the most accurate estimates of LEH defect formation in Neanderthals currently possible. In so doing, we create charts for aging LEH defects in Neanderthals, analogous to those created for modern humans by Reid and Dean (2000) for four Neanderthal anterior tooth types.

MATERIALS AND METHODS

ESTABLISHING GROWTH CHARTS FOR NEANDERTHAL AND INUIT ANTERIOR TOOTH CROWNS

Reid and Dean (2000) created a series of enamel growth charts based on enamel histological sections made from 115 unworn anterior teeth (routinely extracted from dental patients living in the United Kingdom). Data on the ages at which mineralization began for each tooth type were taken from an earlier publication (Reid et al. 1998). These ages were added to the average time taken to form cuspal enamel for each tooth type, giving the age at which cuspal enamel formation was completed. Next, the authors calculated the subsequent lateral enamel formation time, which includes the entire crown height. To calculate lateral enamel formation time, the authors counted the internal striae of Retzius, which crop out on the enamel surface as perikymata, and form with a regular periodicity of six to 12 days in different individuals (Reid and Dean 2006). To determine the periodicity of striae, daily increments known as cross

striations were counted between striae. While periodicities vary across individuals, they are constant for all of the teeth of a single individual (FitzGerald 1998). Thus, by counting all of the striae of Retzius present in lateral enamel and multiplying by their periodicity, lateral enamel formation time was determined. To facilitate the aging of LEH defects, Reid and Dean (2000) divided the crown height into deciles, and used the mean number of striae of Retzius to calculate the mean age at which each decile of crown height was completed. These charts provide a model for establishing enamel growth charts for Neanderthal and Point Hope Inupiaq anterior tooth crowns in the present study.

We used initiation and cuspal enamel formation time estimates from Reid and Dean (2000) to create charts for aging Point Hope defects. However, for the lateral enamel, we used previously published perikymata counts per decile from the Point Hope teeth (Guatelli-Steinberg et al. 2007). Because we did not have enamel sections of these teeth, we used periodicities of eight or nine days, the two most common values for periodicities in a variety of modern human groups (Smith et al. 2007a). Thus, these lateral enamel formation times are estimates based on central tendencies in the data. To create charts for aging Neanderthal defects, initiation and cuspal enamel formation times were taken from data in Smith et al. (2007b, 2010). Methods for determining initiation ages and cuspal enamel formation times follow established conventions and are detailed in these papers. For the lateral enamel, we used previously published perikymata counts per decile from Neanderthal teeth (Guatelli-Steinberg et al. 2007). Again, without enamel sections of these particular teeth, we used the two most common values of seven and eight days for Neanderthals (Smith et al. 2010). Because periodicities can range from six to nine days in Neanderthals (Smith et al. 2010) and six to 12 days in modern humans (Reid and Dean 2006), the lateral enamel formation times given in this paper are estimates.

LEH SAMPLE

Specimens included in this study were limited to permanent anterior teeth with one or more LEH defects and with 80% or more of their completed crown heights estimated to have been present. Previous enamel hypoplasia studies have shown that permanent anterior teeth are more likely than deciduous teeth or permanent posterior teeth to display LEH (see Goodman and Rose 1990, for a review). This phenomenon may be related to several factors: deciduous teeth form *in utero* where they may be buffered against developmental perturbations (Goodman and Rose 1990); deciduous teeth form quickly and exhibit a small number of perikymata on their surfaces (Hillson 1996); posterior permanent teeth contain a relatively greater proportion of cuspal enamel (where perikymata are not visible on the enamel surface and thus LEH cannot appear) than do anterior teeth (Hillson 1996; Hillson and Bond 1997); and, finally, posterior permanent teeth are less likely to display clearly demarcated defects because of their crown growth geometry (Hillson and Bond 1997).

For canines, completed crown height estimates were made by visually extending the converging sides of the worn crown. For incisors, crown height estimates were made by comparing the morphology of unworn crowns to worn crowns. Finally, two of the Krapina Neanderthal teeth included in this study (Krapina 91 and 93) are incomplete crowns on which the majority of the crown appears to have formed. To estimate the completed crown height for these teeth, the lines of curvature on mesial and distal sides of crown near the cervix were visually extended. For Krapina 91 and 93, we estimated that 89% of the crown height had been completed. Some previous studies of LEH prevalence have limited analyses only to those teeth on which perikymata could be at least partially observed (Guatelli-Steinberg 2003, 2004; Guatelli-Steinberg et al. 2004). Such studies have done so because abrasion great enough to remove perikymata from the enamel surface might also remove minor LEH defects, affecting estimates of LEH prevalence. However, in this study the aim is to age defects, not assess prevalence. Thus, here we included all anterior permanent teeth which were estimated to be 80% or more complete, regardless of whether perikymata were observable on them.

LEH defects were identified under conditions of diffuse lighting with a second light source oriented obliquely to the specimen (Goodman and Rose 1990; Lukacs 1989). A 10x hand lens aided in identifying defects. The first author examined the original Point Hope teeth and coated replicas (see below) of the Krapina teeth. The lower limit of defects identified in this study were lines or grooves that appeared to be larger than adjacent perikymata grooves under 10x magnification. The upper limit was prominent lines or grooves of varying depth and width that were clearly visible without magnification.

Defects were measured using Mitutoyo digital calipers from the CEJ to the middle of each defect along the midline of the tooth. To assess measurement error, 25 defects were measured three times consecutively. The average difference between the first and third measurement is 0.18mm (ranging from 0.02mm to 0.47mm), representing an average measurement error of 4%. Subjectivity in where to place the tips of the calipers, particularly in judging the "middle" of a wide defect, seems likely to be the primary source of measurement error. To assign an estimated age at defect formation using the enamel growth charts, distances from the CEJ were divided by actual crown heights in the case of unerupted unworn crowns or by estimated completed crown heights in the case of worn (or the two incomplete) crowns. The result of this division (i.e., the quotient) multiplied by 10 gives the decile in which the defect lies. That decile was located on the enamel growth chart and an age at formation was assigned. Most often defects do not fall exactly at the borders of a decile, such that interpolations between the ages at which a decile is completed must be made. To do so, Martin et al. (2008) used a nonlinear interpolation (to account for the non-linear pattern of tooth growth) as well as a linear interpolation, but these interpolations produced similar estimated ages at defect formation. Thus, here we follow Martin et al. (2008) in using a linear interpolation.

