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Enamel thickness variation in the deciduous dentition of extant large-bodied hominoids

Alejandra Ortiz[1,2], Katherine Schander-Triplett[3], Shara E. Bailey[2,4], Matthew M. Skinner[4,5], Jean-Jacques Hublin[4], Gary T. Schwartz[1]

[1] Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

[2] Center for the Study of Human Origins, Department of Anthropology, New York University, New York, NY, USA

[3] Barrett, The Honors College, College of Liberal Arts and Sciences, Arizona State University

[4] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[5] School of Anthropology and Conservation, University of Kent, Canterbury, United Kingdom

* Corresponding author.

E-mail address: ao706@nyu.edu (A. Ortiz)

Abstract

Objectives

Enamel thickness features prominently in hominoid evolutionary studies. To date, however, studies of enamel thickness in humans, great apes and their fossil relatives have focused on the permanent molar row. Comparatively little research effort has been devoted to tissue proportions within deciduous teeth. Here we attempt to fill this gap by documenting enamel thickness variation in the deciduous dentition of extant large-bodied hominoids.

Materials and Methods

We used microcomputed tomography to image dental tissues in 80 maxillary and 78 mandibular deciduous premolars of *Homo sapiens*, *Pan troglodytes*, *Gorilla*, and *Pongo*. Two-dimensional virtual sections were created from the image volumes to quantify average (AET) and relative (RET) enamel thickness, as well as its distribution across the crown.

Results

Our results reveal no significant differences in enamel thickness among the great apes. Unlike the pattern present in permanent molars, *Pongo* does not stand out as having relatively thicker-enameled deciduous premolars than *Pan troglodytes* and *Gorilla.* Humans, on the other hand, possess significantly thicker deciduous premolar enamel in comparison to great apes. Following expectations from masticatory biomechanics, we also find that the "functional" side (protocone, protoconid) of deciduous premolars generally possesses thicker enamel than the "nonfunctional" side.

Discussion

Our study lends empirical support to anecdotal observations that patterns of AET and RET observed for permanent molars of large-bodied apes do not apply to deciduous premolars. By documenting enamel thickness variation in hominoid deciduous teeth, this study provides the comparative context to interpret rates and patterns of wear of deciduous teeth and their utility in life history reconstructions.

1. Introduction

Enamel thickness and its distribution across the tooth crown have long been recognized as an important source of taxonomic, phylogenetic, and functional information of extinct and extant primates (e.g., Molnar & Gantt, 1977; Martin, 1985; Beynon and Wood, 1986; Shellis, Beynon, Reid, & Hiiemae, 1998; Schwartz, 2000a; Shimizu, 2002; Martin, Olejniczak, & Maas, 2003; Constantino, Lucas, Lee, & Lawn., 2009; McGraw, Pampush, & Daegling, 2012; but see Olejniczak et al., 2008a; Skinner, Alemseged, Gaunitz, & Hublin, 2015 for results suggesting the homoplastic nature of enamel thickness in hominins). Its high percentage of inorganic material (~96%) makes tooth enamel the hardest naturally produced substance in the body, such that teeth are extremely durable and therefore the best-preserved elements in the fossil record. The primary function of enamel is to aid in the mechanical reduction of food particles in the oral cavity. Increases in the quantity of enamel are thought to increase the functional longevity of teeth by slowing the degree of tooth loss due to abrasion and attrition and also by decreasing the likelihood of tooth failure during mastication (Myoung et al., 2009; Chai, 2014). Given the clear association with food bolus reduction, it has been argued that the quantity of enamel overlying the dentine core is an accurate indicator of dietary adaptations, with organisms feeding on hard objects having thicker-enameled teeth than those feeding on leaves and piths (e.g., Kay, 1981; Dumont, 1995; Teaford, 2007; Lucas, Constantino, Wood, & Lawn, 2008).

The prevalence of teeth in the fossil record, coupled with the intimate connection between tooth crown anatomy and dietary proclivities, has resulted in enamel thickness featuring prominently in studies of hominoid evolution. However, this research has focused almost exclusively on the permanent dentition (e.g., for extant hominoids: Molnar & Gantt, 1977; Martin, 1985; Shellis et al., 1998; Gantt, 1986; Schwartz, 2000a; Kono, 2004; Smith, Olejniczak, Martin, & Reid, 2005; Smith, Olejniczak, Reid, Ferrell, & Hublin, 2006; Smith, Olejniczak, Reh, Reid, & Hublin, 2008; Smith, Kupczik, Machanda, Skinner, & Zermeno, 2012a; Kono & Suwa, 2008; Olejniczak, Tafforeau, Feeney, & Martin, 2008b; for fossil apes: Martin et al., 2003; Smith, Martin, & Leakey, 2003; Olejniczak et al., 2008c; Zanolli et al., 2015; for fossil hominins: Beynon & Wood, 1986; Grine & Martin, 1988; Conroy, 1991; Macho & Thackeray, 1992; Olejniczak et al., 2008a,d; Smith et al., 2012b; Skinner et al., 2015; Pan et al., 2016; Martín-Francés et al., 2018; Zanolli et al., 2018). Comparatively little research effort has been devoted to tissue proportions, including the amount of enamel, within deciduous teeth (Aiello, Montgomery, & Dean, 1991; Gantt, Harris, Rafter, & Rahn, 2001; Grine, 2005; Mahoney, 2010, 2013; Fornai et al., 2014). A few general trends can be gleaned about the patterning of enamel thickness within and across the molars of hominoids from these studies. It is well-established that among extant large-bodied hominoids *Homo* has the thickest-enameled permanent molars, followed by *Pongo*, *Pan*, and finally *Gorilla*[1]. This gradient has led to broad classifications, with *Homo* and *Pongo* being characterized as having "thick" enamel, whereas *Pan* and *Gorilla* have been variably characterized as having "thin" or "intermediate" enamel thickness (Martin, 1985; Shellis et al., 1998).

Macho and Berner (1993) were among the first to quantify the uneven distribution of enamel across the permanent molars of recent humans. Since their study, there has been an emphasis on documenting differences in molar enamel distribution in other hominoids and interpreting these differences within a strict functional framework based on integrating knowledge about the mechanics of the mammalian chewing cycle and molar occlusal anatomy (Kay, 1977; Chivers, Wood, & Bilsborough, 1984; Ross et al., 2009; Ungar, 2017). The

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[1] Note that this pattern is based primarily on two-dimensional tooth sections and that it may slightly differ using three-dimensional values of enamel thickness, especially in *Pongo* and *Pan* (e.g., see Kono, 2004).

mammalian, and thus primate, chewing cycle can be divided into a series of movements, or strokes: the closing, power, and opening strokes. The closing stroke, wherein the mandibular arcade is elevated towards the maxillary arcade, brings opposing teeth into close approximation. Because the occlusal tables, and thus the main cusps, of opposing molars contact each other during the power stroke, it is not surprising that the nature of the food being reduced, coupled with the precise manner in which molars move into and out of centric occlusion, should be related to the distribution of enamel. Broadly speaking, enamel is expected to be thicker on the "functional" or "supporting" cusps (i.e., protocone and protoconid) than on the "non-functional" or "guiding" cusps (i.e., paracone and metaconid) (Macho & Berner, 1993; Macho & Spears, 1999; Schwartz, 2000a). Studies of the patterning of enamel thickness distribution in hominoid permanent molars have provided mixed support for these functional expectations (Molnar & Gantt, 1977; Grine & Martin, 1988; Conroy, 1991; Macho & Berner, 1993; Schwartz, 2000a; Kono, 2004; Grine, 2005; Skinner et al., 2015). What has become apparent, however, is that the degree of asymmetry in enamel thickness between the lingual and buccal cusps is less pronounced moving distally along the permanent molar row, a fact that has been associated with more equivalent masticatory loads exerted over the "functional" and "non-functional" regions in the second and third molars (Spears & Macho, 1995).

Other trends in enamel thickness variation along the permanent molar row have been observed. Using standard measures of the total volume of enamel across a molar crown (the indices of average and relative enamel thickness; Martin, 1985), there is a tendency for enamel thickness to increase from M1 to M3 (Macho & Berner, 1993, 1994; Grine & Martin, 1998; Shellis et al., 1998; Schwartz, 2000a,b; Grine et al., 2005; Smith et al., 2005, 2006, 2008; Olejniczak et al., 2008a; Feeney et al., 2010). Biomechanical models of mastication suggest that the mandible acts like a third-class lever (Hylander, 1975; Mansour & Reynick, 1975; but see Spencer, 1998, 1999). Following this model, it has been argued that the mandible experiences higher bite forces posteriorly and that these bite forces have selected for thicker enamel on the posterior molars of humans and other hominoids (Molnar & Ward, 1977; Macho & Berner, 1994; Spears & Macho, 1995, 1998; Macho & Spears, 1999). Alternatively, Grine (Grine, 2002, 2005; Grine et al., 2005) has proposed that the distal-ward increase in enamel thickness from M1 to M3 is simply the result of the differential reduction of the dentine crown component in posterior molars (i.e., morphological hypothesis).

In stark contrast to the great deal that has been learned about the evolutionary and functional significance of permanent molar enamel thickness, our understanding of dental tissue proportions and distribution in hominoid deciduous postcanine teeth (referred to herein as deciduous premolars)[2] is comparatively limited. In the past two decades progress has been made in the characterization of dental tissue proportions – the amount of enamel versus the amount of coronal dentine – in recent humans (Aiello et al., 1991; Harris et al., 1999; Gantt et al., 2001; Grine, 2005; Mahoney, 2010, 2013) and fossil hominins (Zilberman et al., 1992; Zanolli et al., 2010; Benazzi et al., 2011a; Fornai et al, 2014). Because these studies focused primarily either on testing functional and morphological hypotheses related to the amount of enamel within molar crowns (Gantt et al., 2001; Grine, 2005; Mahoney, 2010, 2013) or on taxonomic differences between *Homo sapiens* and other hominin species (Zilberman et al., 1992; Bayle, Braga, Mazurier, & Macchiarelli, 2009; Zanolli et al., 2010; Benazzi et al., 2011a,b; Fornai et al,

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[2] Deciduous postcanine teeth are variably referred to as both “deciduous premolars” (dp) and “deciduous molars” (dm). The latter emphasizes the functional and, in the case of the distalmost deciduous tooth, morphological similarity between these teeth and the permanent molars. The former is used here to emphasize the developmental linkage to the permanent premolars, as the permanent premolars are the succedaneous teeth that result from the successional dental lamina extending directly off of the deciduous premolar primordia.

2014), our knowledge of the functional and/or taxonomic value of deciduous premolar enamel thickness in our closest living relatives – *Pan*, *Gorilla*, and *Pongo* – still has serious deficiencies. What is currently known is based on observations of a single third (dp_3) and fourth (dp_4) mandibular premolar per genus of great apes (Aiello et al., 1991). Although it appears from this study that the trends in enamel thickness observed in permanent molars are also present in the deciduous premolars, it is not entirely clear whether these trends will be observed within larger samples of hominoid deciduous teeth. The lack of research is surprising considering that patterns of deciduous dental wear (relative to that of the permanent molars) represent an important means to infer biological age (e.g., age at death), as well as key aspects of the growth, development, and life history of extinct and extant hominoids (Gustafson, 1950; Miles, 1963, 2001; Wolpoff, 1979; Aiello et al., 1991; Skinner, 1997; Bermúdez de Castro et al., 2003; Trinkaus, 2011; Vieira, Barbosa, Quintão, & Normando, 2015). In particular, the paucity of information on deciduous premolar enamel in apes and early hominins has limited our ability to probe the purported relationship between enamel thickness and rates of wear in the deciduous dentition.

