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Maxillary molar enamel thickness of Plio-Pleistocene hominins

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Abstract. Enamel thickness remains an important morphological character in hominin systematics and is regularly incorporated into dietary reconstructions in hominin species. We expand on a previous study of enamel thickness in mandibular molars by examining a large maxillary molar sample of Plio-Pleistocene hominins (n=62), and a comparative sample of extant non-human apes (n=48) and modern humans (n=29). 2D mesial planes of section were generated through microtomography and standard dental tissue variables were measured to calculate average (AET) and relative (RET) enamel thickness. AET was also examined across the lingual, occlusal and buccal regions of the crown. This study confirms previous findings of increasing enamel thickness throughout the Plio-Pleistocene, being thinnest in *Australopithecus anamensis* and peaking in *Australopithecus boisei*, with early *Homo* specimens exhibiting intermediate enamel thickness. Agreeing with previous findings, 2D plane of section enamel thickness is found to be a poor taxonomic discriminator, with no statistically significant differences observed between fossil hominins. For fossil hominins, modern humans, and *Pongo* the occlusal region of enamel was the thickest, and lingual enamel thickness was greater than buccal. *Pan* and *Gorilla* present the opposite pattern with enamel being thinnest occlusally. Comparison at each molar position between the maxilla and mandible revealed very few significant differences in fossil hominins but some evidence of significantly thicker maxillary enamel (AET) in modern humans and thinner maxillary enamel in *Pan* (RET).

1. Introduction

The thickness and distribution of enamel tissue across tooth crowns are important features in assessing taxonomy, phylogeny, and dietary adaptations in fossil primates. Over three decades of research has elucidated patterns of enamel thickness variation in fossil hominins, and fossil and extant hominoids (Molnar and Gantt, 1977; Martin, 1985; Beynon and Wood, 1986; Gantt, 1986; Shellis et al., 1998; Schwartz, 2000; Kono, 2004; Smith et al., 2003, 2005, 2006a; Kono and Suwa, 2008; Olejniczak et al., 2008b, c, d). Whereas naturally broken teeth or histological thin-sections have been used in many of these studies, researchers have increasingly utilized microtomography to systematically produce homologous mesial planes of section in molars (Conroy, 1991; Grine, 1991; Macho and Thackeray, 1992; Spoor et al., 1993; Schwartz et al., 1998; Martin et al., 2003; Tafforeau, 2004; Olejniczak and Grine, 2006;

Olejniczak et al., 2008a; Smith et al., 2009a, b; 2012a, b, c), leading to more comprehensive taxonomic comparisons (see review in Smith et al., 2012a and Skinner et al., 2015).

This paper is a sequel to a previous study (Skinner et al., 2015) that investigated 2D average enamel thickness (AET) and relative enamel thickness (RET) in mandibular molars of Plio-Pleistocene hominins and extant apes using established protocols (Martin, 1985; Olejniczak et al., 2008a). Skinner et al. (2015) focused on temporal trends, metameric variation, the regional distribution of enamel across the mesial crown, and investigated the utility of 2D enamel thickness data as a taxonomic indicator. Results indicated: 1) a trend in increase in enamel thickness from 4 - 2 million years ago, from *Australopithecus anamensis* to *A. boisei*; 2) a tendency for enamel thickness to increase along the tooth row from first to third molar; and 3) a trend for decreasing enamel thickness through time within the genus *Homo*. Furthermore, there were clear differences in enamel thickness between extant apes and hominins, but few significant differences within the hominin clade. Finally, the regional distribution of enamel across the tooth crown for the majority of extant apes and hominins was characterized by thick occlusal enamel, less thick buccal enamel and least thick lingual enamel; exceptions to this being *Gorilla* (with thicker buccal than occlusal enamel) and *Pan* (with thinnest occlusal enamel).

In this study we extend our analysis of enamel thickness to maxillary molars to: 1) quantify 2D AET and RET in extant apes and Plio-Pleistocene hominin maxillary molars; 2) assess regional distribution of enamel buccolingually across the tooth crown; 3) evaluate whether mandibular and maxillary molars exhibit similar enamel thickness characteristics; and 4) provide individual enamel thickness measurements for extant apes and fossil hominins for use by other researchers.