Hillson (1996, 2014) points out that if a systemic, rath-

TABLE 1. DEFECT SAMPLE SIZES FOR EACH TOOTH TYPE BY POPULATION.

Group	Sample	UI1	UC	LC
Krapina	Matched only[1]	3	0	4
	Expanded sample[2]	5	11	23
Point Hope	Matched only[1]	12	5	13
	Expanded sample[2]	19	16	15

[1]These are defects on one member of an antimeric pair for which it was possible to find a match on the other member.
[2]The expanded sample includes defects on teeth for which no antimere was present.

er than localized, stressor has caused a hypoplastic defect on a tooth, it should be possible to identify defects on all teeth that were forming at the time of the stress episode. He contends that defects that cannot be matched on all the simultaneously forming teeth of an individual should not be counted in assessments of LEH prevalence. In practice, defining precise criteria for determining which defects are chronological matches across tooth types can be difficult for several reasons: initiation ages may differ from those assumed by enamel growth charts, teeth may deviate from the cuspal enamel formation times assumed by enamel growth charts, and there is inherent imprecision involved in estimating exactly how much of the crown height is missing as a result of wear. In addition, differences in crown growth geometry even among anterior teeth can make it difficult to match defects across different tooth types (DGS, TMS personal observations). Thus, in the present study, we matched defects among antimeric pairs only, and therefore present the data by tooth type rather than by individual.

Defects on antimeric pairs were considered to be matches based on their distances from the CEJ. As the greatest measurement error for defect distances from the CEJ was 0.47mm, we considered defects on antimeres to be matched if their distances from the CEJ were not more than 0.5mm different from each other. This is a conservative criterion, because it assumes that tooth growth is identical for each antimere (i.e., each has exactly the same initiation age, cuspal enamel formation time, and lateral enamel formation time). Using this criterion, we determined that out of 63 defects on antimeric pairs in our original sample, 50 defects (79.4%) could be matched. We analyzed the data in two ways. First, we determined which defects could be matched on the two members of an antimeric pair. Then we calculated estimated ages at defect formation for the defects on the most complete antimere of the pair (if antimeres were equally complete, we chose the left antimere). These ages were used in our analyses. This set of analyses, however, is limited to very small sample sizes by tooth type. Second, given that with our conservative criterion the majority of defects could be matched, we expanded the sample to include defects on single teeth, for which no antimere was present.

Table 1 gives the sample sizes used in the analyses by population group and tooth type, for both the sample limited to defects which could be matched and for the expanded sample (which also includes unmatched defects from single teeth for which the antimere was not present). Table 2 lists the Krapina Neanderthal teeth used in this study. The Inupiaq sample to which these Neanderthal samples are compared is housed at the American Museum of Natural History (AMNH), and spans several culture periods (see Guatelli-Steinberg et al. 2004 for a more complete description). The Krapina samples for the 2004 study (Guatelli-Steinberg et al. 2004) and this study are not identical owing to the different selection criteria used in each study. In addition, for three teeth included in both studies there are differences in the number of defects identified. Specifically, in the 2004 study, only one minor line was noted on specimen 120. In the present study an additional, shallow cervical defect was noted for this tooth. In addition, for specimen 121, no defects were noted in the 2004 study, but two minor lines and one shallow cervical defect were identified for this tooth in the present study. Finally, for specimen 36, three defects were noted in this study as opposed to the two noted in the 2004 study.

ESTIMATING AGES AT DEFECT FORMATION

We first report basic statistics regarding the age at which defects formed in the Krapina teeth, using seven-day and eight-day estimated periodicities. Next, we compare the Krapina and Point Hope samples in terms of where defects are located on their crowns. This comparison is informative about relative timing—it reveals when, during each group's enamel formation periods, defects are forming. Here we ask whether there are differences between the population samples in the distribution of defects across their enamel formation periods. We use Mann-Whitney U tests to compare the distributions, rather than t-tests of means, because

TABLE 2. KRAPINA NEANDERTHAL SPECIMENS USED IN THIS STUDY.

Krapina Dental Person	Specimen number	Tooth type	Single tooth or member of antimeric pair	Total LEH	Matched LEH	Unmatched LEH
2	191	ULC	Single tooth	1	0	1
	195	ULI1	Antimere (to 194)	2	1	1
3	119	LLC	Single tooth	4	0	4
4	Mandible D	LLC	Single tooth	2	0	2
	141	URC	Single tooth	1	0	1
6	Mandible H	LRC	Antimere	2	2	0
8	120	LLC	Single tooth	2	0	2
	103	ULC	Single tooth	1	0	1
10	Mandible E	LLC	Single tooth	3	0	3
13	Mandible J	LRC	Antimere	2	2	0
18	36	URC	Single tooth	3	0	3
21	91	URI1	Antimere (to 93)	2	2	0
29	123	ULI1	Single tooth	2	0	2
30	76	URC	Single tooth	1	0	1
31	121	LLC	Single tooth	3	0	3
Unassigned	75	LRC	Single tooth	5	0	5
Unassigned	144	ULC	Single tooth	3	0	3
Unassigned	146	ULC	Single tooth	1	0	1

TABLE 3. ESTIMATED MEAN AGE IN DAYS (1 SD) FOR ENAMEL FORMATION AT EACH DECILE OF CROWN HEIGHT FOR NEANDERTHAL ANTERIOR TEETH
(sample size indicates the specimens used to count the number of perikymata in each decile).