Here, we employ non-destructive microcomputed tomographic techniques to examine enamel thickness and its distribution in 158 deciduous premolars of extant large-bodied hominoids, including specimens representing the genera *Homo*, *Pan*, *Gorilla*, and *Pongo*. Our goals are: 1) to document and compare measures of average and relative enamel within and among humans and great apes; 2) to assess patterns of metameric and inter-arcade variation in enamel thickness within each genus; 3) to characterize the patterning of enamel thickness distribution across the lingual, occlusal, and buccal tooth regions in each genus; and 4) to analyze whether intra- and inter-generic trends of enamel thickness found in great ape and human deciduous premolars follow those identified for permanent molars. By addressing these questions in the largest, taxonomically diverse sample of hominoid deciduous teeth examined to date, this study can serve as a benchmark for understanding deciduous enamel variation within and between members of the hominoid clade and its implications for systematics and dietary functional morphology.

2. Materials and methods

2.1. Sample

Enamel thickness was examined in 80 maxillary (dp^3 and dp^4) and 78 mandibular (dp_3 and dp_4) deciduous third and fourth premolars of *Homo sapiens*, *Pan troglodytes*, *Gorilla* sp., and *Pongo* sp. Sample sizes per premolar type and taxon are provided in Table 1. No intra-individual antimeres were included. We made no attempt to record the sex of the individuals; it should be noted, however, that enamel thickness of deciduous premolars does not appear to differ between males and females (Aiello et al., 1991; Harris et al., 1999; Grine, 2005; but see Gantt et al., 2001).

The *H. sapiens* sample mainly included individuals of African ancestry, followed by a small number of individuals from European ancestry or of unknown geographic provenience. Due to small sample sizes for great apes and, in many cases, the lack of exact provenance, no subspecies delineation was made for *P. troglodytes*, and no species delineation was made for *Gorilla* and *Pongo*. Specific details of the collections used and their institutions are provided in SOM Table S1.

2.2. Methods

We used microcomputed tomography to image dental tissues virtually and create two-dimensional (2D) sections from the three-dimensional (3D) image volumes. Although several studies on permanent teeth have recently documented dental tissue proportions in 3D (e.g., Kono, Suwa, & Tanijiri, 2002; Kono, 2004; Kono & Suwa, 2008; Olejniczak et al., 2008a,c), deciduous tooth enamel is comparatively thinner and more porous, and thus likely to wear at a faster rate not long after reaching functional occlusion (Aiello et al., 1991; Sumikawa, Marshall, Gee, & Marshall, 1999; Gantt et al., 2001). This means that a comprehensive 3D study requiring only unworn or lightly worn specimens would be difficult, if not impossible, to undertake. Individuals from the R.A. Dart Collection were scanned at the University of the Witwatersrand with a Nikon Metrology XTH 225/320 LC industrial CT system using the following parameters: 70kV, 120µA, 1.0 mm aluminum filter, and isometric voxel size of 50-85 microns. Great ape specimens curated at the Museum of Comparative Zoology at Harvard University were imaged with an X-Tek HMXST Micro-CT system (125 kV, 80µA, 1.0 mm aluminum filter, and isometric voxel size of 45-65 microns), whereas those in the Institute of Human Origins at Arizona State University were scanned with a Skyscan 1173 (110 kV, 72µA, 1.0 mm aluminum filter, and an isometric voxel size of 35.8 microns). All other specimens were scanned at the Max Planck Institute for Evolutionary Anthropology with either a BIR ACTIS 225/300 (130 kV, 100 µA, 0.25 mm brass filter) or a Skyscan 1172 (100 kV, 94 µA, 2.0 mm aluminum and copper) scanner at isometric voxel size of 27-70 microns.

Each microCT dataset was filtered using a three-dimensional median and mean-of-least-variance filter and then imported into Amira v6.3 (Mercury Computer Systems) for dental tissue segmentation and enamel-dentine junction (EDJ) and outer enamel surface (OES) surface generation following well-established protocols detailed elsewhere (Skinner et al., 2008; Ortiz, Skinner, Bailey, & Hublin, 2012). The segmentation process was performed by AO. Only teeth with no or minor wear were included (equivalent to Molnar's [1971] first four wear stages). The wear stage associated with each tooth in our study sample is provided in SOM Table S1. Note, however, that assessments of dental wear were based on the entire tooth crown and that observed wear facets and dentine patches do not necessarily occur at the location of the slices used for enamel thickness calculations. Given the difficulty of reconstructing missing enamel in 3D (Skinner et al., 2015), no attempts were made to reconstruct cusp tips at the OES. Dentine horns, on the other hand, are relatively sharper structures that can be more easily and accurately reconstructed in 3D using specialized imaging software. Our sample included therefore specimens with reconstructed dentine horns, when necessary. Reconstructions were performed in Geomagic Wrap (3D Systems Design) by AO prior to making the virtual slices used for calculating dental tissue data. Intra-observer error associated with EDJ reconstruction was calculated in the dp^4 of one *H. sapiens* and one *P. troglodytes*. Error calculation followed Skinner et al. (2015) and was negligible (~1-3%) based on EDJ surface areas retrieved from the different reconstructions. When necessary, cusp tips at the OES where reconstructed in 2D in Adobe® Photoshop® by AO. Error associated with 2D enamel reconstruction was on average 1.7%, tested using an unworn (Molnar's [1971] grade 1) dp^4 of *H. sapiens* cropped virtually at four different heights (SOM Fig. S1).

As per Skinner et al. (2015), each 3D digital model was rotated manually into anatomical position, where we subsequently created a virtual section perpendicular to the occlusal plane through the mesial cusps (Fig. 1a). Specifically, the plane passed through the dentine horns of the protocone and paracone of dp^3s and dp^4s, and through the dentine horns of the protoconid and metaconid of dp_3s and dp_4s, with the exception of great ape dp_3s, which generally possess a main single cusp (protoconid) and require a different slicing protocol. Thus, for great ape dp_3s, we followed Benazzi et al.'s (2014) protocol for premolars with no lingual cusp present whereby sections passed through the protoconid dentine horn and points on the labial and lingual cervical enamel at the widest labiolingual bi-cervical diameter. A scaled 2D image of each cross-section was saved as a TIFF format.

As illustrated in Fig. 1 and described in detail in Table 2, the following variables were calculated in Adobe® Photoshop®: 1) total area of the tooth crown section, 2) area of enamel cap, 3) area of dentine crown, 4) length of the EDJ, and 5) bi-cervical diameter. We used these variables to obtain two widely used indices of enamel thickness (Martin, 1985; Grine & Martin, 1988): average enamel thickness (AET) and relative enamel thickness (RET). AET is defined as the area of enamel cap divided by the length of the EDJ. The index RET is generated by dividing AET by the square root of the dentine crown area (multiplied by 100). RET provides therefore a dimensionless estimate of total enamel volume, allowing comparisons between groups of different tooth and body sizes. To document the patterning of enamel thickness distribution, we calculated the following linear measurements on upper and lower dp4s: lingual cervical wall thickness, mid-occlusal basin thickness, and buccal cervical wall thickness (Schwartz, 2000a). We did not collect these linear measurements on dp3s given that our sample sizes were considerably smaller and that great apes generally possess a single cusp in their dp_3s.

The sectioning process was carried out by AO in Amira v6.3, whereas all measurements were taken by KS-T using Adobe® Photoshop®. To test for error throughout the entire process from slicing to measurement gathering, a randomly selected subsample of eight molars (one dp^3 and one dp^4 per genus) was reprocessed from start to finish by both authors using a blind study protocol in which any taxonomic and specimen identification was removed. Error in enamel thickness measures between the first and second sessions (separated by ~one month) was on average 3.2%. Significant differences between groups were assessed using Mann-Whitney *U* test and Kruskal-Wallis test with post-hoc pairwise comparisons. All analyses were performed in PAST (Hammer, Harper, & Ryan, 2001) and JMP (SAS Institute).

3. Results

Table 3 provides the descriptive statistics (including the mean, standard deviation, and coefficient of variation) for the different measurements of deciduous premolar enamel thickness for all hominoid taxa. The individual measurements for each of the specimens analyzed are reported in SOM Table S1. Scaled schematic diagrams illustrating differences in dental tissue proportions in maxillary and mandibular deciduous fourth premolars are shown in Figure 2. Figure 3 presents pie charts showing 2D tissue proportions per tooth type and taxon, while boxplots demonstrating intergeneric differences in AET and RET indices are shown in Figure 4. The relative area of enamel per unit crown area is greater in *Homo sapiens* (~26%-34% enamel) than in great apes (~15%-24%), and tissue proportions in *P. troglodytes* and *Pongo* sp. are strikingly similar in all tooth types analyzed (Fig. 3). Mean values for both AET and RET are highest, without exception, in *H. sapiens,* providing clear support for modern humans possessing the thickest postcanine deciduous enamel among extant large-bodied hominoids. AET and RET indices among the great apes are very similar. From thinnest to thickness, the following pattern of AET (by tooth position based on mean values) is observed: dp^3s: *Gorilla* sp. < *P. troglodytes* = *Pongo* sp.; dp^4s: *P. troglodytes* < *Pongo* sp. < *Gorilla* sp.; dp_3s: *P. troglodytes* < *Gorilla* sp. < *Pongo* sp.; and dp_4s: *P. troglodytes* < *Pongo* sp. < *Gorilla* sp. (Table 3, Fig. 4). This pattern appears to be influenced by size, however (Table 3, Figs. 4): When the effects of size are taken into account through calculation of RET, *Gorilla* sp. deciduous premolars are slightly more thinly enameled that those of *P. troglodytes* and *Pongo* sp., whose RET indices are, in turn, more similar to each other. The following pattern for RET is observed among the great apes (based on mean values): *Gorilla* sp. < *Pongo* sp. ≤ *P. troglodytes* for maxillary and mandibular deciduous premolars (Table 2, Fig. 4). *Pongo* sp. exhibits the highest coefficients of variation (CV) for both AET and RET, followed by *Gorilla* sp., *Homo sapiens*, and *Pan troglodytes*. In some cases, CVs for AET and RET of *Pan troglodytes* are considerably smaller than those found for all other groups analyzed (Table 3).

The results of the Kruskal-Wallis test and associated post-hoc pairwise comparisons for AET and RET are presented in SOM Table S2 and Table 4, respectively. All pairwise group differences for AET and RET in dp_3 are non-significant, except for *H. sapiens* vs. *Gorilla* sp. It should be noted, however, that the lack of significance among groups could be at least partially attributed to small sample sizes, as among the four tooth types analyzed, our dp_3 sample is the smallest. As shown in Table 4, differences in AET and RET for dp^3, dp^4, and dp_4 between *H. sapiens* and each of the great apes are, in all cases, significant, except for between *H. sapiens* and *Pongo* sp. dp^3s. Contrary to the results for humans, Kruskal-Wallis post-hoc pairwise comparisons reveal that all differences in enamel thickness among the great apes are non-significant..

