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News and Views

Crown-formation time in Neandertal anterior teeth revisited

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Introduction

Our knowledge on the growth of anterior teeth in extant and extinct humans has recently been broadened. Two studies have compared Neandertal dental growth with that of Upper Paleolithic–Mesolithic humans and with modern contemporary humans. Neandertals clearly show fewer perikymata in their anterior teeth than do Upper Paleolithic–Mesolithic people of Europe, as reported by Ramírez Rozzi and Bermúdez de Castro (2004). However, when modern human populations are compared with a sample of Neandertal teeth used by Guatelli-Steinberg et al. (2005), the number of perikymata in this extinct human group is encompassed within the modern human range of variation.

Using histological sections of anterior teeth, Guatelli-Steinberg et al. (2005, 2007a,b) obtained the total number of perikymata in two modern human populations (Newcastle and South Africa). However, faced with the impossibility of sectioning fossil teeth, they followed a different methodology to determine the total number of perikymata in their sample of Neandertal anterior teeth. Here we present some observations about the methods Guatelli-Steinberg et al. used to analyze their sample of Neandertal teeth and show that their results are inaccurate and thus cannot be used as comparative data in future studies.

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Several points about Guatelli-Steinberg et al.'s samples and methods

Aside from its intrinsic importance, dental developmental criteria provide a good proxy for estimating general growth in individuals. Specifically, dental enamel preserves incremental lines that enable chronological aspects of dental growth to be determined. Cross-striations are incremental lines with a circadian (daily) periodicity. Striae of Retzius are longer-term markers that appear at intervals (or periodicity) ranging between 6 and 11 days in modern humans (FitzGerald, 1998). A tooth crown can be divided into two portions following the striae of Retzius arrangement. In lateral (or imbricational) enamel, Retzius lines are oblique, running from the enamel-dentine junction to the outer surface of the enamel where they crop out, forming perikymata. In cuspal (or appositional) enamel, all Retzius lines are buried under subsequently formed enamel. The first stria to reach the surface of the tooth divides the crown into appositional and imbricational regions.

The most reliable approach to characterize the pattern of dental growth in any given species would be the analysis of enamel histology. However, because it is undesirable to section fossil hominid teeth, the study of dental growth in fossil *Homo* from the middle and late Pleistocene has focused on the analyses of perikymata—the surface manifestations of striae of Retzius.

Here, we discuss Guatelli-Steinberg et al.'s (2005) results in the context of the samples and methods they used and consider the implications of the use of these results in future studies. There are several points that merit consideration:

(1) In contrast to Ramírez Rozzi and Bermúdez de Castro's (2004) study, which included 146 Neandertal teeth from

55 individuals, Guatelli-Steinberg et al.'s (2005) study included only 55 teeth from 30 individuals.

(2) Guatelli-Steinberg et al. (2005) included the anterior teeth from the Tabun II mandible in their Neandertal sample, disregarding the fact that some scholars consider Tabun II to be representative of anatomically modern humans (Rak et al., 2002).

(3) Guatelli-Steinberg et al. (2005) incorrectly stated that the first molar of Tabun II was sectioned in previous histological work by Dean and colleagues (2001), when in fact the molar was from the specimen Tabun I.

(4) Krapina 194 and 195 were included in Guatelli-Steinberg et al.'s (2005) analysis as different individuals when, in fact, they are the left and right maxillary first incisors, respectively, of the specimen KDP 2 (Radovčić et al., 1988).

(5) Guatelli-Steinberg et al. (2005: 14199) indicated that they followed "the same method of Ramírez-Rozzi and Bermudez de Castro." Both works estimated crown height in worn teeth, but some important differences in methodology exist between them (see below).

(6) Ramírez Rozzi and Bermúdez de Castro (2004) obtained the number of perikymata *only* in those deciles where perikymata were clearly observable, whereas Guatelli-Steinberg et al. (2005, 2007a,b) estimated perikymata number even in areas of the tooth where perikymata are not visible in order to obtain an estimate of the total number of perikymata. This difference prevents a direct comparison between the results of these two works.