Age at	Upper central incisor (n=9)		Upper lateral Incisor (n=9)		Upper canine (n=14)		Lower canine (n=10)	
Initial mineralization[1]	44		205		102		93	
Cuspal enamel completion[1]	239		426		297		278	
Percent of crown height completed[2]	7-day periodicity	8-day periodicity	7-day periodicity	8-day periodicity	7-day periodicity	8-day periodicity	7-day periodicity	8-day periodicity
10%	316 (14)	327 (16)	496 (7)	506 (8)	360 (7)	369 (8)	355 (7)	366 (8)
20%	407 (14)	431 (16)	566 (7)	586 (8)	430 (7)	449 (8)	439 (14)	462 (16)
30%	519 (14)	559 (16)	643 (7)	674 (8)	507 (14)	537 (16)	530 (7)	566 (8)
40%	631 (14)	687 (16)	727 (7)	770 (8)	591 (14)	633 (16)	628 (14)	678 (16)
50%	743 (14)	815 (16)	825 (7)	882 (8)	689 (21)	745 (24)	733 (14)	798 (16)
60%	883 (21)	975 (24)	930 (14)	1002 (16)	794 (21)	865 (24)	852 (21)	934 (24)
70%	1016 (14)	1127 (16)	1049 (14)	1138 (16)	906 (21)	993 (24)	985 (21)	1086 (24)
80%	1142 (7)	1271 (8)	1161 (7)	1266 (8)	1025 (14)	1129 (16)	1125 (21)	1246 (24)
90%	1268 (14)	1415 (16)	1287 (14)	1410 (16)	1144 (14)	1265 (16)	1272 (35)	1414 (40)
100%	1366 (14)	1527 (16)	1427 (7)	1570 (8)	1263 (14)	1401 (16)	1405 (35)	1566 (40)

[1]Based on data from Smith et al. (2007b, 2010) on age at initial mineralization and cuspal enamel formation time. Cuspal enamel completion is the sum of the age at initial mineralization and cuspal enamel formation time.
[2]Based on data from Guatelli-Steinberg et al. (2005, 2007) on perikymata numbers.

the distributions are not normally distributed in most cases.

Next, using the enamel growth charts, we compare estimated ages at defect formation between the two population samples, under the assumption of equivalent average periodicities (eight days) or different average periodicities of seven days for the Krapina sample and nine days for the Point Hope sample. Again, we use Mann-Whitney U tests to compare the distributions. In this analysis, we only compare defects that would have formed during periods of enamel formation overlap between the samples. Otherwise, ages at defect formation would partially reflect differences between the two samples in the age span during which their enamel is forming, rather than simply differences between the samples in the ages at which defects are forming. The Point Hope sample dictates the minimum ages of the periods of overlap, as modern human teeth initiate later. Because some teeth that were 80% complete were included in the sample, we set the minimum ages for the period of overlap for each tooth type by the average ages at which the Point Hope sample's second decile of enamel was completed. Deciles are numbered from incisal to cervical, reflecting the direction of enamel growth. Neanderthal ages at enamel completion dictate the maximum ages for the periods of overlap, as Neanderthal teeth are completed at earlier ages than our estimates for the completion of the Pt. Hope teeth. In addition, because we included two Neanderthal central incisors that had not completed crown formation, maximum ages were altered accordingly for this tooth type.

RESULTS

ENAMEL GROWTH CHARTS

Estimates of enamel formation time (in days) for anterior tooth types are reported for Neanderthals and the Point Hope sample in Tables 3 and 4, respectively. These estimates are presented for the four anterior tooth types in Neanderthals (upper central incisors, upper lateral incisors, upper canine, and lower canine) for which we have data on initiation age and cuspal enamel formation time. Data

TABLE 4. ESTIMATED MEAN AGE IN DAYS (1 SD) FOR ENAMEL FORMATION AT EACH DECILE OF CROWN HEIGHT FOR ANTERIOR TEETH IN THE POINT HOPE SAMPLE
(sample size indicates the specimens used to count the number of perikymata in each decile).

Age at	Upper central incisor (n=10)		Upper lateral Incisor (n=10)		Upper canine (n=9)		Lower central incisor (n=12)		Lower lateral incisor (n=14)		Lower canine (n=10)	
Initial mineralization[1]	128		383		274		90		146		200	
Cuspal enamel completion[1]	417		657		629		346		358		548	
Percent of crown height completed	8-day periodicity	9-day periodicity	8-day periodicity	9-day periodicity	8-day periodicity	9-day periodicity	8-day periodicity	9-day periodicity	8-day periodicity	9-day periodicity	8-day periodicity	9-day periodicity
10%	489 (8)	498 (9)	721 (8)	729 (9)	693 (8)	701 (9)	402 (8)	409 (9)	422 (8)	430 (9)	628 (8)	638 (9)
20%	569 (8)	588 (9)	793 (8)	810 (9)	765 (8)	782 (9)	466 (8)	481 (9)	486 (8)	502 (9)	716 (8)	737 (9)
30%	657 (16)	687 (18)	865 (8)	891 (9)	845 (8)	872 (9)	530 (16)	553 (18)	558 (8)	583 (9)	820 (16)	854 (18)
40%	761 (16)	804 (18)	945 (16)	981 (18)	941 (8)	980 (9)	602 (16)	634 (18)	638 (16)	673 (18)	940 (24)	989 (27)
50%	881 (24)	939 (27)	1041 (24)	1089 (27)	1045 (16)	1097 (18)	690 (16)	733 (18)	734 (16)	781 (18)	1076 (24)	1142 (27)
60%	1009 (24)	1083 (27)	1145 (16)	1206 (18)	1173 (32)	1241 (36)	794 (16)	850 (18)	846 (16)	907 (18)	1244 (24)	1331 (27)
70%	1169 (32)	1263 (36)	1289 (32)	1368 (36)	1333 (40)	1421 (45)	914 (24)	985 (27)	982 (16)	1060 (18)	1436 (16)	1547 (18)
80%	1361 (32)	1479 (36)	1457 (24)	1557 (27)	1517 (32)	1628 (36)	1050 (16)	1138 (18)	1134 (16)	1231 (18)	1660 (16)	1799 (18)
90%	1569 (24)	1713 (27)	1657 (24)	1782 (27)	1725 (40)	1862 (45)	1210 (32)	1318 (36)	1302 (16)	1420 (18)	1900 (32)	2069 (36)
100%	1785 (32)	1956 (36)	1873 (32)	2025 (36)	1933 (32)	2096 (36)	1386 (24)	1516 (27)	1478 (24)	1618 (27)	2140 (40)	2339 (45)

[1]Based on data from Reid and Dean (2006) on age at initial mineralization and cuspal enamel formation time in northern Europeans. Cuspal enamel completion is the sum of the age at initial mineralization and cuspal enamel formation time.