Table 3 and Figure 4 also reveal some interesting intra-taxon patterns. On average, within each hominoid group, dp^4s and dp_4s consistently possess greater AET and RET indices than their mesial metameres –dp^3s and dp_3s – respectively. We also note some trends in enamel thickness between maxillary and mandibular antagonistic pairs (i.e., dp^3 vs. dp_3; dp^4 vs. dp_4). In almost all cases, AET and RET means within each taxon are higher in dp^3 and dp^4 relative to their mandibular counterparts, with this trend being more marked in *H. sapiens*, followed by *Pongo* sp. The only two exceptions to this trend occur in *P. troglodytes* (AET means for dp^4 and dp_4 are the same) and in *Gorilla* sp. (enamel is thicker in dp_3 relative to dp^3 based on RET means and similar based on AET).

Finally, we examined the patterning of enamel thickness distribution in each taxon using linear measurements (LCW, MOB, BCW). Consistent with functional expectations for maxillary teeth, linear measurements of dp^4 reveal that enamel is consistently thickest on the lingual region in all groups (Fig. 5). Although the trend is less pronounced in dp_4 than in dp^4 as the difference between BCW and LCW is small, Fig. 5 also shows that the functional cusp of dp_4 (protoconid) tends to have thicker enamel than the non-functional cusp (metaconid). Occlusal enamel thickness of both deciduous premolars (dp^4 and dp_4) consistently provides the smallest values (Fig. 5).

4. Discussion

Extant large-bodied hominoids exhibit the following pattern of permanent molar enamel thickness (from thinnest to thickest): *Gorilla* < *Pan* < *Pongo* < *Homo*, where molars in *Gorilla* and *Pan* are characterized as having “thin” or “intermediate” enamel, and *Pongo* and *H. sapiens* are characterized as having “thick” enamel. Aiello et al.’s (1991) preliminary observations, on the other hand, noted a different pattern for the deciduous dentition, wherein enamel thickness did not greatly differ among the great apes. In agreement with Aiello et al. (1991), our results based on a large sample of deciduous premolars – the functional analog of permanent molars – found no significant differences in RET values among living members of the *Pan*, *Gorilla*, and *Pongo* clades. Broadly, our results for RET suggest the following trend for deciduous enamel (from thinnest to thickest): *Gorilla* < *Pongo* ≤ *Pan* < *Homo*. Thus, contrary to what is observed in the permanent molars, *Pongo* does not stand out as having more thickly enameled deciduous premolars compared to African apes. *Gorilla* deciduous teeth, however, tend to have slightly thinner (but not significantly different) enamel than those of *Pan* and *Pongo*, and *H. sapiens* possesses significantly thicker enamel in their deciduous dentition compared to *Gorilla, Pan*, and *Pongo*. Differences in 2D tissue proportions (% of enamel and dentine in the tooth crown) between *H. sapiens* and great apes are also evident in all tooth types examined, with enamel comprising ~26%34% of the total crown area in *H. sapiens* and only ~15%-24% in extant large-bodied apes. Interestingly, Olejniczak et al. (2008d) noted clear differences in relative tissue proportions between *H. sapiens* and Neanderthal permanent molars when analyzed in 3D, but not in 2D. In this regard, it remains to be tested whether differences in tissue proportions found in our study hold true when 3D data are considered.

Schwartz (2000a) posited that the range of variation in RET for permanent molars was larger in the so-called thick-enameled hominoids (i.e., *Pongo* and *Homo*) than in *Pan* and *Gorilla*. This was not the case in deciduous teeth. CVs for AET and RET were greater in *Pongo* and *Gorilla* than in *P. troglodytes* and to a lesser extent in *H. sapiens*. Caution is warranted, however, since our *Pongo* and *Gorilla* samples likely included specimens from more than one species, which could have resulted in a higher CVs relative to our species-level human and chimpanzee samples. Comparative analyses have noted that measures of enamel thickness are generally more variable in deciduous than in permanent molars (Gantt et al., 2001; Grine, 2005). Overall, the levels of intra-generic and intra-tooth variation in enamel thickness found here are similar to, or smaller than, those reported in previous studies of recent human deciduous premolars (Gantt et al., 2001; Grine, 2005). According to Gantt et al. (2001), however, the inclusion of even minimally worn teeth likely artificially increased the range of variation in their reported enamel thickness measurements. Thinly enameled bunodont teeth, such as those analyzed here, wear down quickly, a fact that might have increased some of the CV values in our study.

Although human and great ape deciduous premolars do not appear to follow the same patterns of inter-generic enamel thickness variation than their permanent functional analogs (i.e., the permanent molars), inter-arcade (i.e., antagonistic) and metameric trends appear to be both relatively stable between deciduous and permanent teeth and consistent across hominoids. Studies in recent humans have suggested that maxillary deciduous premolars and permanent molars have thicker enamel than their mandibular counterparts (Gantt, 1986; Gantt et al., 2001). This observation is supported by our study as comparisons between antagonistic pairs (dp^3 vs. dp_3, and dp^4 vs. dp_4) reveal, in most cases, higher AET and RET means in maxillary than in mandibular deciduous teeth, especially in *H. sapiens* and *Pongo* sp. Furthermore, hominoid dental tissue research has provided strong evidence for a posterior increase in enamel thickness along the permanent molar row (Grine & Martin, 1998; Macho and Berner, 1993, 1994; Spears & Macho, 1995; Shellis et al., 1998; Schwartz, 2000b; Grine et al., 2005; Smith et al., 2005, 2006, 2008, 2012a; Olejniczak et al., 2008a; Feeney et al., 2010; Skinner et al., 2015; Pan et al., 2016). Although enamel is considerably thinner on deciduous than on permanent teeth, a distal increase in deciduous premolar enamel thickness has been documented previously in fossil and recent humans (Zilberman et al., 1992; Harris et al., 1999; Grine, 2005; Gantt et al., 2001; Bayle et al., 2009; Zanolli et al., 2010; Mahoney, 2010, 2013; Benazzi et al., 2011a,b). In this regard, our results showing an increase in the amount of enamel from dp3 to dp4 are not only concordant with previous studies of the human deciduous dentition, but also provide empirical support to anecdotal observations for great apes reported by Aiello et al. (1991).

By invoking functional models of masticatory biomechanics, several researchers have argued that anterior-posterior gradients in enamel thickness along the permanent molar row reflect an increase in bite force magnitudes (Molnar & Ward, 1977; Macho & Berner, 1994; Spears & Macho, 1995, 1998; Macho and Spears, 1999). Although functional interpretations of the distal-ward increase in enamel thickness are controversial and clinical data on bite force in children are limited (Spencer, 1998; Grine, 2005; Mahoney, 2010; Mountain, Wood, & Toumba, 2011; Edmonds & Glowacka, 2014), this argument has also been used by Gantt et al. (2001) and Mahoney (2013) to explain the presence of thickest enamel on the more posterior deciduous teeth. As dp4s possess both greater dentine and enamel areas than relatively smaller dp3s, the overall percentage of the tooth crown formed by enamel is ~3-7% greater in dp4 crowns. Grine (2005) and Mahoney (2010) noted that enamel thickness changes along the premolar/molar series are the result of different odontogenic processes operating in deciduous and permanent human molars. They suggest that the quantity of both enamel and dentine increase from dp3 to dp4, whereas increases in RET from M1 to M3 are due to a reduction in dentine in the posterior-most molars. In this vein, our results are consistent with their statement on deciduous premolars.

Overall, differences in the distribution of enamel across the molar crown found here lend support to the hypothesis that “functional” cusps possess thicker enamel than their “non-functional” counterparts to prolong a tooth crown’s functional longevity. Although this hypothesis was first proposed for permanent teeth of humans and other hominoids (Molnar & Gantt, 1977; Macho and Berner, 1993; Macho and Spears, 1999; Schwartz, 2000a; Kono, et al., 2002), enamel thickness differentials between the “functional” and “non-functional” cusps have also been previously found for human deciduous premolars (Gantt et al., 2001; Grine, 2005; but see Mahoney, 2010). In addition, we found that, in all instances, hominoid deciduous premolars possess less enamel across their occlusal basin than on the lingual and buccal regions, with this trend being more marked in our *P. troglodytes* and *H. sapiens* samples. This is not only consistent with regional patterns reported for *H. sapiens* dp^4s (Grine, 2005), but also with Kono and Suwa's (2008) observations on the presence of extremely thin occlusal enamel in the permanent molars of bonobos and common chimpanzees.

For decades, tooth wear has been used as a tool for age determination in archaeological and living human individuals (e.g., Gustafson, 1950; Miles, 1963, 2001; Kim, Kho, & Lee, 2000; Mays, 2002; Vieira et al., 2015). Paleoanthropologists have also used tooth wear (generally in combination with other features such as stages of dental eruption) as a coarse measure of the rate of growth and development of fossil and recent hominoid species, most often to reconstruct key aspects of their life history such as weaning age, interbirth intervals, mortality rates, and lifespan (Wolpoff, 1979; Aiello et al., 1991; Skinner, 1997; Bermúdez de Castro et al., 2003; Caspari & Lee, 2004; Nargolwalla, Begun, Dean, Reid, & Kordos, 2005; Smith, Toussaint, Reid, Olejniczak, & Hublin, 2007; Trinkaus, 2011). Although enamel thickness is a key factor influencing rates and patterns of dental wear (Molnar & Gantt, 1977; Molnar & Ward, 1977; Aiello et al., 1991), it is surprising that estimates of species' life history extrapolating from rates of dental wear do not explicitly take into account the influence of enamel thickness on wear rates (reviewed in Smith, 2013).

Although most life history inferences based on archaeological and fossil dental remains rely on evidence from permanent teeth, Aiello et al. (1991) noted the potential importance of deciduous teeth for inferring two key aspects of hominoids' life history: age at weaning and interbirth intervals. Acknowledging that their conclusions were preliminary given both their small samples and unknown age at death of the specimens used, Aiello et al. (1991) proposed that the pattern and magnitude of wear (attrition) found among hominoid deciduous teeth were suggestive of an earlier weaning and shorter interbirth interval in gorillas than in chimpanzees and orangutans. In this vein, the data presented here can be used to test the observed preliminary pattern in a more comprehensive manner. While there is now clearer evidence that weaning in apes is a complex and long process (Pusey, 1983; Smith, 2013; Smith et al., 2013; Smith, Austin, Hinde, Vogel, & Arora, 2017; Joannes-Boyau et al., 2019) and that recent minimally invasive state-of-the-art research offers a new exciting glimpse into weaning age in our hominin ancestors (Joannes-Boyau et al., 2019), we believe that exploring this life history trait using complementary lines of evidence, including the non-destructive approach of dental wear, is warranted considering that nursing behavior among apes is difficult to infer and systematically investigate both in the wild and in the fossil record.