(7) Ramírez Rozzi and Bermúdez de Castro (2004) calculated mean values and 95% confidence intervals for each decile of the tooth surface, whereas Guatelli-Steinberg et al. (2005) presented only the total number of perikymata for each tooth.

(8) Although mean values for each tooth class are presented in Guatelli-Steinberg et al.'s (2005) Figure 2, the mean and its 95% confident limits are calculated for a sample in which all of the anterior teeth are pooled. The statistics for this pooled sample are meaningless.

(9) Guatelli-Steinberg et al. (2005, 2007a,b) performed an ANOVA in order to compare the total perikymata counts. Since some samples are represented by individuals derived from a wide geographic and temporal range and some subsamples are very small, the homogeneity of variances cannot be assumed and should be demonstrated by statistical tests.

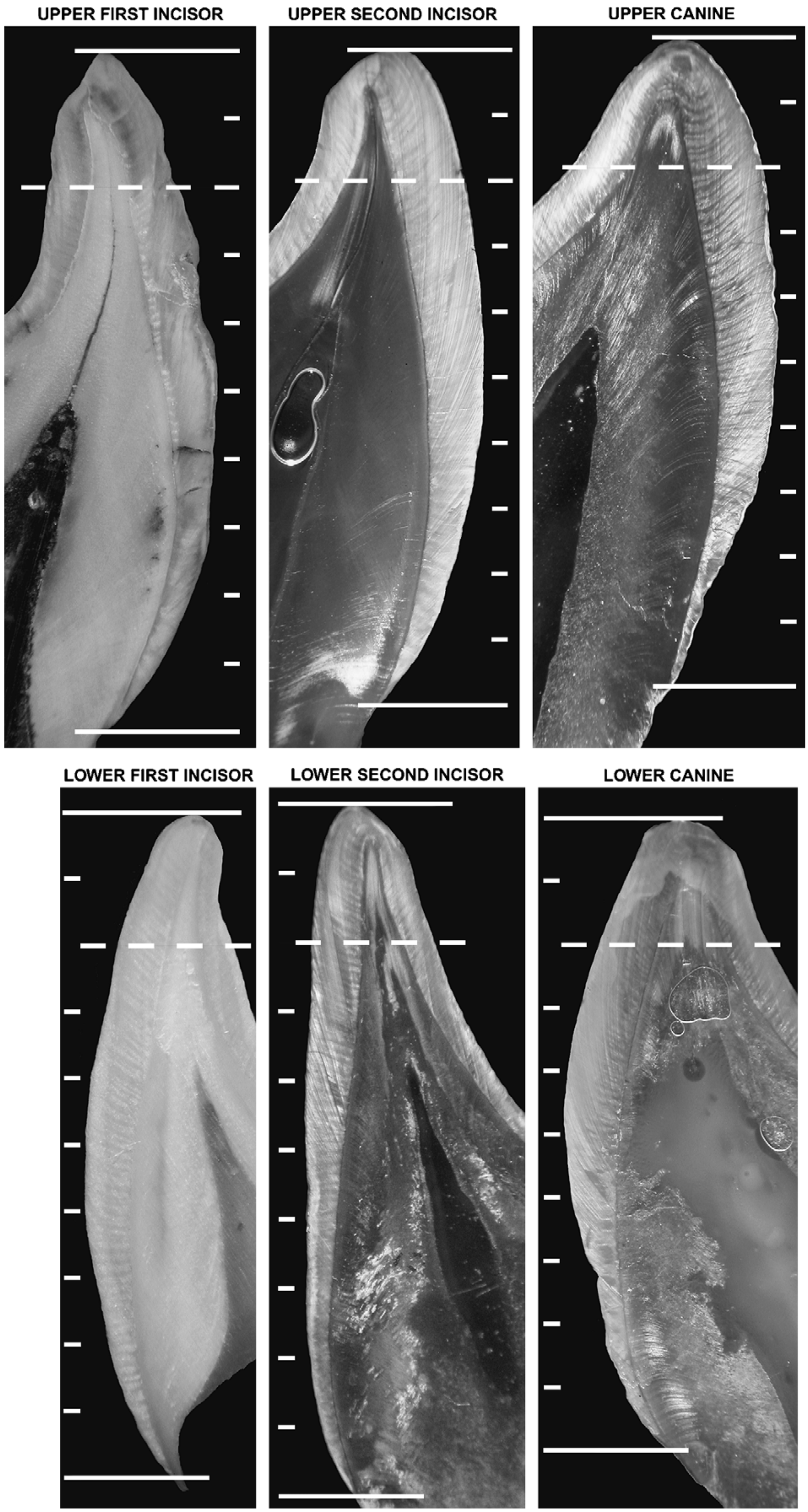
(10) Guatelli-Steinberg et al. (2005, 2007a,b) lumped all tooth classes together in their analysis. Because teeth from different classes develop at the same time, the units are not independent, and thus ANOVA is not a valid test.