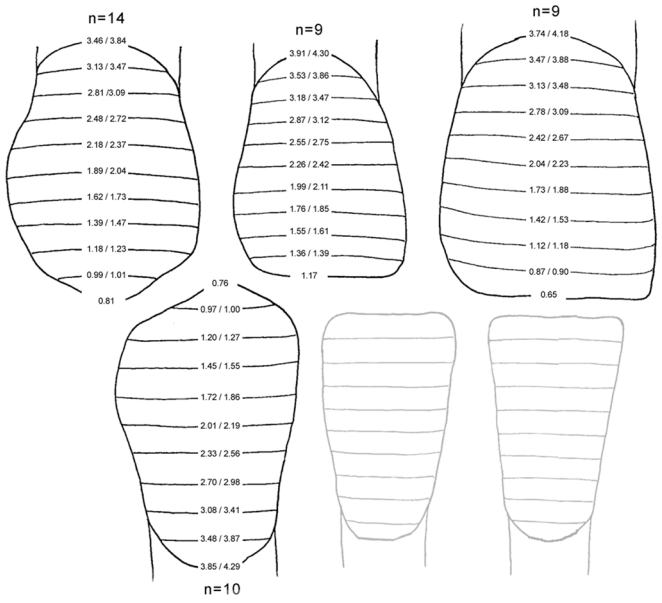

Figure 1. Enamel growth charts for Neandertal anterior teeth in this study. Estimated ages (in years) at the completion of enamel formation for each decile of crown height for both 7-day/8-day periodicities. The first (unpaired) value at the cusp of each tooth is the estimated age at the completion of cuspal enamel formation.

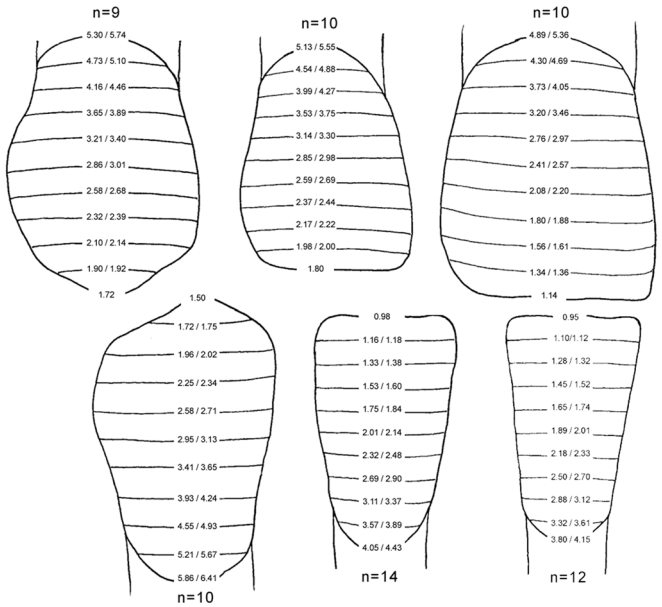

Figure 2. Enamel growth charts for Point Hope anterior teeth. Estimated ages (in years) at the completion of enamel formation for each decile of crown height for both 8-day/9-day periodicities. The first (unpaired) value at the cusp of each tooth is the estimated age at the completion of cuspal enamel formation.

are presented for all anterior tooth types for the Point Hope sample. Components of total enamel formation time are reported cumulatively. These include age at initiation of mineralization, age at cuspal enamel completion, and mean ages of completion for each decile of crown height beginning at the cusp of the tooth and ending at the CEJ. Decile growth estimates are based on the most common periodicities for each group, seven and eight days for Neanderthals (Smith et al. 2010) and eight and nine days for the Point Hope sample (the most common periodicities in modern humans, Smith et al. 2007a). The estimates of enamel formation time from this table have been converted into years in the enamel growth charts given in Figures 1 and 2.

ESTIMATED AGES AT DEFECT FORMATION IN KRAPINA ANTERIOR TEETH

Table 5 gives the age estimates for Krapina defects both for the matched LEH defects and for the expanded sample (which includes matched LEH defects as well as unmatched defects from single teeth). Based on a seven-day periodicity, the earliest age at which a defect could be detected was 1.1 years, while based on an eight-day periodicity, the latest age at which a defect could be detected was 4.1 years. These ages span the majority of estimated lateral enamel formation time, beginning at 0.65 years in the UI1 (the end of cuspal enamel formation based on a seven-day periodicity) and ending at 4.3 years for the LC (lateral

TABLE 5. ESTIMATED AGES AT KRAPINA NEANDERTHAL LEH FORMATION.

Sample	Tooth type	Number of defects	Age in years based on 7-day periodicity		Age in years based on 8-day periodicity	
			Range	Median	Range	Median
Matched	UI1	3	1.9-2.9	2.6	2.1-3.2	2.8
	LC	4	1.9-2.6	2.3	2.1-2.8	2.5
Expanded	UI1	5	1.9-3.1	2.6	2.1-3.5	2.8
	UC	11	1.9-2.9	2.3	2.0-3.2	2.5
	LC	23	1.1-3.7	2.5	1.2-4.1	2.8