Finally, although testing Aiello et al.'s (1991) hypothesis of age at weaning in gorillas is beyond the scope of the present study, our results support the argument that the greater degrees of dental wear on gorilla deciduous teeth relative to those of chimpanzees and orangutans cannot be attributed to differences in enamel thickness. That is, we found no significant differences in relative and average enamel thickness among the great apes, meaning that the enamel on the deciduous postcanine dentition of *Gorilla* is not significantly thinner than in *Pan* and *Pongo*. One additional conclusion derived from this study is that *Pongo* does not possess thicker-enameled deciduous premolars than African great apes. Patterns of food consumption during the early life of great ape individuals are complex and slight differences have been noted among populations and species, but in a very general sense, infants from both *Pan* and *Pongo* start eating solid food by 0.5-1 years of age, which then constitutes an appreciable component of their diet by the time they reach about 1-2 years of age (Smith et al., 2013, 2017). It is known, however, that orangutans experience longer and sometimes cyclical periods of offspring dependence and later weaning ages relative to other apes (Pusey, 1983; van Noordwijk, Willems, Utami Atmoko, Kuzawa, & van Schaik, 2013; Smith et al., 2017). Thus, from the functional perspective, investment in postcanine deciduous teeth with thicker enamel in orangutans would be unexpected considering 1) that orangutans have the most prolonged nursing period than any other apes, 2) that milk consumption is considerably less challenging for the masticatory apparatus than solid food, and 3) that deciduous premolars among great apes remain in functional occlusion for roughly the same amount of time (based on estimates of the timing of dp3-4 and P3-4 emergence; see Smith, Crummett, & Brandt, 1994). Further research is needed to better understand the evolutionary, functional, and developmental implications of the patterns of enamel thickness variation in hominoid deciduous teeth, and our study represents an important first step in this direction by providing the comparative context within which to interpret deciduous tooth wear and its usefulness for inferring age at weaning in great apes and fossil hominins.

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Figure legends

Fig 1. Protocol used to collect enamel thickness data. (a) occlusal view of a three-dimensional model of a tooth with dentine in yellow and enamel rendered transparent. The red line indicates the plane of section, passing through the dentine horns of the two mesial cusps. (b) two-dimensional image of a cross-section from which enamel thickness measurements were collected. (c) area of total section (dashed lines). (d) area of enamel cap (dashed lines). (e) area of dentine crown (dashed lines). (f) length of enamel-dentine junction (black line) and bi-cervical diameter (red arrow). (g) length of lingual cervical wall, mid-occlusal basin, and buccal cervical wall (red arrows). Right dp_4 of *H. sapiens* depicted. Not to scale.

Fig 2. Cross sections through the mesial cusps of (a) dp^4 and (b) dp_4 with examples of dental tissue proportions in humans and great apes. Right premolars depicted.

Fig. 3. Pie charts showing 2D dental tissue proportions for (a) *H. sapiens*, (b) *P. troglodytes*, (c) *Gorilla* sp., (d) *Pongo* sp. Dentine in dark gray. Enamel in light gray.

Fig 4. Box plots of (a-b) average enamel thickness (AET), and (c-d) relative enamel thickness (RET) for upper and lower deciduous premolars per taxon.

Fig. 5. Patterning of enamel thickness distribution using LCW, MOB, and BCW linear measurements for (a) dp^4 and (b) dp_4. See Table 2 for abbreviations.

Enamel thickness variation in the deciduous dentition of extant large-bodied hominoids

Alejandra Ortiz[1,2], Katherine Schander-Triplett[3], Shara E. Bailey[2,4], Matthew M. Skinner[4,5], Jean-Jacques Hublin[4], Gary T. Schwartz[1]

[1] Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

[2] Center for the Study of Human Origins, Department of Anthropology, New York University, New York, NY, USA

[3] Barrett, The Honors College, College of Liberal Arts and Sciences, Arizona State University

[4] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[5] School of Anthropology and Conservation, University of Kent, Canterbury, United Kingdom

* Corresponding author.

E-mail address: ao706@nyu.edu (A. Ortiz)

Abstract

Objectives

Enamel thickness features prominently in hominoid evolutionary studies. To date, however, studies of enamel thickness in humans, great apes and their fossil relatives have focused on the permanent molar row. Comparatively little research effort has been devoted to tissue proportions within deciduous teeth. Here we attempt to fill this gap by documenting enamel thickness variation in the deciduous dentition of extant large-bodied hominoids.

Materials and Methods

We used microcomputed tomography to image dental tissues in 80 maxillary and 78 mandibular deciduous premolars of *Homo sapiens*, *Pan troglodytes*, *Gorilla*, and *Pongo*. Two-dimensional virtual sections were created from the image volumes to quantify average (AET) and relative (RET) enamel thickness, as well as its distribution ~~patterning~~ across the crown.

Results

Our results reveal no significant differences in enamel thickness among the great apes. Unlike the pattern present in permanent molars, *Pongo* does not stand out as having relatively thicker-enameled deciduous premolars than *Pan troglodytes* and *Gorilla.* Humans, on the other hand, possess significantly thicker deciduous premolar enamel in comparison to great apes. Following expectations from masticatory biomechanics, we also find that the “functional” side (protocone, protoconid) of deciduous premolars generally possesses thicker enamel than the “nonfunctional” side.

Discussion

Our study lends empirical support to anecdotal observations that patterns of AET and RET observed for permanent molars of large-bodied apes do not apply to deciduous premolars. By documenting enamel thickness variation in hominoid deciduous teeth, this study provides the comparative context to interpret rates and patterns of wear of deciduous teeth and their utility in life history reconstructions.

1. Introduction

Enamel thickness and its distribution across the tooth crown have long been recognized as an important source of taxonomic, phylogenetic, and functional information of extinct and extant primates (e.g., Molnar & Gantt, 1977; Martin, 1985; Beynon and Wood, 1986; Shellis, Beynon, Reid, & Hiiemae, 1998; Schwartz, 2000a; Shimizu, 2002; Martin, Olejniczak, & Maas, 2003; Constantino, Lucas, Lee, & Lawn., 2009; McGraw, Pampush, & Daegling, 2012; but see Olejniczak et al., 2008a; Skinner, Alemseged, Gaunitz, & Hublin, 2015 for results suggesting the homoplastic nature of enamel thickness in hominins). Its high percentage of inorganic material (~96%) makes tooth enamel the hardest naturally produced substance in the body, such that teeth are extremely durable and therefore the best-preserved elements in the fossil record. The primary function of enamel is to aid in the mechanical reduction of food particles in the oral cavity. Increases in the quantity of enamel are thought to increase the functional longevity of teeth by slowing the degree of tooth loss due to abrasion and attrition and also by decreasing the likelihood of tooth failure during mastication (Myoung et al., 2009; Chai, 2014). Given the clear association with food bolus reduction, it has been argued that the quantity of enamel overlying the dentine core is an accurate indicator of dietary adaptations, with organisms feeding on hard objects having thicker-enameled teeth than those feeding on leaves and piths (e.g., Kay, 1981; Dumont, 1995; Teaford, 2007; Lucas, Constantino, Wood, & Lawn, 2008).

The prevalence of teeth in the fossil record, coupled with the intimate connection between tooth crown anatomy and dietary proclivities, has resulted in enamel thickness featuring prominently in studies of hominoid evolution. However, this research has focused almost exclusively on the permanent dentition (e.g., for extant hominoids: Molnar & Gantt, 1977; Martin, 1985; Shellis et al., 1998; Gantt, 1986; Schwartz, 2000a; Kono, 2004; Smith, Olejniczak, Martin, & Reid, 2005; Smith, Olejniczak, Reid, Ferrell, & Hublin, 2006; Smith, Olejniczak, Reh, Reid, & Hublin, 2008; Smith, Kupczik, Machanda, Skinner, & Zermeno, 2012a; Kono & Suwa, 2008; Olejniczak, Tafforeau, Feeney, & Martin, 2008b; for fossil apes: Martin et al., 2003; Smith, Martin, & Leakey, 2003; Olejniczak et al., 2008c; Zanolli et al., 2015; for fossil hominins: Beynon & Wood, 1986; Grine & Martin, 1988; Conroy, 1991; Macho & Thackeray, 1992; Olejniczak et al., 2008a,d; Smith et al., 2012b; Skinner et al., 2015; Pan et al., 2016; Martín-Francés et al., 2018; Zanolli et al., 2018). Comparatively little research effort has been devoted to tissue proportions, including the amount of enamel, within deciduous teeth (Aiello, Montgomery, & Dean, 1991; Gantt, Harris, Rafter, & Rahn, 2001; Grine, 2005; Mahoney, 2010, 2013; Fornai et al., 2014). A few general trends can be gleaned about the patterning of enamel thickness within and across the molars of hominoids from these studies. It is well-established that among ~~that~~ extant large-bodied hominoids *Homo* has the thickest-enameled permanent molars, followed by *Pongo*, *Pan*, and finally *Gorilla*[1]. This gradient has led to broad classifications, with *Homo* and *Pongo* being characterized as having “thick” enamel, whereas *Pan* and *Gorilla* have been variably characterized as having “thin” or “intermediate” enamel thickness (Martin, 1985; Shellis et al., 1998).

Macho and Berner (1993) were among the first to quantify the uneven distribution of enamel across the permanent molars of recent humans. Since their study, there has been an emphasis on documenting differences in molar enamel distribution in other hominoids and interpreting these differences within a strict functional framework based on integrating knowledge about the mechanics of the mammalian chewing cycle and molar occlusal anatomy (Kay, 1977; Chivers, Wood, & Bilsborough, 1984; Ross et al., 2009; Ungar, 2017). The

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[1] Note that this pattern is based primarily on two-dimensional tooth sections and that it may slightly differ using three-dimensional values of enamel thickness, especially in *Pongo* and *Pan* (e.g., see Kono, 2004).

mammalian, and thus primate, chewing cycle can be divided into a series of movements, or strokes: the closing, power, and opening strokes. The closing stroke, wherein the mandibular arcade is elevated towards the maxillary arcade, brings opposing teeth into close approximation. ~~The power stroke involves the movement of the mandible such that opposing teeth move into and then back out of centric occlusion.~~ Because the occlusal tables, and thus the main cusps, of opposing molars contact each other during the power stroke, it is not surprising that the nature of the food being reduced, coupled with the precise manner in which molars move into and out of centric occlusion, should be related to the distribution of enamel. Broadly speaking, enamel is expected to be thicker on the “functional” or “supporting” cusps (i.e., protocone and protoconid) than on the “non-functional” or “guiding” cusps (i.e., paracone and metaconid) (Macho & Berner, 1993; Macho & Spears, 1999; Schwartz, 2000a). Studies of the patterning of enamel thickness distribution in hominoid permanent molars have provided mixed support for these functional expectations (Molnar & Gantt, 1977; Grine & Martin, 1988; Conroy, 1991; Macho & Berner, 1993; Schwartz, 2000a; Kono, 2004; Grine, 2005; Skinner et al., 2015). What has become apparent, however, is that the degree of asymmetry in enamel thickness between the lingual and buccal cusps is less pronounced moving~~as we move~~ distally along the permanent molar row, a fact that has been associated with more equivalent masticatory loads exerted over the “functional” and “non-functional” regions in the second and third molars (Spears & Macho, 1995).