There are further methodological problems in Guatelli-Steinberg et al.'s work that need to be discussed in more detail. For instance, some individuals are represented by many teeth in the analysis (e.g., six teeth from the Le Moustier specimen), whereas other individuals are represented by only one tooth (e.g., the Neandertal from Devil's Tower). This procedure attributes greater importance to those individuals represented by more teeth. Moreover, Guatelli-Steinberg et al. (2005) clustered six different tooth classes (maxillary and mandibular incisors and canines) to obtain a mean number of perikymata. Given that crown-formation times are significantly different among anterior teeth, they should have considered the possibility that the observed differences in the total number of perikymata between Neandertals and modern humans were the result of including different proportions of tooth types in each sample. Since canine crowns take longer to form (mandibular canine = 5.11 years; maxillary canine = 3.83 yrs) than the crowns of mandibular first incisors (3.34 years; Reid and Dean, 2006: Table 4, northern Europeans), the number of perikymata is higher in the former than in the latter. Therefore, the analysis of a sample that includes a greater number of canines would show a higher number of perikymata than a sample that contains a greater number of mandibular first incisors. This is indeed the case in Guatelli-Steinberg et al's (2005) work. In their analysis, canines represent 43% of the Neandertal sample, while mandibular first incisors only represent 9% (Table 1). Their South African sample included canines and mandibular first incisors with proportions of 37% and 15%, respectively, and in the Newcastle sample, canines constituted 45% of the sample, whereas mandibular first incisors accounted for only 13%.

While different proportions of tooth classes in different human groups can affect Guatelli-Steinberg et al.'s (2005) results, variation in tooth wear must also be considered. Guatelli-Steinberg et al. (2005: 14198) stated that "only teeth estimated to have 80% or more of their crown heights intact (i.e., minimally worn teeth) were selected for analysis." Furthermore, they stated that "teeth were excluded from the study if more than one decile beyond the first two deciles contained indistinct perikymata" (Guatelli-Steinberg et al., 2005: 14199). Anterior teeth with crowns that have been reduced by 20% due to wear would exhibit dentine exposures no larger than a third of the occlusal surface (Fig. 1). When the sample of Neandertal teeth included in the Guatelli-Steinberg et al.'s analysis is carefully scrutinized (Guatelli-Steinberg et al., 2005: Table 2; see also Guatelli-Steinberg et al., 2007a,b), it is clear that their sample contained many teeth that show a very advanced degree of wear and that are likely to have lost more than 20% of their crowns (Figs. 2, 3). Because Guatelli-Steinberg et al. carried out their analysis on the total number of

Table 1
Number and proportion of Neandertal and modern human teeth included in Guatelli-Steinberg et al.'s (2005) work