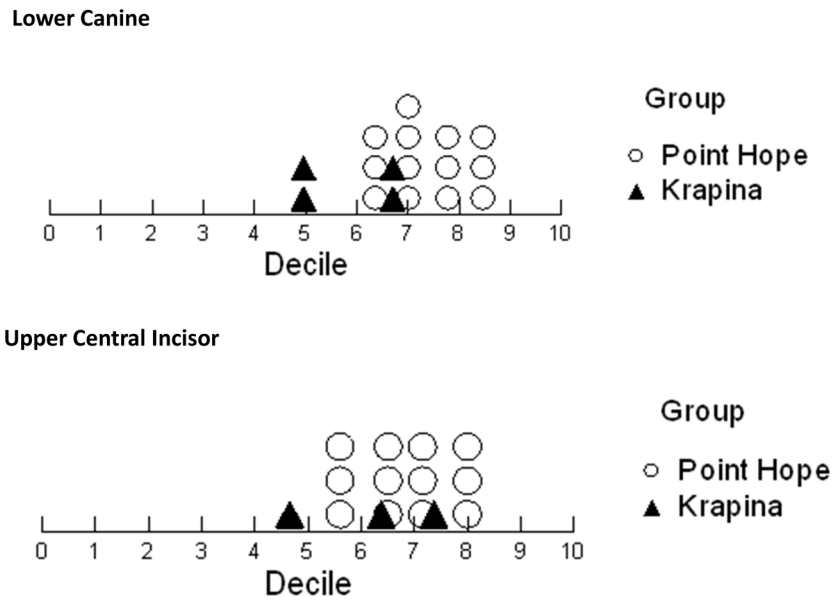

Figure 3. Decile comparison for defects with matches on antimeres.

enamel completed based on an eight-day periodicity). The earlier ages recorded on the lower canines are likely to be a function of the fact that some of these lower canines were unerupted teeth, such that the complete crown height was present. The later ages recorded on the lower canines are likely to reflect the later ages at which this tooth type completes enamel formation as compared to the upper canine or upper central incisor. Despite these differences, the median age at defect formation is fairly consistent across tooth types. Based on a seven-day periodicity, the median age ranges from 2.3 to 2.6 years, while based on an eight-day periodicity, the median age ranges from 2.5 to 2.8 years.

In one instance it was possible to estimate the precise age of defects for the Krapina individual known as Krapina Dental Person (KDP) 2 (Maxilla B, K191, 194, 195, 196), as the periodicity had previously been determined to be 7 days using synchrotron X-ray imaging (Smith et al. 2010). Assuming that the upper canine initiated at 102 days, which is the value calculated from the Scladina individual (Smith et al. 2007b), a pair of anterior tooth defects in KDP 2 matched across three incisors were estimated to have formed at 1.6 and 2.3 years of age, followed by a deep furrow that lasted until ~2.6 years of age.

COMPARISON WITH POINT HOPE SAMPLE

Location of defects within deciles

Although the matched defects sample is small, there appears to be a slight difference in the location of defects in the deciles of the Krapina and Point Hope teeth. As can be seen in Figure 3, the Point Hope defects appear to be shifted to later-forming deciles as compared to the Krapina defects, particularly for the lower canine.

This difference between the Krapina and Inuit samples in the location of their defects is even more pronounced in the expanded sample. As seen in Figure 4, for the lower canine, the 23 Krapina defects range from the second through tenth deciles, with a strong peak in the seventh decile. The 15 Point Hope defects on the lower canine are confined to the seventh through ninth deciles. The median decile for the Krapina defects is 6.5 (the midpoint of decile seven), while that for the Point Hope defects is 7.4 (close to the midpoint of decile eight).The difference in the distributions the two samples is statistically significant (Mann-Whitney U=262.0, p=0.008, df=1). Figure 4 also shows the distribution

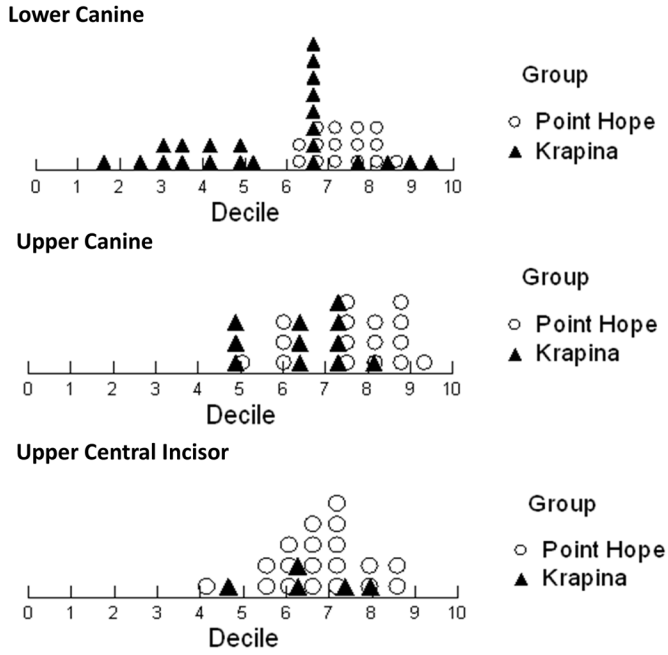

Figure 4. Decile comparison for expanded sample (defects with matches on antimeres and defects on single teeth).

TABLE 6. PERIODS OF ENAMEL FORMATION OVERLAP.

	8-day periodicity assumed for both samples		7-day periodicity assumed for Krapina; 9-day for Point Hope	
Tooth type	**Period of overlap start days (years)**	**Period of overlap end days (years)**	**Period of overlap start days (years)**	**Period of overlap end days (years)**
UI1	569 days (1.6 yrs)	1401 days (3.8 yrs)	588 days (1.6 yrs)	1255 days (3.4 yrs)
UC	765 days (2.1 yrs)	1401 days (3.8 yrs)	782 days (2.1 yrs)	1263 days (3.5 yrs)
LC	716 days (2.0 yrs)	1566 days (4.3 yrs)	737 days (2.0 yrs)	1405 days (3.8 yrs)

of defects on the upper canine and the upper central incisor. The difference in defect distribution is less pronounced for these teeth than for the lower canine; nevertheless, the Krapina defects tend to be shifted to earlier-forming deciles than the Point Hope defects. This shift is also significant for the upper canine (Mann-Whitney U=132.0, p=0.030, df=1), while it is not statistically significant for the upper incisors (Mann-Whitney U=56.0, p=0.412, df=1). Although not shown because there are no Krapina teeth to compare them with, defects on the UI2, LI1, and LI2 of the Point Hope teeth were all limited to deciles six through ten, consistent with the distribution of defects on other tooth types.