2. Materials and methods

The study sample includes maxillary molars (n= 139) belonging to extant hominoids and fossil hominins (Supplementary Online Material (SOM) Table S1 contains a complete list of all specimens and includes information about the basis for molar position and taxonomic affiliation). Specimens which did not preserve an intact mesial crown, exhibited pathologies of enamel growth, or had insufficient radiographic contrast between enamel and dentine were excluded. Specimens displaying wear that exposed large areas of dentine were excluded from the study. Owing to the widely accepted difficulty of assigning sex to many fossil hominin teeth, sex was not incorporated as a factor for this study. Extant hominoid taxa include *Homo sapiens*, *Pongo*, *Gorilla*, and *Pan* (note: due to the small sample sizes for some molar positions, no sub-generic division was made for non-human ape samples although individual data for *Pan paniscus* and *Pan troglodytes* are listed in SOM Table S1). The fossil hominin sample includes *A. anamensis*, *A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, and *Homo* sp.

Fossil hominin specimens derive from collections housed at the following institutions: National Museum of Ethiopia, Addis Ababa, Ethiopia; National Museums of Kenya, Nairobi, Kenya; University of Witwatersrand, Johannesburg, South Africa; Ditsong National Museum of Natural History, Pretoria, South Africa. The hominoid samples derive from the Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science (ZMB), Berlin, Germany; the Royal Museum for Central Africa (MRAC), Tervuren, Belgium; and the Max Planck Institute for Evolutionary Anthropology (MPI), Leipzig, Germany. The modern human sample derives from the 'Francisc J. Rainer' Anthropology Institute (R), Bucharest, Romania; and the Max Planck Institute for Evolutionary Anthropology (M), Leipzig, Germany.

All enamel thickness measurements were collected from a µCT derived 2D mesial plane of section. Specimens were scanned using either a BIR Actis 300/225 FP or SkyScan 1172 microtomographic scanner with a resultant isometric voxel size of 15-65 mm^3. To produce the plane of section each molar was first loaded into Avizo (v6.3, www.thermofisher.com) and visually rotated into anatomical position. This rotation was conducted in Avizo using the trackball in the transform editor module and viewing the molar simultaneously in three views. The aim of this rotation is to achieve an orientation that approximates the orientation of the molar in occlusion with regard to tilting in mesiodistal and buccolingual directions. First, a virtual 2D plane was placed perpendicular to the occlusal plane and passing through the tip of the protocone dentine horn. This plane was then rotated to pass through the paracone dentine horn. In cases where enamel was missing, reconstructions were done using segmentation tools in Avizo to augment sample size of unworn fossil teeth for most hominin species (note: our reconstruction of relevant teeth can be evaluated in the images in the SOM). Intraobserver error was evaluated by having one of us (A.L.) repeat the processing sequence for an *A. africanus* specimen five times over several months and was calculated as the average deviation from the mean of five measurements. Values of 2.03% for AET and 1.38% for RET are consistent with error rates reported in Skinner et al. (2015).

On each 2D section four variables were measured including: area of enamel cap (mm^2); area of coronal dentine (mm^2), defined by a line drawn between the most cervical enamel extensions; and length of the enamel-dentine junction (EDJ) (mm). The mesial crown section was divided into lingual, occlusal and buccal regions by connecting the tip of each dentine horn to the cusp tip of the outer enamel surface. All measurements were calculated in ImageJ. AET was calculated by dividing the area of the enamel cap by EDJ length. RET, which provides a scale free value of enamel thickness, allowing for comparisons of taxa of differing tooth and body size, was calculated as AET divided by the square root of dentine area and multiplied by 100. For regional AET values, the area for each region was divided by its corresponding EDJ length. A Kruskal-Wallis test with post-hoc pairwise comparisons was used to test for significance in AET and RET differences between taxa using SPSS 22. The same test was also used to test for significance in intra-taxon differences in AET and RET and between mandibular and maxillary molars of extant apes, *A. africanus* and *A. robustus* --taxa for which the sample size is relatively large.