Tooth class	Neandertal		South African		Inuit		Newcastle	
	n	%	*n*	%	*n*	%	*n*	%
Maxillary								
I1	10	18	20	15	10	15	19	17
I2	9	16	21	16	10	15	16	14
C	14	25	26	19	9	14	39	34
Mandibular								
I1	5	9	20	15	12	18	15	13
I2	8	14	23	17	14	22	13	11
C	10	18	24	18	10	15	13	11


UPPER FIRST INCISOR
UPPER SECOND INCISOR
UPPER CANINE
LOWER FIRST INCISOR
LOWER SECOND INCISOR
LOWER CANINE

perikymata, the following question can be asked: How have they obtained the total number of perikymata in these teeth?

Of the 55 crowns included in Guatelli-Steinberg et al.'s (2005) analysis, only 13 are unaffected by wear. These 13 teeth come from only 6 individuals. Indeed, Krapina 194 and 195 (left and right I^1), Krapina 191 (maxillary canine), and Krapina 196 (I^2) belong to the same individual, KDP 2. Individual KDP 3 comprises Krapina 102 (maxillary canine), 119 (mandibular canine), and 131 (I^2). Krapina 103 (maxillary canine) and 120 (mandibular canine) belong to KDP 8, and Krapina 90 (I_2) and 121 (mandibular canine) are grouped in KDP 31. Other teeth without wear come from KDP 35 (Krapina 130, an I^2) and Devil's Tower (I^1).

Guatelli-Steinberg et al.'s results

As noted, the Neandertal sample chosen by Guatelli-Steinberg and coworkers can provide the total number of perikymata in only a few teeth from even fewer individuals. Furthermore, in unworn teeth, perikymata counts remain difficult to obtain, and in almost all teeth, the total number of perikymata has to be estimated.

It is reasonable to think that the mean values for the total number of perikymata for each tooth class suggested by Guatelli-Steinberg et al. have been obtained by counting perikymata only in unworn teeth. In fact, there are very few unworn teeth in each tooth class—three maxillary canines, three I^2s, two I^1s, three mandibular canines, and one I_2 (there are no unworn I_1s)—from which total perikymata counts can be derived at all, thus indicating that some caution is warranted regarding the method employed to analyze these data and how the results derived from them are used.

At small sample sizes (i.e., $n < 4$), means and variances cannot be considered representative of a population, and thus it is not valid to use them to calculate confidence intervals or to test statistical hypotheses. Indeed, the standard error becomes so large that it increases the probability of making a type II error when means of two or more samples are compared. Since the sample size of unworn teeth in Guatelli-Steinberg et al.'s (2005, 2007a,b) study is limited to $n = 3$ in the best-represented tooth classes, mean values are meaningless and cannot be used to carry out statistical tests (i.e., *t*-test or ANOVA). Small samples only allow for descriptive analysis.

Unfortunately, Guatelli-Steinberg et al. (2005, 2007a,b) did not provide individual values, and thus results presented as means are unusable for comparisons between Neandertals and other human populations in future studies.

Discussion

Dental analyses examine many aspects of tooth microstructure, and a complete understanding of dental growth is only achieved when as many of these aspects as possible are included in a study. However, it is often impossible to make histological sections of fossil hominid teeth, which prevents an in-depth study of dental growth in many fossil species, including middle and late Pleistocene *Homo*. This obstacle inevitably limits analysis of enamel to the external manifestation of internal incremental markings (i.e., perikymata). Fortunately, numbers of perikymata and the perikymata-packing pattern can be analyzed in fossil hominid species.

Perikymata-packing patterns enable us to distinguish between fossil hominid groups (e.g., *Australopithecus* vs. *Paranthropus*; Bromage and Dean, 1985; Dean, 1987). In addition, dividing the crown height into deciles enables us to compare specific areas of a tooth across different groups in which perikymata can be counted (Ramírez Rozzi and Bermúdez de Castro, 2004).