Comparison of estimated age at defect formation within periods of enamel formation overlap

Results are presented for the expanded sample only, since the sample sizes of matched defects are quite limited for this comparison. We used average periodicities of seven and eight for Neanderthals, and of eight and nine for the Point Hope sample to construct the enamel growth charts (see Figures 1–2). During their periods of overlapping enamel formation (see Methods), samples are compared in terms of ages at which defects formed assuming the minimum and maximum difference in these average periodicities. Hence, to minimize differences, Krapina and Point Hope defects are compared based upon periodicities of eight. Then, to maximize differences between the two samples, ages at defect formation were compared based upon a seven-day periodicity for the Krapina sample and a nine-day periodicity for the Point Hope sample. Table 6 gives the period of enamel formation overlap over which estimated defect ages were compared. Figure 5 shows the estimated age distribution of defects assuming an eight-day periodicity, while Figure 6 shows the estimated age distribution of defects assuming a seven-day periodicity for Krapina and a nine-day periodicity for Point Hope.

Under the assumption of an eight-day periodicity for both samples, the period of enamel formation overlap for the lower canine ranges from 2.0 to 4.3 years of age. Krapina defects range from 2.0 to 4.1 years, while those for Point Hope range from 3.5 to 4.3 years under this assumption. The estimated median age of 16 Krapina defects is 2.9 years, while that for the 10 Point Hope teeth is 3.9 years. The difference in these distributions is statistically significant (Mann-Whitney U=148, p=0.000, df=1). For the upper canine, the period of enamel formation overlap is from 2.1 years to 3.8 years of age. Estimated defect ages for the upper canine range from 2.5 to 3.2 years for the Krapina defects and 2.9 to 3.3 years for the Point Hope defects. The estimated median age is 2.8 years for the eight Krapina defects and 3.2 years for the four Point Hope defects. These are also statistically significantly different age distributions (Mann-Whitney U=28.0, p=0.042, df=1). The difference in central incisor distributions (median estimated ages of 2.8 years for five Krapina defects, and 3.1 years for 18 Point Hope defects) is not statistically significant (Mann-Whitney U=56.0, p=0.412, df=1).

Figure 6 shows the estimated age distribution of defects during the overlap period assuming a seven-day average periodicity for the Krapina sample and a nine-day average periodicity for the Point Hope sample. With a seven-day periodicity for the Krapina sample, the period of overlap is truncated such that most of the Point Hope defects now lie outside of the overlap period. Small sample sizes for this comparison precluded statistical testing. While sample sizes per tooth type are small for the Point Hope sample, the overall impression of these graphs is that there is now a further separation of estimated defect ages for the Point Hope and Krapina samples, as would be expected under the assumption of a seven-day periodicity for Krapina and a nine-day periodicity for Point Hope.

DISCUSSION

In the current study, we undertook a comparison of estimated ages at defect formation in the anterior teeth of Krapina Neanderthals and Point Hope Inupiaq. To do so, we constructed enamel growth charts for estimating ages at defect formation in both groups based on currently avail-

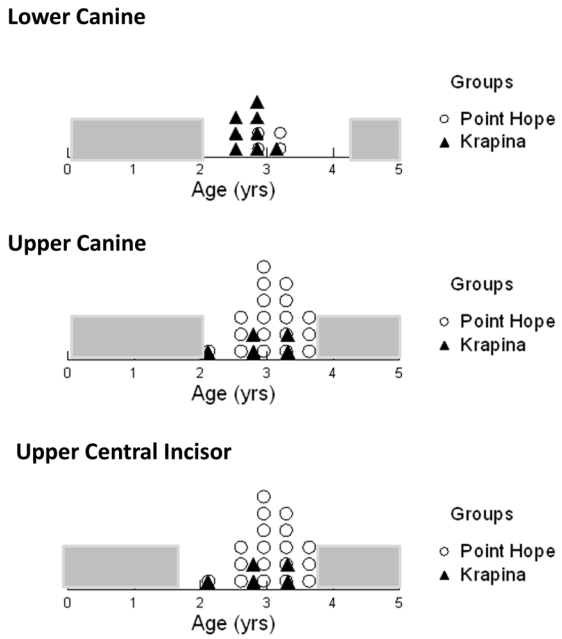

Figure 5. Age distribution of defects in the expanded sample (defects with matches on antimeres and defects on single teeth), assuming an 8-day periodicity for both groups. Areas in grey represent either periods of time when lateral enamel is not forming or when lateral enamel is forming in only one of the groups (i.e., in only Point Hope or Neandertal teeth with 80% or more of their crown heights complete/intact).

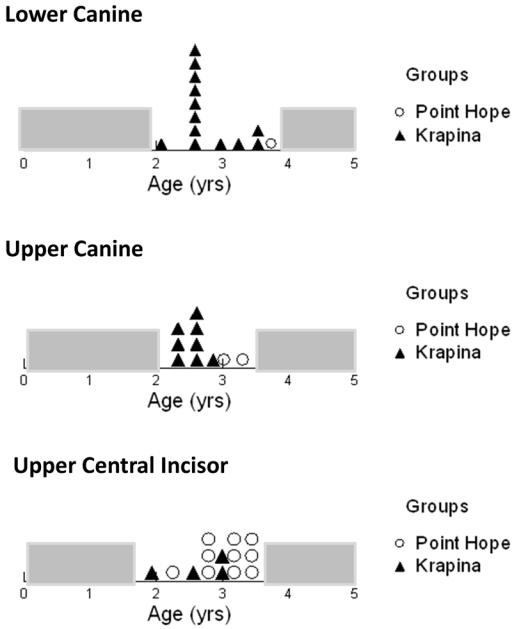

Figure 6. Age distribution of defects in the expanded sample (defects with matches on antimeres and defects on single teeth), assuming a 7-day periodicity for Neandertals and a 9-day periodicity for the Point Hope sample. Areas in grey represent either periods of time when lateral enamel is not forming or when lateral enamel is forming in only one of the groups (i.e., in only Point Hope or Neandertal teeth with 80% or more of their crown heights complete/intact).

able information. The Neanderthal growth charts are based on data on the initiation of mineralization, cuspal enamel formation time, and periodicity of Neanderthal teeth (Smith et al. 2007b, 2010). They are also based on perikymata counts in deciles of the lateral enamel of Neanderthals (Guatelli-Steinberg et al. 2007). It is important to note that these charts reflect central tendencies in the data for all of these variables. The standard deviations in the Neanderthal enamel growth charts given here, do, however reflect known variability in Neanderthal perikymata numbers (Guatelli-Steinberg et al. 2007). For the Point Hope sample, we used data on periodicities, initiation and cuspal enamel formation times from modern Europeans (Reid and Dean 2000, 2006) because we did not have specific data from the Point Hope sample for these variables. Nevertheless, the Point Hope enamel growth charts do include data on perikymata numbers specifically from the Point Hope dental sample, and variability in those numbers is reflected in the enamel growth charts.

