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Enamel thickness variation of deciduous first and second upper molars in modern humans and Neanderthals

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ABSTRACT

Enamel thickness and dental tissue proportions have been recognized as effective taxonomic discriminators between Neanderthal and modern humans teeth. However, most of the research on this topic focused on permanent teeth, and little information is available for the deciduous dentition. Moreover, although worn teeth are more frequently found than unworn teeth, published data for worn teeth are scarce and methods for the assessment of their enamel thickness need to be developed. Here, we addressed this issue by studying the 2D average enamel thickness (AET) and 2D relative enamel thickness (RET) of Neanderthal and modern humans unworn to moderately worn upper first deciduous molars (dm^1s) and upper second deciduous molars (dm^2s). In particular, we used 3D μCT data to investigate the mesial section for dm^1s and both mesial and buccal sections for dm^2s. Our results confirmed previous findings of an Neanderthal derived condition of thin enamel, and thinner enamel in dm^1s than dm^2s in both Neanderthal and modern humans. We demonstrated that the Neanderthal 2D RET indices are significantly lower than those of modern humans at similar wear stages in both dm^1s and dm^2s ($p < 0.05$). The discriminant analysis showed that using 2D RET from dm^1 and dm^2 sections at different wear stages up to 93% of the individuals are correctly classified. Moreover, we showed that the dm^2 buccal sections, although non-conventionally used, might have an advantage on mesial sections since they distinguish as well as mesial sections but tend to be less worn. Therefore, the 2D analysis of enamel thickness is suggested as a means for taxonomic discrimination between modern humans and Neanderthal unworn to moderately worn upper deciduous molars.

Introduction

Tooth enamel thickness and enamel distribution in primate teeth have been extensively analyzed for their functional implications and for life history assessment (e.g., Martin, 1985; Gantt and Rafter, 1998; Schwartz, 2000; Shimizu et al., 2005; Macchiarelli et al., 2006; Mahoney, 2013; Strait et al., 2013). Various aspects of enamel thickness have been the focus of anthropological research for their taxonomic and phylogenetic relevance (e.g., Grine and Martin, 1988; Macho and Thackeray, 1992; Martin et al., 2003; Hlusko et al., 2004). Analyses of enamel thickness and dental tissue proportions have been carried out to investigate dental morphological variation among hominoids (Kono, 2004; Suwa and Kono, 2005; Smith et al., 2005, 2012a; Alba et al., 2010) and within the genus *Homo* (Kono et al., 2002; Smith et al., 2012b). In particular, it has been recognized that enamel thickness distinguishes between modern human and Neanderthal permanent and deciduous teeth (Zilberman et al., 1992; Olejniczak et al., 2008a; Smith et al., 2009, 2010; Bayle et al., 2009a,b, 2010; Crevecoeur et al., 2010; Toussaint et al., 2010; Benazzi et al., 2011a), as Neanderthal teeth showed a derived condition of thinner enamel respect to modern humans, as recognized previously by some scholars

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(Zilberman et al., 1992; Zilberman and Smith, 1992; Molnar et al., 1993; Rozzi, 1996). This matter was thoroughly investigated by Olejniczak et al. (2008a) who explained the differences between the two taxa showing that Neanderthals possessed a comparable absolute enamel volume to modern humans, but distributed on a larger coronal dentine area (in accordance with Grine, 2002, 2005; Macchiarelli et al., 2006). Previous investigation on deciduous teeth (Macchiarelli et al., 2006; Bayle et al., 2009a,b, 2010; Toussaint et al., 2010; Zanolli et al., 2010; Benazzi et al., 2011a,b) confirmed this trend of derived thinner enamel in Neanderthals. However our knowledge on dental tissues variability in Neanderthal and modern human deciduous teeth is still very limited (Macchiarelli et al., 2006). Furthermore, most scholars have focused on unworn or slightly worn teeth (Grine, 2002, 2005; Smith et al., 2005; Olejniczak et al., 2008a; among the others), because dental wear causes an alteration on the proportions of dental tissues (see discussion in Benazzi et al., 2011a; and our illustration in Fig. S1 in Supplementary Online Material [SOM]). Since wear most often affects fossil teeth to various degrees, investigating dental tissues variability in worn teeth is crucial for evaluating enamel thickness as a means of taxonomic discrimination.

Imaging techniques based on microcomputed tomography (μCT) have made it possible to investigate the dental surfaces and inner tooth structures, avoiding destructive interventions and allowing for digital procedures for the analysis of enamel thickness. These virtual techniques build upon protocols developed for physical sections by Martin (1985) and later adapted to suit the purposes of dental analyses on virtual images. While enamel thickness has been traditionally measured on mesial sections (Martin, 1983, 1985), imaging techniques allow consideration of other sections or multiple sections (2D enamel thickness: Smith et al., 2006; Olejniczak et al., 2008a,b,c,d; Bayle et al., 2009a,b, 2010; Crevecoeur et al., 2010; Zanolli et al., 2010; Benazzi et al., 2011a; Fornai et al., 2012), as well as the whole crown (3D enamel thickness: Martin et al., 2003; Olejniczak et al., 2008b,c,d; Bayle et al., 2009a,b, 2010; Crevecoeur et al., 2010; Zanolli et al., 2010; Benazzi et al., 2011c, 2013). The various digital protocols used so far for the orientation and isolation of the dental crown (for both 2D and 3D enamel thickness), and identification of the coronal sections have been comparatively reviewed by Benazzi et al. (2014b) who, based on preexisting methods (Martin, 1985; Olejniczak et al., 2008a), proposed also accurate and standardized methods for molar enamel thickness analysis. The guidelines by Benazzi et al. (2014b) provide instructions only for the image processing of teeth in which the dentine is not yet exposed. Therefore, a reliable approach for the quantification of tissue proportions in moderately worn teeth is still needed.