The large variation in the number of perikymata found in modern humans by Guatelli-Steinberg and colleagues contributes greatly to our knowledge about modern human variation, particularly the low values reported for their South African sample. However, their results for total numbers of perikymata in Neandertal anterior teeth must be considered unreliable. The 42 worn teeth, the majority of which exhibit high degrees of wear (much higher than claimed by Guatelli-Steinberg and colleagues; see Figure 2), represent 76% of the Neandertal sample analyzed by Guatelli-Steinberg et al. The total number of perikymata in the 13 unworn teeth is overwhelmed by the estimated and reconstructed numbers obtained from the 42 worn teeth. The mean values proposed by Guatelli-Steinberg et al. (2005, 2007a,b) for Neandertal teeth must therefore be considered inaccurate.

Conclusion

Close scrutiny of the work on Neandertal anterior teeth by Guatelli-Steinberg et al. (2005, 2007a,b) reveals several problems in methodology and sample composition. Guatelli-Steinberg et al. analyzed the total number of perikymata in a relatively small sample of Neandertal anterior teeth, which included many specimens with a high degree of wear. This suggests that Guatelli-Steinberg and coworkers needed to estimate the total number of perikymata for a considerable number of teeth included in their sample. It is therefore difficult to ascertain what proportion of the number of perikymata obtained for Neandertals by Guatelli-Steinberg and coworkers are reconstructed and what proportion are real counts. It may be that Guatelli-Steinberg et al. used unworn Neandertal teeth to calculate mean values for regions where perikymata are missing. In this case, the small sample size of unworn teeth is so low that mean values determined in this way are bound to be unreliable in terms of estimating the population parameter.

Fig. 1. Sections of anterior modern human teeth. The height of the crown is divided by deciles and the most occlusal 20% of crown height is indicated by the dashed white line. Guatelli-Steinberg et al. (2005: 14198) stated: "Only teeth estimated to have 80% or more of their crown heights intact (i.e., minimally worn teeth) were selected for analysis." Thus, the teeth included in their analysis should not exhibit wear greater than that shown in the figure. When crowns are 20% worn, the dentine exposure in the midline of the crown constitutes at least one third of the occlusal wear facet.