Enamel growth in the Neanderthal sample differs from that of the Point Hope sample in several ways. A major difference is in the average age span encompassed by enamel formation. Specifically, Neanderthals in this sample began and completed enamel formation at earlier estimated ages than members of the Point Hope sample. There are several reasons for this difference. Neanderthals had an earlier age at mineralization initiation, shorter cuspal enamel formation time for each tooth type, and lower average long-period line periodicity than observed among modern humans (Smith et al. 2010). There are also disparities between these groups in the duration of enamel formation within equivalent divisions of crown height. These stem largely from two factors. First, lower average striae of Retzius periodicities in Neanderthals result in generally shorter periods of enamel growth per decile. However, even if identical periodicities are assumed for both groups, differences in the average number of perikymata per decile lead to differences in growth. As can be seen in Figure 7, Neanderthals exhibit a more uniform distribution of perikymata across their enamel surfaces while the Point Hope samples have more densely packed perikymata in the cervical halves of their teeth (Guatelli-Steinberg et al. 2007). For the Point Hope sample, this leads to a longer period of growth in the cervical deciles of anterior teeth (deciles six through ten) relative to that observed for Krapina Neanderthals.

Here, we find that estimated median ages at defect formation on the Krapina anterior teeth cluster between 2.3 and 2.8 years of age, depending on tooth type and on whether a seven or eight-day periodicity is used. Previous studies have estimated older median or peak ages at enamel hypoplasia formation in Neanderthal samples across all permanent teeth when using modern human standards to age defects (Brennan 1991; Ogilvie et al. 1989; Skinner 1996). Ogilvie et al. (1989) reported a peak age of four years in their Neanderthal sample (which includes Krapina). Skinner (1996) found a peak age of 3.5 years for a Middle

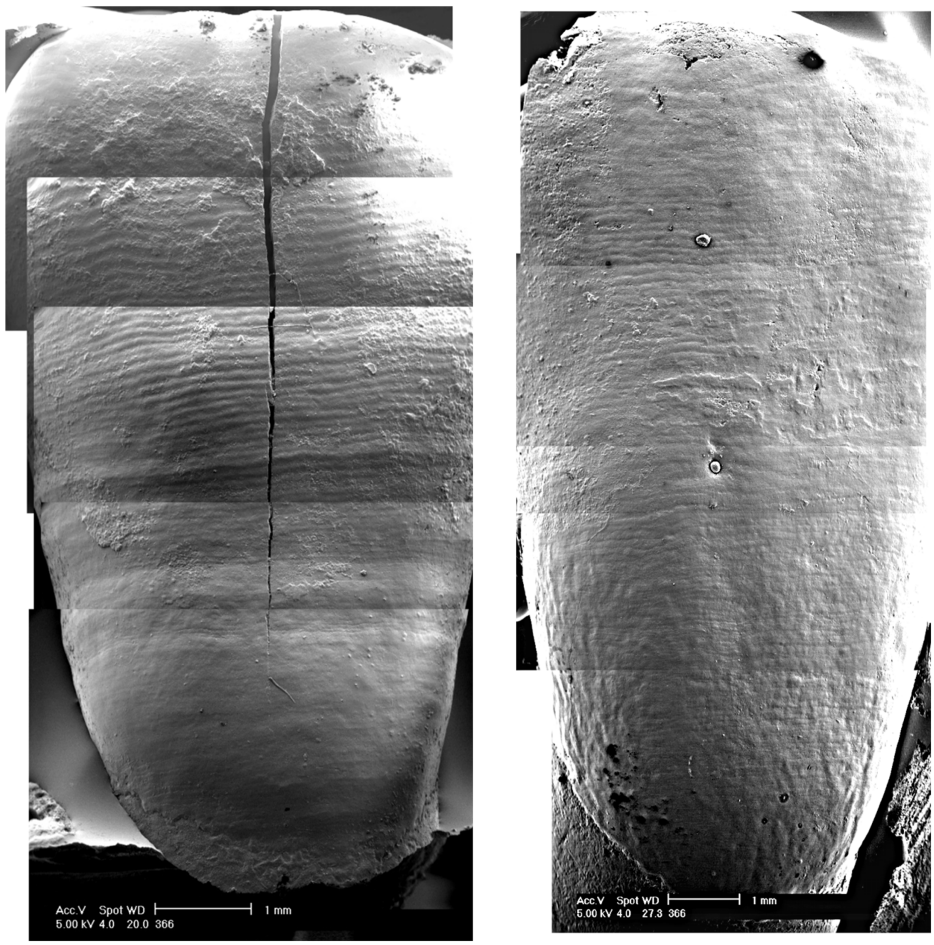

Figure 7. Montages made from SEM images taken at 20x magnification of one Inupiaq lower I2 (replica) at left (Point Hope 411) and one Neandertal lower I2 (replica) at right (Krapina 90). The replicas are scaled to the same size.

Paleolithic sample that included anatomically modern human teeth from Qafzeh and Jebel Ihroud, in addition to those of Krapina and other Neanderthals. Skinner's (1996) Upper Paleolithic samples, by contrast, exhibit a higher proportion of stress episodes during the first two years of life. Brennan (1991) found that the majority of defects in her Mousterian Neanderthal sample (which did not include Krapina) formed after 2.5 years of age, while the majority of defects in her Magdalenian sample occurred prior to this age.