Other trends in enamel thickness variation along the permanent molar row have been observed. Using standard measures of the total volume of enamel across a molar crown (the indices of average and relative enamel thickness; Martin, 1985), there is a tendency for enamel thickness to increase from M1 to M3 (Macho & Berner, 1993, 1994; Grine & Martin, 1998;

Shellis et al., 1998; Schwartz, 2000a,b; Grine et al., 2005; Smith et al., 2005, 2006, 2008; Olejniczak et al., 2008a; Feeney et al., 2010). Biomechanical models of mastication suggest that the mandible acts like a third-class lever (Hylander, 1975; Mansour & Reynick, 1975; but see Spencer, 1998, 1999). Following this model, it has been argued that the mandible experiences higher bite forces posteriorly and that these bite forces have selected for thicker enamel on the posterior molars of humans and other hominoids (Molnar & Ward, 1977; Macho & Berner, 1994; Spears & Macho, 1995, 1998; Macho & Spears, 1999). Alternatively, Grine (Grine, 2002, 2005; Grine et al., 2005) has proposed that the distal-ward increase in enamel thickness from M1 to M3 is simply the result of the differential reduction of the dentine crown component in posterior molars (i.e., morphological hypothesis).

In stark contrast to the great deal that has been learned about the evolutionary and functional significance of permanent molar enamel thickness, our understanding of dental tissue proportions and distribution in hominoid deciduous postcanine teeth (referred to herein as deciduous premolars)[2] is comparatively limited. In the past two decades progress has been made in the characterization of dental tissue proportions – the amount of enamel versus the amount of coronal dentine – in recent humans (Aiello et al., 1991; Harris et al., 1999; Gantt et al., 2001; Grine, 2005; Mahoney, 2010, 2013) and fossil hominins (Zilberman et al., 1992; Zanolli et al., 2010; Benazzi et al., 2011a; Fornai et al, 2014). Because these studies focused primarily either on testing functional and morphological hypotheses related to the amount of enamel within molar crowns (Gantt et al., 2001; Grine, 2005; Mahoney, 2010, 2013) or on taxonomic

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[2] Deciduous postcanine teeth are variably referred to as both “deciduous premolars” (dp) and “deciduous molars” (dm). The latter emphasizes the functional and, in the case of the distalmost deciduous tooth, morphological similarity between these teeth and the permanent molars. The former is used here to emphasize the developmental linkage to the permanent premolars, as the permanent premolars are the succedaneous teeth that result from the successional dental lamina extending directly off of the deciduous premolar primordia.

differences between *Homo sapiens* and other hominin species (Zilberman et al., 1992; Bayle, Braga, Mazurier, & Macchiarelli, 2009; Zanolli et al., 2010; Benazzi et al., 2011a,b; Fornai et al, 2014), our knowledge of the functional and/or taxonomic value of deciduous premolar enamel thickness in our closest living relatives – *Pan*, *Gorilla*, and *Pongo* – still has serious deficiencies. What is currently known is based on observations of a single third (dp_3) and fourth (dp_4) mandibular premolar per genus of great apes (Aiello et al., 1991). Although it appears from this study that the trends in enamel thickness observed in permanent molars are also present in the deciduous premolars, it is not entirely clear whether these trends will be observed within larger samples of hominoid deciduous teeth. The lack of research is surprising considering that patterns of deciduous dental wear (relative to that of the permanent molars) represent an important means to infer biological age (e.g., age at death), as well as key aspects of the growth, development, and life history of extinct and extant hominoids (Gustafson, 1950; Miles, 1963, 2001; Wolpoff, 1979; Aiello et al., 1991; Skinner, 1997; Bermúdez de Castro et al., 2003; Trinkaus, 2011; Vieira, Barbosa, Quintão, & Normando, 2015). In particular, the paucity of information on deciduous premolar enamel in apes and early hominins has limited our ability to probe the purported relationship between enamel thickness and rates of wear in the deciduous dentition.

Here, we employ non-destructive microcomputed tomographic techniques to examine enamel thickness and its distribution in 158 deciduous premolars of extant large-bodied hominoids, including specimens representing the genera *Homo*, *Pan*, *Gorilla*, and *Pongo*. Our goals are: 1) to document and compare measures of average and relative enamel within and among humans and great apes; 2) to assess patterns of metameric and inter-arcade variation in enamel thickness within each genus; 3) to characterize the patterning of enamel thickness distribution across the lingual, occlusal, and buccal tooth regions in each genus; and 4) to analyze whether intra- and inter-generic trends of enamel thickness found in great ape and human deciduous premolars follow those identified for permanent molars. By addressing these questions in the largest, taxonomically diverse sample of hominoid deciduous teeth examined to date, this study can serve as a benchmark for understanding deciduous enamel variation within and between members of the hominoid clade and its implications for systematics and dietary functional morphology.

2. Materials and methods

2.1. Sample

Enamel thickness was examined in 80 maxillary (dp^3 and dp^4) and 78 mandibular (dp_3 and dp_4) deciduous third and fourth premolars of *Homo sapiens*, *Pan troglodytes*, *Gorilla* sp., and *Pongo* sp. Sample sizes per premolar type and taxon are provided in Table 1. No intra-individual antimeres were included. We made no attempt to record the sex of the individuals; it should be noted, however, that enamel thickness of deciduous premolars does not appear to differ between males and females (Aiello et al., 1991; Harris et al., 1999; Grine, 2005; but see Gantt et al., 2001).

The *H. sapiens* sample mainly included individuals of African ancestry, followed by a small number of individuals from European ancestry or of unknown geographic provenience. Due to small sample sizes for great apes and, in many cases, the lack of exact provenance, no subspecies delineation was made for *P. troglodytes*, and no species delineation was made for *Gorilla* and *Pongo*. Specific details of the collections used and their institutions are provided in SOM Table S1.

2.2. Methods

We used microcomputed tomography to image dental tissues virtually and create two-dimensional (2D) sections from the three-dimensional (3D) image volumes. Although several studies on permanent teeth have recently documented dental tissue proportions in 3D (e.g., Kono, Suwa, & Tanijiri, 2002; Kono, 2004; Kono & Suwa, 2008; Olejniczak et al., 2008a,c), deciduous tooth enamel is comparatively thinner and more porous, and thus likely to wear at a faster rate not long after reaching functional occlusion (Aiello et al., 1991; Sumikawa, Marshall, Gee, & Marshall, 1999; Gantt et al., 2001). This means that a comprehensive 3D study requiring only unworn or lightly worn specimens would be difficult, if not impossible, to undertake. Individuals from the R.A. Dart Collection were scanned at the University of the Witwatersrand with a Nikon Metrology XTH 225/320 LC industrial CT system using the following parameters: 70kV, 120µA, 1.0 mm aluminum filter, and isometric voxel size of 50-85 microns. Great ape specimens curated at the Museum of Comparative Zoology at Harvard University were imaged with an X-Tek HMXST Micro-CT system (125 kV, 80µA, 1.0 mm aluminum filter, and isometric voxel size of 45-65 microns), whereas those in the Institute of Human Origins at Arizona State University were scanned with a Skyscan 1173 (110 kV, 72µA, 1.0 mm aluminum filter, and an isometric voxel size of 35.8 microns). All other specimens were scanned at the Max Planck Institute for Evolutionary Anthropology with either a BIR ACTIS 225/300 (130 kV, 100 µA, 0.25 mm brass filter) or a Skyscan 1172 (100 kV, 94 µA, 2.0 mm aluminum and copper) scanner at isometric voxel size of 27-70 microns.

Each microCT dataset was filtered using a three-dimensional median and mean-of-least-variance filter and then imported into Amira v6.3 (Mercury Computer Systems) for dental tissue segmentation and enamel-dentine junction (EDJ) and outer enamel surface (OES) surface generation following well-established protocols detailed elsewhere (Skinner et al., 2008; Ortiz, Skinner, Bailey, & Hublin, 2012). The segmentation process was performed by AO. Only teeth with no or minor wear were included (equivalent to Molnar's [1971] first four wear stages). The wear stage associated with each tooth in our study sample is provided in SOM Table S1. Note, however, that assessments of dental wear were based on the entire tooth crown and that observed wear facets and dentine patches do not necessarily occur at the location of the slices used for enamel thickness calculations. Given the difficulty of reconstructing missing enamel in 3D (Skinner et al., 2015), no attempts were made to reconstruct cusp tips at the OES. Dentine horns, on the other hand, are relatively sharper structures that can be more easily and accurately reconstructed in 3D using specialized imaging software. Our sample included therefore specimens with reconstructed dentine horns, when necessary. Reconstructions were performed in Geomagic Wrap (3D Systems Design) by AO prior to making the virtual slices used for calculating dental tissue data. Intra-observer error associated with EDJ reconstruction was calculated in the dp^4 of one *H. sapiens* and one *P. troglodytes*. Error calculation followed Skinner et al. (2015) and was negligible (~1-3%) based on EDJ surface areas retrieved from the different reconstructions. When necessary, cusp tips at the OES where reconstructed in 2D in Adobe® Photoshop® by AO. Error associated with 2D enamel reconstruction was on average 1.7%, tested using an unworn (Molnar's [1971] grade 1) dp^4 of *H. sapiens* cropped virtually at four different heights (SOM Fig. S1).

As per Skinner et al. (2015), each 3D digital model was rotated manually into anatomical position, where we subsequently created a virtual section perpendicular to the occlusal plane through the mesial cusps (Fig. 1a). Specifically, the plane passed through the dentine horns of the protocone and paracone of dp^3s and dp^4s, and through the dentine horns of the protoconid and metaconid of dp_3s and dp_4s, with the exception of great ape dp_3s, which generally possess a main single cusp (protoconid) and require a different slicing protocol. Thus, for great ape dp_3s, we followed Benazzi et al.'s (2014) protocol for premolars with no lingual cusp present whereby sections passed through the protoconid dentine horn and points on the labial and lingual cervical enamel at the widest labiolingual bi-cervical diameter. A scaled 2D image of each cross-section was saved as a TIFF format.

As illustrated in Fig. 1 and described in detail in Table 2, the following variables were calculated in Adobe® Photoshop®: 1) total area of the tooth crown section, 2) area of enamel cap, 3) area of dentine crown, 4) length of the EDJ, and 5) bi-cervical diameter. We used these variables to obtain two widely used indices of enamel thickness (Martin, 1985; Grine & Martin, 1988): average enamel thickness (AET) and relative enamel thickness (RET). AET is defined as the area of enamel cap divided by the length of the EDJ. The index RET is generated by dividing AET by the square root of the dentine crown area (multiplied by 100). RET provides therefore a dimensionless estimate of total enamel volume, allowing comparisons between groups of different tooth and body sizes. To document the patterning of enamel thickness distribution, we calculated the following linear measurements on upper and lower dp4s: lingual cervical wall thickness, mid-occlusal basin thickness, and buccal cervical wall thickness (Schwartz, 2000a). We did not collect these linear measurements on dp3s given that our sample sizes were considerably smaller and that great apes generally possess a single cusp in their dp_3s.