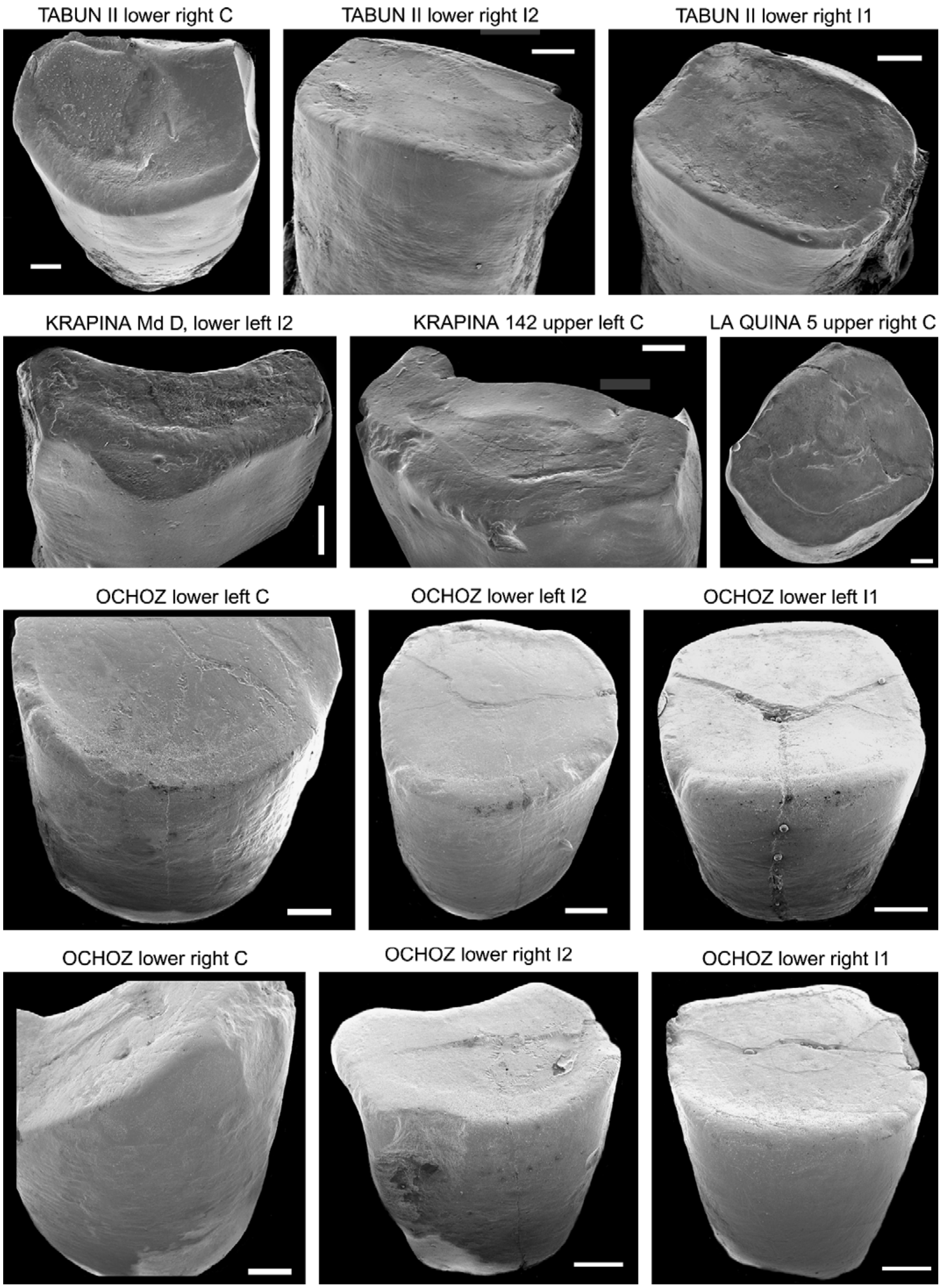


Fig. 2. Anterior teeth included in the Guatelli-Steinberg et al.'s work. Guatelli-Steinberg et al. (2005) calculated the total number of perikymata in Neandertal teeth using teeth that were estimated to retain 80% of their original crown height. Guatelli-Steinberg et al. (2005: 14199) excluded teeth "if more than one decile beyond the first two deciles contained indistinct perikymata." However, many teeth, such as those presented in this figure, show a degree of wear that has clearly affected more than 20% of the crown (for other worn Krapina teeth, see also Figures 93, 98, 100, 102, 155, 157, 167 in Radovčić et al., 1988). Since Guatelli-Steinberg et al. did not state which antimere was used for analysis, the six mandibular anterior teeth from Ochoz are shown. The question is: How did Guatelli-Steinberg et al. obtain the total number of perikymata in these teeth?

In short, the data and results presented by Guatelli-Steinberg et al. for Neandertal anterior teeth are at best highly questionable.

Thus, although it is now clear that overlap in the number of perikymata in Neandertal and modern human teeth exists (Mann et al., 1990; Tillier et al., 1995; Ramírez Rozzi and Bermúdez de Castro, 2004; Ramírez Rozzi, 2005), the results presented by Guatelli-Steinberg et al. (2005) cannot be regarded as a reliable indicator of how Neanderthal anterior teeth compare with those of modern human populations.