To some extent the differences between this study and previous studies in median or peak estimated ages at defect formation are likely to reflect the fact that later calcifying teeth (premolars and second and third molars) were included in these studies, while the present study is limited to the earlier-forming anterior teeth. However, an additional reason for the difference is that in the present study, estimated defect ages were based on Neanderthal rather than modern human enamel growth standards. The effect of this difference in growth standards is clear. For example, on Krapina specimen 144, an upper left canine, there are three LEH defects noted by the current study and by the study of Ogilvie et al. (1989), with both studies reporting similar measurements from the CEJ on which defect ages were based. The ages for these defects are given as 3, 4, and 4.5 years in Ogilvie et al. (1989) while the corresponding ages in this study are 1.9, 2.3, and 2.7 years for a seven-day periodicity, and 2.0, 2.5, and 2.9 years for an eight-day periodicity. If the measurements of Ogilvie et al. (1989) were translated into ages at LEH formation based on the Neanderthal growth charts presented here, they would all be shifted to earlier ages. The same would, of course, also be true of the measurements made by Skinner (1996) and Brennan (1991), such that there would be less of a difference between the ages at defect formation between their Neanderthal and Upper Paleolithic samples than they reported. As Ogilvie et al. (1989) and Brennan (1991) interpreted differences in LEH timing to reflect (at least in part) differences in weaning ages between Neanderthals and their Upper Paleolithic populations, it is clear that their interpretations require revision.

We found significant differences in estimated ages at defect formation between Krapina and Point Hope samples during overlapping periods of enamel formation. Even if an eight-day periodicity is assumed for both samples, most of the Point Hope defects were estimated to have occurred

at later ages than the Krapina defects. As an example, for the lower canine expanded sample (matched plus single defects), there is a difference of one year between the median estimated age at defect formation during the period of enamel formation overlap (2.9 years for Krapina vs. 3.9 years for Point Hope). This difference partially reflects the difference between the two samples in the distribution of defects on the crown. Point Hope defects occur predominantly in the cervical half of the crown (i.e., later in crown development) while Krapina defects are less constrained to this region.

The causes of the difference between the Krapina and Point Hope samples in the distribution of LEH defects on their crowns, and ages at defect formation, are not clear. While LEH defects reflect growth disruption, the formation of defects is constrained by crown growth geometry (Hillson and Bond 1997). Specifically, the angles that Retzius planes (enamel growth planes) make with the enamel surface appear to affect the depth and definition of defects. Generally, when these angles are acute, perikymata are more widely spaced on the enamel surface, and LEH defects are shallower and less well defined (Guatelli-Steinberg 2008; Hillson and Bond 1997). As shown in Figure 7, perikymata appear more widely spaced in the incisal half of the Point Hope tooth than they are on the incisal half of the Krapina Neanderthal tooth. If this wider spacing reflects more acute Retzius plane angles, then well-defined LEH defects would be less evident in this region of Point Hope teeth than in the Krapina teeth.

While differences between the Point Hope and Krapina teeth in crown growth geometry may explain the difference in LEH age distribution between them, it is also possible that there are differences between the two groups in the ages at which stress events themselves are occurring. These differences could occur for any number of reasons, having to do with the sufficiency of infant nutrition, the availability of weaning foods, and/or exposure and susceptibility to pathogens. As noted, previous studies attributed peak LEH ages in Neanderthals to weaning stress (Brennan 1991; Ogilvie et al. 1989). While we have no information, as yet, on weaning ages in Krapina Neanderthals, weaning ages for the Point Hope Inupiaq may have been late relative to other modern human groups. For 113 non-industrialized societies, Sellen (2001) reported an average age for the termination of breastfeeding of 29 months (2.14 yrs) +/- 10 months. In an 1890 census report on the "Population and Resources of Alaska," Porter writes of the region in which Point Hope is located: "Children are rarely weaned until they become 4 or 5 years old, and it is no uncommon sight to see a woman pull a child of 8 or 9 years under her shirt to nurse it…" (1893: 137). A weaning age of 4 years of age is not far from the estimated median ages at LEH formation in the Point Hope teeth obtained in this study. The possibility that the Krapina Neanderthals and Point Hope populations may have differed from each other in weaning ages is intriguing insofar as what it would imply about interbirth intervals and population growth in these two groups. However, at present an equally plausible, and possibly sufficient, explanation for differences between these groups in the estimated ages at which their LEH defects form can be found in their crown growth geometry.

The emphasis in previous studies on ages at peak LEH occurrence is related to the assumption that peak ages are reflective of the weaning process. Although this assumption might be valid, comparison of ranges and age distributions of defects during periods of enamel formation overlap provides a clearer picture of sample differences in the timing of LEHs, whatever their cause(s).

CONCLUSIONS

In the current study, we present anterior tooth enamel growth charts that can be used to estimate age at LEH formation in Neanderthals more accurately than previously possible. We used these charts to compare estimated defect ages between the Krapina and Point Hope samples during the period of time that both were forming lateral enamel on their anterior teeth. The estimated ages at which defects formed differ between these two groups, either as a result of differences in their crown growth geometry, differences in the ages at which children experienced stress, or both. To differentiate among these explanations, it will be useful to gain independent evidence about ages at weaning in these samples, which might be possible using laser ablation to analyze strontium-calcium ratios (Humphrey et al. 2008) or, as more recently done, with barium-calcium ratios (Austin et al. 2013), provided diagenesis is not an issue. It would also be useful to measure and compare Retzius plane angles in sections of the Point Hope and Neanderthal teeth to determine if these are consistent with an explanation based on crown growth geometry. Finally, future directions should include histological approaches, which when permitted on fossil material, would make it possible to more precisely age hypoplastic defects (Smith et al. 2007b). Moreover, with histology, it will be possible to examine accentuated striae, potentially expanding the range of enamel formation overlap back to birth. An additional advantage of examining accentuated striae is that their expression appears to be less dependent on tooth type and crown growth geometry than is the case for linear enamel hypoplasias.

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