The sectioning process was carried out by AO in Amira v6.3, whereas all measurements were taken by KS-T using Adobe® Photoshop®. To test for error throughout~~of~~ the entire process from slicing to measurement gathering, a randomly selected subsample of eight molars (one dp^3 and one dp^4 per genus) was~~ere~~ reprocessed from start to finish by both authors using a blind study protocol in which any taxonomic and specimen identification was removed. Error in enamel thickness measures between the first and second sessions (separated by ~one month) was on average 3.2%. Significant differences between groups were assessed using Mann-Whitney *U* test and Kruskal-Wallis test with post-hoc pairwise comparisons. All analyses were performed in PAST (Hammer, Harper, & Ryan, 2001) and JMP (SAS Institute).

3. Results

Table 3 provides the descriptive statistics (including the mean, standard deviation, and coefficient of variation) for the different measurements of deciduous premolar enamel thickness for all hominoid taxa. The individual measurements for each of the specimens analyzed are reported in SOM Table S1. Scaled schematic diagrams illustrating differences in dental tissue proportions in maxillary and mandibular deciduous fourth premolars are shown in Figure 2. Figure 3 presents pie charts showing 2D tissue proportions per tooth type and taxon, while boxplots demonstrating intergeneric differences in AET and RET indices are shown in Figure 4. The relative area of enamel per unit crown area is greater in *Homo sapiens* (~26%-34% enamel) than in great apes (~15%-24%), and tissue proportions in *P. troglodytes* and *Pongo* sp. are strikingly similar in all tooth types analyzed (Fig. 3). Mean values for both AET and RET are highest, without exception, in *H. sapiens,* providing clear support for modern humans possessing the thickest postcanine deciduous enamel among extant large-bodied hominoids. AET and RET indices among the great apes are very similar. From thinnest to thickness, the following pattern of AET (by tooth position based on mean values) is observed: dp^3s: *Gorilla* sp. < *P. troglodytes* = *Pongo* sp.; dp^4s: *P. troglodytes* < *Pongo* sp. < *Gorilla* sp.; dp_3s: *P. troglodytes* < *Gorilla* sp. < *Pongo* sp.; and dp_4s: *P. troglodytes* < *Pongo* sp. < *Gorilla* sp. (Table 3, Fig. 4). This pattern appears to be influenced by size, however (Table 3, Figs. 4): When the effects of size are taken into account through calculation of RET, *Gorilla* sp. deciduous premolars are slightly more thinly enameled that those of *P. troglodytes* and *Pongo* sp., whose RET indices are, in turn, more similar to each other. The following pattern for RET is observed among the great apes (based on mean values): *Gorilla* sp. < *Pongo* sp. ≤ *P. troglodytes* for maxillary and mandibular deciduous premolars (Table 2, Fig. 4). *Pongo* sp. exhibits the highest coefficients of variation (CV) for both AET and RET, followed by *Gorilla* sp., *Homo sapiens*, and *Pan troglodytes*. In some cases, CVs for AET and RET of *Pan troglodytes* are considerably smaller than those found for all other groups analyzed (Table 3).

The results of the Kruskal-Wallis test and associated post-hoc pairwise comparisons for AET and RET are presented in SOM Table S2 and Table 4, respectively. All pairwise group differences for AET and RET in dp_3 are non-significant, except for *H. sapiens* vs. *Gorilla* sp. It should be noted, however, that the lack of significance among groups could be at least partially attributed to small sample sizes, as among the four tooth types analyzed, our dp_3 sample is the smallest. As shown in Table 4, differences in AET and RET for dp^3, dp^4, and dp_4 between *H. sapiens* and each of the great apes are, in all cases, significant, except for between *H. sapiens* and *Pongo* sp. dp^3s. Contrary to the results for humans, Kruskal-Wallis post-hoc pairwise comparisons reveal that all differences in enamel thickness among the great apes are non-significant..

Table 3 and Figure 4 also reveal some interesting intra-taxon patterns. On average, within each hominoid group, dp^4s and dp_4s consistently possess greater AET and RET indices than their mesial metameres –dp^3s and dp_3s – respectively. We also note some trends in enamel thickness between maxillary and mandibular antagonistic pairs (i.e., dp^3 vs. dp_3; dp^4 vs. dp_4). In almost all cases, AET and RET means within each taxon are higher in dp^3 and dp^4 relative to their mandibular counterparts, with this trend being more marked in *H. sapiens*, followed by *Pongo* sp. The only two exceptions to this trend occur in *P. troglodytes* (AET means for dp^4 and dp_4 are the same) and in *Gorilla* sp. (enamel is thicker in dp_3 relative to dp^3 based on RET means and similar based on AET).

Finally, we examined the patterning of enamel thickness distribution in each taxon using linear measurements (LCW, MOB, BCW). Consistent with functional expectations for maxillary teeth, linear measurements of dp^4 reveal that enamel is consistently thickest on the lingual region in all groups (Fig. 5). Although the trend is less pronounced in dp_4 than in dp^4 as the difference between BCW and LCW is small, Fig. 5 also shows that the functional cusp of dp_4 (protoconid) tends to have thicker enamel than the non-functional cusp (metaconid). Occlusal enamel thickness of both deciduous premolars (dp^4 and dp_4) consistently provides the smallest values (Fig. 5).

4. Discussion

Extant large-bodied hominoids exhibit the following pattern of permanent molar enamel thickness (from thinnest to thickest): *Gorilla* < *Pan* < *Pongo* < *Homo*, where molars in *Gorilla* and *Pan* are characterized as having “thin” or “intermediate~~average~~” enamel, and *Pongo* and *H. sapiens* are characterized as having “thick” enamel. Aiello et al.’s (1991) preliminary observations, on the other hand, noted a different pattern for the deciduous dentition, wherein enamel thickness did not greatly differ among the great apes. In agreement with Aiello et al. (1991), our results based on a large sample of deciduous premolars – the functional analog of permanent molars – found no significant differences in RET values among living members of the

Pan, *Gorilla*, and *Pongo* clades. Broadly, our results for RET suggest the following trend for deciduous enamel (from thinnest to thickest): *Gorilla* < *Pongo* ≤ *Pan* < *Homo*. Thus, contrary to what is observed in the permanent molars, *Pongo* does not stand out as having more thickly enameled deciduous premolars compared to African apes. *Gorilla* deciduous teeth, however, tend to have slightly thinner (but not significantly different) enamel than those of *Pan* and *Pongo*, and *H. sapiens* possesses significantly thicker enamel in their deciduous dentition compared to *Gorilla, Pan*, and *Pongo*. Differences in 2D tissue proportions (% of enamel and dentine in the tooth crown) between *H. sapiens* and great apes are also evident in all tooth types examined, with enamel comprising ~26%34% of the total crown area in *H. sapiens* and only ~15%-24% in extant large-bodied apes. Interestingly, Olejniczak et al. (2008d) noted clear differences in relative tissue proportions between *H. sapiens* and Neanderthal permanent molars when analyzed in 3D, but not in 2D. In this regard, it remains to be tested whether differences in tissue proportions found in our study hold true when 3D data are considered.

Schwartz (2000a) posited that the range of variation in RET for permanent molars was larger in the so-called thick-enameled hominoids (i.e., *Pongo* and *Homo*) than in *Pan* and *Gorilla*. This was not the case in deciduous teeth. ~~Coefficients of variation (~~CVs~~)~~ for AET and RET were greater in *Pongo* and *Gorilla* ~~and *Pongo*~~ than in *P. troglodytes* and to a lesser extent in *H. sapiens*. Caution is warranted, however, since our *Pongo* and *Gorilla* ~~and *Pongo*~~ samples likely included specimens from more than one species, which could have resulted in a higher CVs relative to our species-level human and chimpanzee samples. Comparative analyses have noted that measures of enamel thickness are generally more variable in deciduous than in permanent molars (Gantt et al., 2001; Grine, 2005). Overall, the levels of intra-generic and intra-tooth variation in enamel thickness found here are similar to, or smaller than, those reported in previous studies of recent human deciduous premolars (Gantt et al., 2001; Grine, 2005). According to Gantt et al. (2001), however, the inclusion of even minimally worn teeth likely artificially increased the range of variation in their reported enamel thickness measurements. Thinly enameled bunodont teeth, such as those analyzed here, wear down quickly, a fact that might have increased some of the CV values in our study.

Although human and great ape deciduous premolars do not appear to follow the same patterns of inter-generic enamel thickness variation than their permanent functional analogs (i.e., the permanent molars), inter-arcade (i.e., antagonistic) and metameric trends appear to be both relatively stable between deciduous and permanent teeth and consistent across hominoids. Studies in recent humans have suggested that maxillary deciduous premolars and permanent molars have thicker enamel than their mandibular counterparts (Gantt, 1986; Gantt et al., 2001). This observation is supported by our study as comparisons between antagonistic pairs (dp^3 vs. dp_3, and dp^4 vs. dp_4) reveal, in most cases, higher AET and RET means in maxillary than in mandibular deciduous teeth, especially in *H. sapiens* and *Pongo* sp. Furthermore, hominoid dental tissue research has provided strong evidence for a posterior increase in enamel thickness along the permanent molar row (Grine & Martin, 1998; Macho and Berner, 1993, 1994; Spears & Macho, 1995; Shellis et al., 1998; Schwartz, 2000b; Grine et al., 2005; Smith et al., 2005, 2006, 2008, 2012a; Olejniczak et al., 2008a; Feeney et al., 2010; Skinner et al., 2015; Pan et al., 2016). Although enamel is considerably thinner on deciduous than on permanent teeth, a distal increase in deciduous premolar enamel thickness has been documented previously in fossil and recent humans (Zilberman et al., 1992; Harris et al., 1999; Grine, 2005; Gantt et al., 2001; Bayle et al., 2009; Zanolli et al., 2010; Mahoney, 2010, 2013; Benazzi et al., 2011a,b). In this regard, our results showing an increase in the amount of enamel from dp3 to dp4 are not only concordant with previous studies of the human deciduous dentition, but also provide empirical support to anecdotal observations for great apes reported by Aiello et al. (1991).

By invoking functional models of masticatory biomechanics, several researchers have argued that anterior-posterior gradients in enamel thickness along the permanent molar row reflect an increase in bite force magnitudes (Molnar & Ward, 1977; Macho & Berner, 1994; Spears & Macho, 1995, 1998; Macho and Spears, 1999). Although functional interpretations of the distal-ward increase in enamel thickness are controversial and clinical data on bite force in children are limited (Spencer, 1998; Grine, 2005; Mahoney, 2010; Mountain, Wood, & Toumba, 2011; Edmonds & Glowacka, 2014), this argument has also been used by Gantt et al. (2001) and Mahoney (2013) to explain the presence of thickest enamel on the more posterior deciduous teeth. As dp4s possess both greater dentine and enamel areas than relatively smaller dp3s, the overall percentage of the tooth crown formed by enamel is ~3-7% greater in dp4 crowns. Grine (2005) and Mahoney (2010) noted that enamel thickness changes along the premolar/molar series are the result of different odontogenic processes operating in deciduous and permanent human molars. They suggest that the quantity of both enamel and dentine increase from dp3 to dp4, whereas increases in RET from M1 to M3 are due to a reduction in dentine in the posterior-most molars. In this vein, our results are consistent with their statement on deciduous premolars.