Here, we carried out the analysis of 2D enamel thickness in mesial and buccal sections of Neanderthal and modern human upper first deciduous molars (dm^1s) and upper second deciduous molars (dm^2s) at different wear stages (1–3 according to Molnar, 1971). For the identification of the 2D sections we referred to the guidelines by Benazzi et al. (2014b), but we established new methods for the identification of 2D mesial and buccal sections in (deciduous) molars presenting exposed patches of dentine. In the current work, we analyzed the sample systematically on the basis of its degree of wear to investigate the range of variability of enamel thickness in modern human and Neanderthal dm^1s and dm^2s. Furthermore, we aimed to assess whether enamel thickness is suitable for the taxonomic discrimination of moderately worn modern human and Neanderthal dm^1s and dm^2s. In this contribution, we provided also the raw data for the values of the enamel tissue components for the entire sample, which may serve future studies on the subject. We evaluated the enamel thickness and dental tissue proportions from the mesial sections (for both dm^1s and dm^2s) and buccal section (for dm^2s) as taxonomic discriminators between *Homo sapiens* and Neanderthals and compared the outcome for dm^2 buccal sections with that of the most traditionally used mesial sections.

Materials and methods

Our sample comprised both dm^1s and dm^2s from European specimens of recent modern humans (RHS; $dm^1 = 23$; $dm^2 = 32$), Upper Paleolithic modern humans (UPHS; $dm^1 = 2$; $dm^2 = 2$), and Neanderthals ($dm^1 = 4$; $dm^2 = 9$), as listed in Table 1. We included only teeth with a wear stage not exceeding 3 according to Molnar's classification (1971). Teeth showing severe damage in the areas of interest (e.g., cracks, decay) were excluded, as well as teeth showing signs of enamel hypoplasia, while minor damage on the

Table 1
List of dm^1s and dm^2s considered for the investigation of the enamel thickness and dental tissue proportions.

Taxon	dm^1				dm^2				
	Individual	Provenience	Source for CT	Wear at mesial section	Individual	Provenience	Source for CT	Wear at mesial section	Wear at buccal section
RHS	Medieval and contemporary ($n = 23$*)	Central Europe	C. d. M[a]	Stage 1 = 4	Medieval and contemporary ($n = 32$*)	Central Europe	C. d. M.[a]	Stage 1 = 14	Stage 1 = 14
			P.H.R.C.T. Lab[b]	Stage 2 = 4			P.H.R.C.T. Lab[b]	Stage 2 = 9	Stage 2 = 18
			Vienna CT Lab[c]	Stage 3 = 16			Vienna CT Lab[c]	Stage 3 = 11	Stage 3 = 6
UPHS	Dolní Věstonice 36-2	Czech Republic	Vienna CT Lab[c]	Stage 1	Dolní Věstonice 36-3	Czech Republic	Vienna CT Lab[c]	Stage 1	Stage 1
	La Rochette	France	P.H.R.C.T. Lab[b]	Stage 3	La Rochette	France	P.H.R.C.T. Lab[b]	Stage 1	Stage 2
N	Krapina d181	Croatia	NESPOS[d]	Stage 3	Krapina d185	Croatia	NESPOS[d]	Stage 1	Stage 1
	Krapina d183	Croatia	NESPOS[d]	Stage 3	Krapina d186	Croatia	NESPOS[d]	Stage 2	Stage 1
	Roc de Marsal 1 L	France	NESPOS[d]	Stage 3	Krapina d187	Croatia	NESPOS[d]	Stage 3	Stage 3
	Pech-de-l'Azé I L	France	NESPOS[d]	Stage 3	Krapina d188	Croatia	NESPOS[d]	Stage 2	Stage 1
					Krapina d189	Croatia	NESPOS[d]	Stage 3	Stage 3
					Krapina d190	Croatia	NESPOS[d]	Stage 3	Stage 3
					Pech-de-l'Azé I L	France	NESPOS[d]	Stage 3	Stage 1
					Roc de Marsal 1 L	France	NESPOS[d]	Stage 2	Stage 1
					Subalyuk-2 L	Hungary	Vienna CT Lab[c]	Stage 3	Stage 3

We report the provenience, source of the CT data, and wear stage (according to Molnar, 1971) at the sections of interest.
*The number of sections do not sum up to the number of individuals because we used both antimeres from the same individual when they showed different wear stages.
L = left; RHS = recent modern humans; UPHS = Upper Paleolithic modern humans; N = Neanderthals.
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