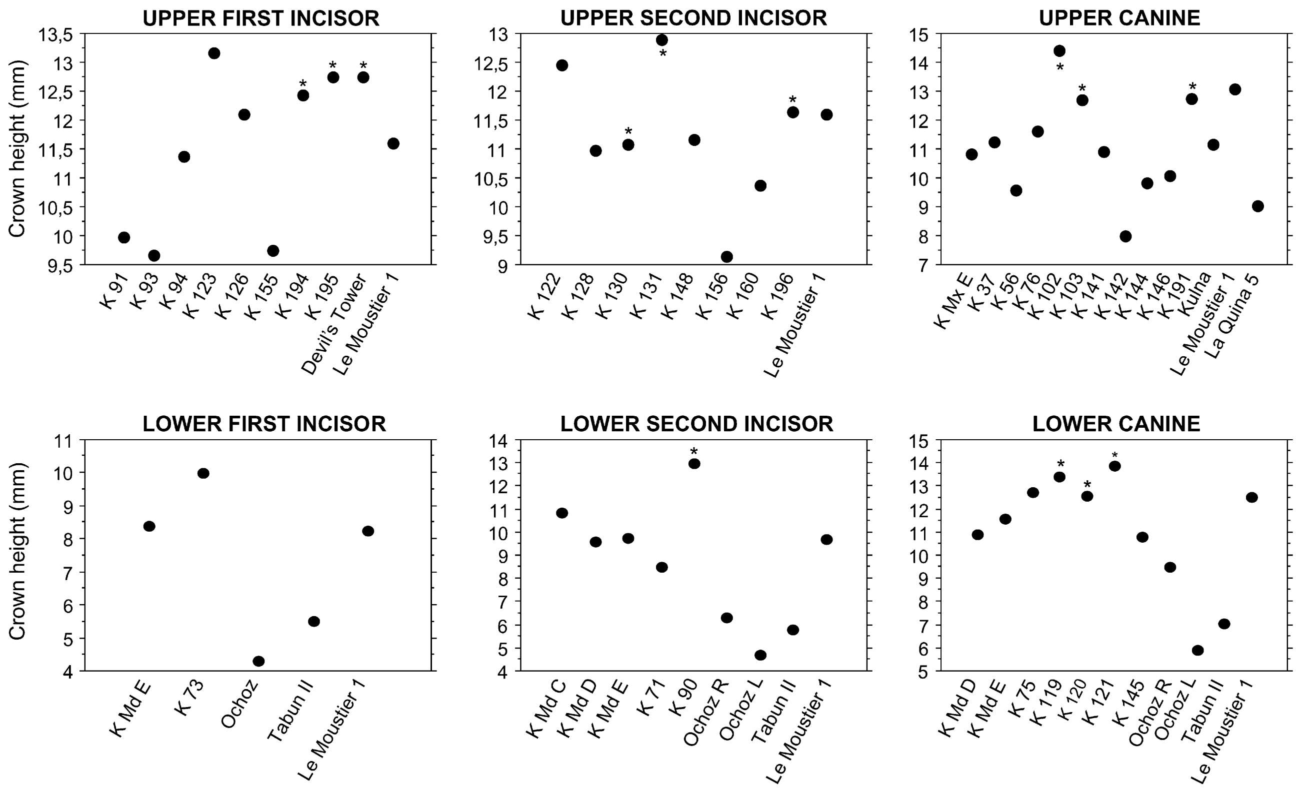


Fig. 3. Crown heights of anterior teeth included in Guatelli-Steinberg et al.'s work. The crown height is given for each crown in each tooth class. The asterisk (*) indicates the 13 unworn teeth from six individuals that can be used a priori to obtain the total number of perikymata. We counted 114 perikymata in the maxillary first incisor from Devil's Tower; this value is very close to the total of 119 perikymata reported by Dean et al. (1986). Although variation exists in the crown height in unworn teeth, the low position of many teeth in graphs clearly indicates an advanced degree of wear (see also Fig. 2). Abbreviations: K = Krapina, Mx = maxilla, Md = mandible, R = right, L = left.

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