Overall, differences in the distribution of enamel across the molar crown found here lend support to the hypothesis that “functional” cusps possess thicker enamel than their “non-functional” counterparts to prolong a tooth crown’s functional longevity. Although this hypothesis was first proposed for permanent teeth of humans and other hominoids (Molnar & Gantt, 1977; Macho and Berner, 1993; Macho and Spears, 1999; Schwartz, 2000a; Kono, et al., 2002), enamel thickness differentials between the “functional” and “non-functional” cusps have also been previously found for human deciduous premolars (Gantt et al., 2001; Grine, 2005; but see Mahoney, 2010). In addition, we found that, in all instances, hominoid deciduous premolars possess less enamel across their occlusal basin than on the lingual and buccal regions, with this trend being more marked in our *P. troglodytes* and *H. sapiens* samples. This is not only consistent with regional patterns reported for *H. sapiens* dp^4s (Grine, 2005), but also with Kono and Suwa's (2008) observations on the presence of extremely thin occlusal enamel in the permanent molars of bonobos and common chimpanzees.

For decades, tooth wear has been used as a tool for age determination in archaeological and living human individuals (e.g., Gustafson, 1950; Miles, 1963, 2001; Kim, Kho, & Lee, 2000; Mays, 2002; Vieira et al., 2015). Paleoanthropologists have also used tooth wear (generally in combination with other features such as stages of dental eruption) as a coarse measure of the rate of growth and development of fossil and recent hominoid species, most often to reconstruct key aspects of their life history such as weaning age, interbirth intervals, mortality rates, and lifespan (Wolpoff, 1979; Aiello et al., 1991; Skinner, 1997; Bermúdez de Castro et al., 2003; Caspari & Lee, 2004; Nargolwalla, Begun, Dean, Reid, & Kordos, 2005; Smith, Toussaint, Reid, Olejniczak, & Hublin, 2007; Trinkaus, 2011). Although enamel thickness is a key factor influencing rates and patterns of dental wear (Molnar & Gantt, 1977; Molnar & Ward, 1977; Aiello et al., 1991), it is surprising that estimates of species' life history extrapolating from rates of dental wear do not explicitly take into account the influence of enamel thickness on wear rates (reviewed in Smith, 2013).

Although most life history inferences based on archaeological and fossil dental remains rely on evidence from permanent teeth, Aiello et al. (1991) noted the potential importance of deciduous teeth for inferring two key aspects of hominoids' life history: age at weaning and interbirth intervals. Acknowledging that their conclusions were preliminary given both their small samples and unknown age at death of the specimens used, Aiello et al. (1991) proposed that the pattern and magnitude of wear (attrition) found among hominoid deciduous teeth were suggestive of an earlier weaning and shorter interbirth interval in gorillas than in chimpanzees and orangutans. In this vein, the data presented here can be used to test the observed preliminary pattern in a more comprehensive manner. While there is now clearer evidence that weaning in apes is a complex and long process (Pusey, 1983; Smith, 2013; Smith et al., 2013; Smith, Austin, Hinde, Vogel, & Arora, 2017; Joannes-Boyau et al., 2019~~8~~) and that recent minimally invasive state-of-the-art research offers a new exciting glimpse into weaning age in our hominin ancestors (Joannes-Boyau et al., 2019~~8~~), we believe that exploring this life history trait using complementary lines of evidence, including the non-destructive approach of dental wear, is warranted considering that nursing behavior among apes is difficult to infer and systematically investigate both in the wild and in the fossil record.

Finally, although testing Aiello et al.'s (1991) hypothesis of age at weaning in gorillas is beyond the scope of the present study, our results support the argument that the greater degrees of dental wear on gorilla deciduous teeth relative to those of chimpanzees and orangutans cannot be attributed to differences in enamel thickness. That is, we found no significant differences in relative and average enamel thickness among the great apes, meaning that the enamel on the deciduous postcanine dentition of *Gorilla* is not significantly thinner than in *Pan* and *Pongo*. One additional conclusion derived from this study is that *Pongo* does not possess thicker-enameled deciduous premolars than African great apes. Patterns of food consumption during the early life of great ape individuals are complex and slight differences have been noted among populations and species, but in a very general sense, infants from both *Pan* and *Pongo* start eating solid food by 0.5-1 years of age, which then constitutes an appreciable component of their diet by the time they reach about 1-2 years of age (Smith et al., 2013, 2017). It is known, however, that orangutans experience longer and sometimes cyclical periods of offspring dependence and later weaning ages relative to other apes (Pusey, 1983; van Noordwijk, Willems, Utami Atmoko, Kuzawa, & van Schaik, 2013; Smith et al., 2017). Thus, from the functional perspective, investment in postcanine deciduous teeth with thicker enamel in orangutans would be unexpected considering 1) that orangutans have the most prolonged nursing period than any other apes, 2) that milk consumption is considerably less challenging for the masticatory apparatus than solid food, and 3) that deciduous premolars among great apes remain in functional occlusion for roughly the same amount of time (based on estimates of the timing of dp3-4 and P3-4 emergence; see Smith, Crummett, & Brandt, 1994). Further research is needed to better understand the evolutionary, functional, and developmental implications of the patterns of enamel thickness variation in hominoid deciduous teeth, and our study represents an important first step in this direction by providing the comparative context within which to interpret deciduous tooth wear and its usefulness for inferring age at weaning in great apes and fossil hominins.

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Figure legends

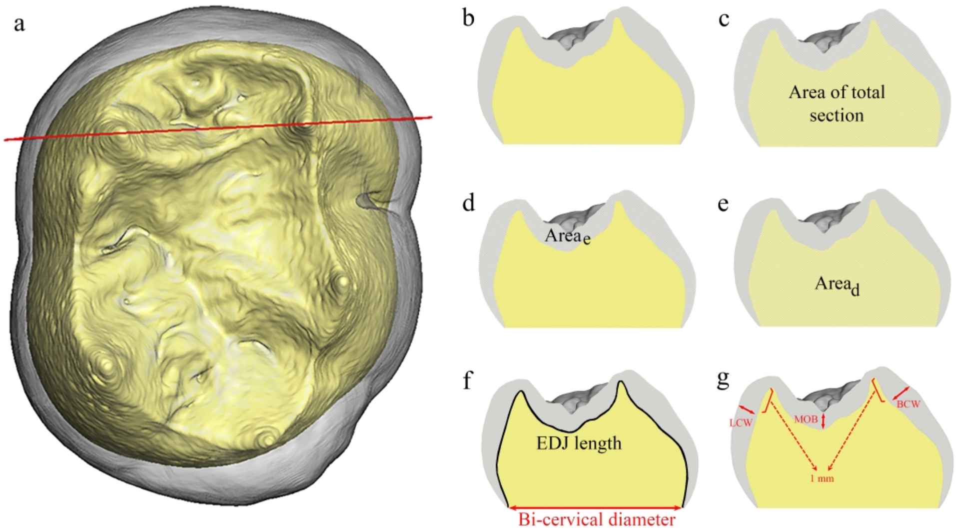
Fig 1. Protocol used to collect enamel thickness data. (a) occlusal view of a three-dimensional model of a tooth with dentine in yellow and enamel rendered transparent. The red line indicates the plane of section, passing through the dentine horns of the two mesial cusps. (b) two-dimensional image of a cross-section from which enamel thickness measurements were collected. (c) area of total section (dashed lines). (d) area of enamel cap (dashed lines). (e) area of dentine crown (dashed lines). (f) length of enamel-dentine junction (black line) and bi-cervical diameter (red arrow). (g) length of lingual cervical wall, mid-occlusal basin, and buccal cervical wall (red arrows). Right dp_4 of *H. sapiens* depicted. Not to scale.

Fig 2. Cross sections through the mesial cusps of (a) dp^4 and (b) dp_4 with examples of dental tissue proportions in humans and great apes. Right premolars depicted.

Fig. 3. Pie charts showing 2D dental tissue proportions for (a) *H. sapiens*, (b) *P. troglodytes*, (c) *Gorilla* sp., (d) *Pongo* sp. Dentine in dark gray. Enamel in light gray.

Fig 4. Box plots of (a-b) average enamel thickness (AET), and (c-d) relative enamel thickness (RET) for upper and lower deciduous premolars per taxon.

Fig. 5. Patterning of enamel thickness distribution using LCW, MOB, and BCW linear measurements for (a) dp^4 and (b) dp_4. See Table 2 for abbreviations.



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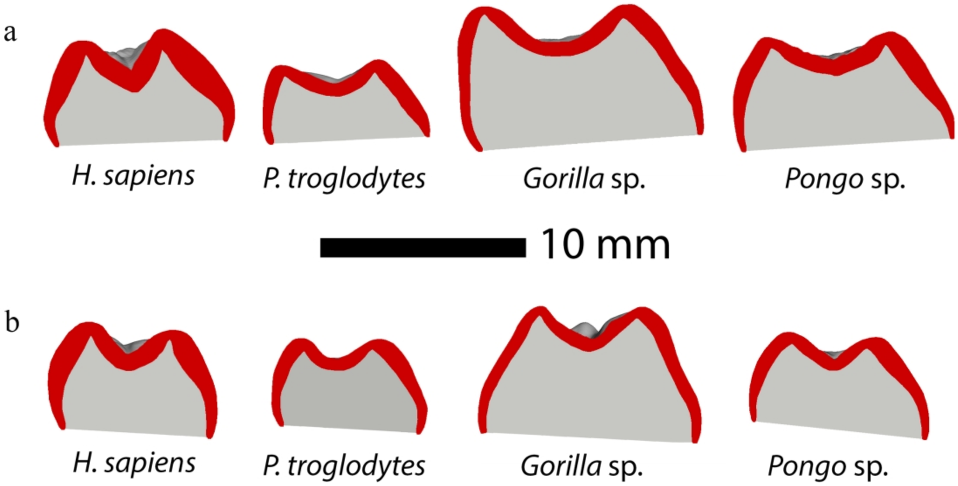

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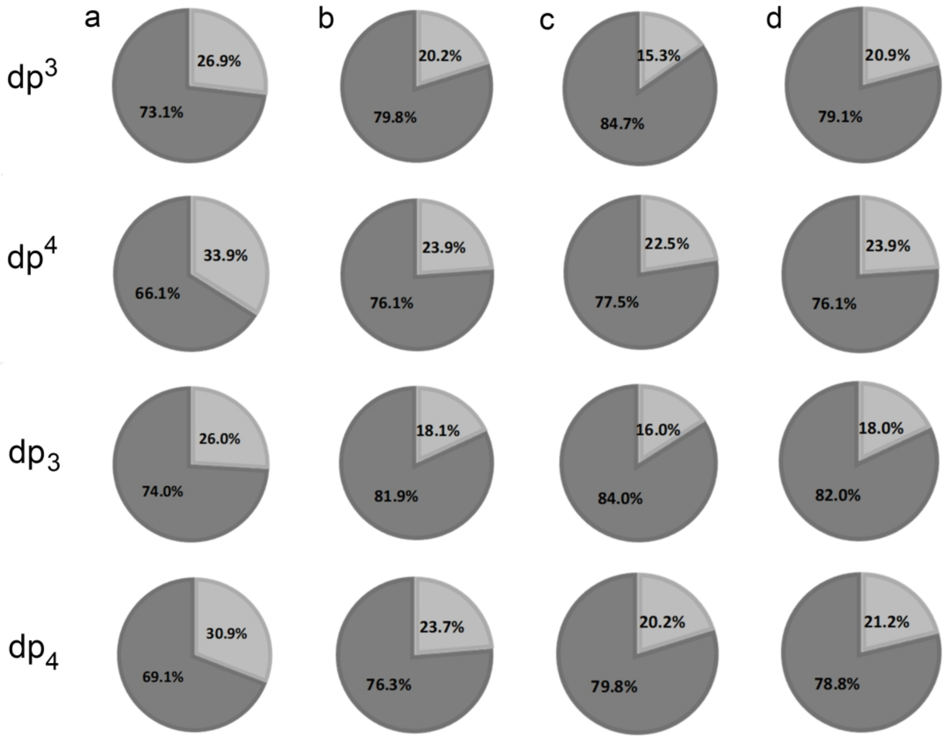

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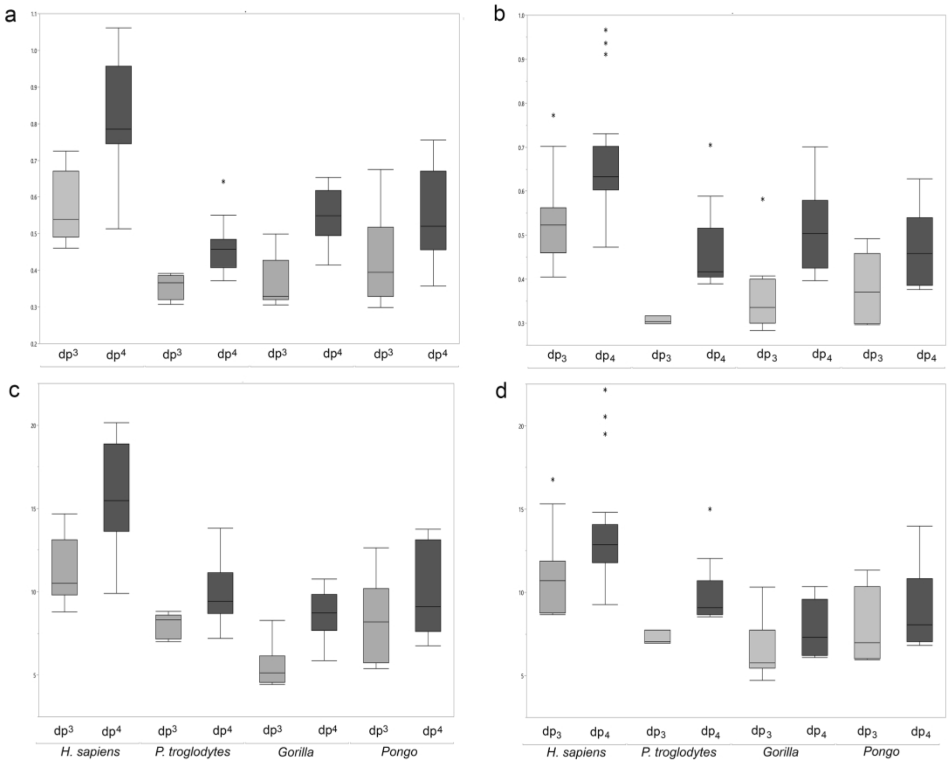

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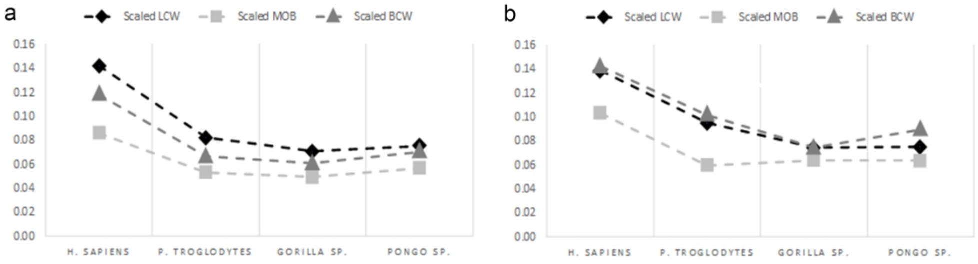

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Table 1. Sample composition by taxon and tooth type.

Taxon	dp^3	dp^4	dp_3	dp_4
H. sapiens	13	12	12	24
P. troglodytes	9	15	3	9
Gorilla sp.	6	11	8	11
Pongo sp.	6	8	5	6

Table 2. Variables used for analysis of enamel thickness variation and distribution.

Measurement	Description
Total section	Area of total section (in mm^2), including area of enamel cap and area of dentine crown
$Area_e$	Area of enamel cap (in mm^2), including lingual, occlusal, and buccal enamel
$Area_d$	Area of dentine crown (in mm^2): area of coronal dentine between the EDJ and a straight line along the lingual and buccal cervical margins
EDJ	Length of the enamel-dentine junction (in mm)
BCD	Bi-cervical diameter (in mm): linear distance between the lingual and buccal cervical margins
AET	Average enamel thickness (in mm): area of enamel cap divided by the length of the EDJ
RET	AET divided by the square root of the dentine crown area and multiplied by 100
LCW	Lingual cervical wall (in mm): linear thickness of enamel along the lingual wall of the protocone (dp^3 and dp^4) or metaconid (dp_3 and dp_4), 1mm from dentine horn
MOB	Midocclusal basin (in mm): linear thickness of enamel in the most inferior portion of the occlusal basin
BCW	Buccal cervical wall (in mm): linear thickness of enamel along the buccal wall of the paracone (dp^3 and dp^4) or protoconid (dp_3 and dp_4), 1mm from dentine horn

Table 3. Mean, standard deviation, and coefficient of variation for the different measures of enamel thickness in hominoid deciduous premolars.

Taxon	Tooth	n	Total section		$Area_e$		$Area_d$		BCD		EDJ		AET			RET		
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	CV	mean	SD	CV
H. sapiens	dp^3	13	35.30	4.03	9.48	1.52	25.82	3.28	7.71	0.26	16.62	1.11	0.57	0.09	0.16	11.31	2.00	0.18
	dp^4	12	41.56	4.19	14.12	2.42	27.44	3.00	8.72	0.46	17.23	1.41	0.82	0.15	0.18	15.81	3.14	0.20
	dp_3	12	32.05	2.90	8.30	1.39	23.75	2.75	6.18	0.41	15.54	0.96	0.54	0.11	0.2	11.12	2.59	0.23
	dp_4	24	36.41	4.88	11.21	1.76	25.20	4.00	7.04	0.44	16.88	1.61	0.67	0.12	0.18	13.50	3.12	0.23
P. troglodytes	dp^3	9	24.72	1.56	4.99	0.45	19.74	1.25	6.39	0.41	14.01	0.45	0.36	0.03	0.08	8.02	0.71	0.09
	dp^4	15	28.87	4.65	6.81	1.09	22.06	4.17	8.10	0.51	14.77	1.32	0.46	0.07	0.15	9.98	1.90	0.19
	dp_3	3	21.98	2.78	3.97	0.40	18.01	2.39	4.80	0.44	12.94	1.03	0.31	0.01	0.03	7.25	0.43	0.06
	dp_4	9	28.68	2.79	6.83	1.45	21.85	1.75	6.43	0.51	14.76	0.78	0.46	0.11	0.24	9.93	2.18	0.22
Gorilla sp.	dp^3	6	53.11	7.43	8.08	1.46	45.03	6.94	9.95	0.85	22.28	2.17	0.37	0.07	0.19	5.51	1.41	0.26
	dp^4	11	54.03	11.91	11.97	2.18	42.06	10.48	10.84	1.12	21.89	2.38	0.55	0.08	0.15	8.59	1.53	0.18
	dp_3	8	37.89	4.65	6.05	1.51	31.84	4.32	7.26	0.95	16.55	1.13	0.37	0.10	0.27	6.56	1.83	0.28
	dp_4	11	54.60	8.32	10.92	1.88	43.68	7.71	9.14	0.98	20.99	1.98	0.52	0.09	0.17	8.02	1.74	0.22
Pongo sp.	dp^3	6	35.03	6.55	7.24	2.13	27.79	5.82	8.82	0.36	17.08	1.93	0.43	0.13	0.30	8.27	2.72	0.33
	dp^4	8	39.69	5.94	9.47	2.12	30.22	5.14	9.90	0.89	17.44	1.72	0.55	0.13	0.24	10.06	2.72	0.27
	dp_3	5	28.40	3.51	5.04	0.77	23.36	3.70	6.62	0.32	13.54	1.28	0.38	0.08	0.21	7.95	2.34	0.29
	dp_4	6	36.40	5.10	7.57	0.93	28.83	5.13	8.05	0.35	16.30	1.77	0.47	0.09	0.19	8.98	2.67	0.30

Abbreviations: SD: standard deviation; CV: coefficient of variation. CV presented only for AET and RET

Table 4. Kruskal-Wallis test with postdoc pairwise comparisons of enamel thickness indices (AET bottom/RET top). Significant *p*-values bolded.

dp^3	*H. sapiens*	*P. troglodytes*	*Gorilla* sp.	*Pongo* sp.
H. sapiens	-	**<0.001**	**<0.01**	N.S.
P. troglodytes	**<0.001**	-	N.S.	N.S.
Gorilla sp.	**<0.05**	N.S.	-	N.S.
Pongo sp.	N.S.	N.S.	N.S.	-
dp^4	*H. sapiens*	*P. troglodytes*	*Gorilla* sp.	*Pongo* sp.
H. sapiens	-	**<0.001**	**<0.001**	**<0.01**
P. troglodytes	**<0.001**	-	N.S.	N.S.
Gorilla sp.	**<0.01**	N.S.	-	N.S.
Pongo sp.	**<0.01**	N.S.	N.S.	-
dp_3	*H. sapiens*	*P. troglodytes*	*Gorilla* sp.	*Pongo* sp.
H. sapiens	-	N.S.	**<0.01**	N.S.
P. troglodytes	N.S.	-	N.S.	N.S.
Gorilla sp.	**<0.05**	N.S.	-	N.S.
Pongo sp.	N.S.	N.S.	N.S.	-
dp_4	*H. sapiens*	*P. troglodytes*	*Gorilla* sp.	*Pongo* sp.
H. sapiens	-	**<0.05**	**<0.001**	**<0.05**
P. troglodytes	**<0.01**	-	N.S.	N.S.
Gorilla sp.	**<0.01**	N.S.	-	N.S.
Pongo sp.	**<0.05**	N.S.	N.S.	-

N.S.: non-significant