3. Results

Table 1 presents the mean and standard deviation of measured and calculated variables for each taxon and for each tooth type. Both AET and RET were significantly different (p=<0.001) among the study taxa, with post-hoc pairwise comparisons revealing that this is predominantly driven by differences between thinly enamelled extant non-human ape taxa (i.e., *Gorilla* and *Pan*) and more thickly enamelled hominin taxa (Table 2). No differences were found among extant non-human apes, while modern humans differed in AET from *A. robustus* (M^1, p=0.009; M^2, p = 0.024), *A. boisei* (M^1, p=0.009; M^3, p=0.019), *A. africanus* (M^3, p=0.045), and in RET from *A. robustus* (M^1, p=0.041) and *A. boisei* (M^1,p=0.035). It should be stressed that very small sample sizes for many hominins at multiple tooth positions prevent meaningful statistical assessment of AET and RET differences.

Figure. 1 displays boxplots of AET and RET results for each taxon and tooth type. A general trend is observed from *A. anamensis* to *A. boisei* with increasing AET enamel thickness throughout the Pliocene from ~4 - 2 million years ago. This pattern is similar for RET with the exception of *A. afarensis* third molars that are similar to those of *A. boisei*. The *Homo* sp. sample exhibits AET and RET similar to *A. robustus*. AET for modern humans tends to fall below other hominins and above non-human apes, while RET values are similar to *A. africanus* and *A. robustus*. *Pan* exhibits the lowest AET values, however, when scaled by dentine area *Pan* has relatively thicker enamel than *Gorilla* (with *Pongo* exhibiting the highest AET and RET values for extant non-human apes). Regarding metameric variation, there is a trend for increasing AET and RET from first to third molars with the exceptions of *A. robustus*, where the second molar AET and RET values are highest, and *Gorilla*, where first molar AET and RET values are higher than in the second molar.

Table 3 lists the mean and standard deviation of the lingual, occlusal and buccal regional measurements for AET for each taxon. Figure 2 shows that fossil hominins, modern humans and *Pongo* have thickest enamel in the occlusal basin as is the case for mandibular molars (Skinner et al., 2015). Contrasting with regional patterning across the mandibular molars, the lingual rather than buccal side of the crown has the thickest enamel in maxillary molars for most taxa. *Pan* and *Gorilla* have the thinnest enamel in the occlusal region.

Using data from Skinner et al. (2015), Figure 3 compares AET and RET between mandibular and maxillary molars for *A. africanus*, *A. robustus*, *H. sapiens*, *Gorilla*, *Pan*, and *Pongo*. Acknowledging that there are issues of statistical independence (as some individuals contribute both maxillary and mandibular molars; see SOM Table S1), pairwise comparisons reveal evidence for significantly thicker maxillary molar enamel in *Homo sapiens* (AET M2 [p=0.005] and M3 [p=0.034] and RET M2 [p=0.037]). This is different than the apparent trend in the other study taxa, most of which indicate the opposite pattern or a large degree of overlap between maxillary and mandibular molars (Table 4). Significantly thicker mandibular than maxillary RET are present in *A. robustus* (M3 [p=0.028]) and *Pan* (M1 [p=0.008] and M2 [p=0.054]).

4. Discussion

Maxillary molar enamel thickness trends are similar to those for mandibular molars with an increase from *A. anamensis to A. boisei*, and with early *Homo* specimens exhibiting relatively thick enamel similar to that in *A. africanus* and *A. robustus*. As noted in Skinner et al. (2015) this is consistent with isotopic evidence for an increase in C4 consumption in australopiths (Cerling et al., 2013; Sponheimer et al., 2013; Wynn et al., 2013; Alemseged, 2015; Levin et al., 2015). In this study, no statistically significant differences in enamel thickness were observed between the Plio-Pleistocene taxa we considered. This could be attributable to small sample sizes in a number of species and molar positions, but also related to the high levels of variation at each molar type compared to extant taxa (Fig. 1). This variation can in turn be explained by a number of factors including spatiotemporal variation, the possibility that some of our taxa (e.g., *Homo* sp.) sample multiple species, and the potential influence of molar crown shape/cusp positioning variation and its impact on resultant 2D planes of section. Additionally, sexual dimorphism, which can affect dental tissue proportions (Saunders et al., 2007), cannot be taken into account due to the difficulty in assigning sex to most hominin specimens. Nonetheless, our results are consistent with other large scale analyses of hominin enamel thickness (Olejniczak 2008 a,c; Smith et al., 2012a,b; Skinner et al., 2015) and suggest that while 2D enamel thickness by itself will be of limited taxonomic value at the species level, it can be used as one line of evidence in conjunction with data sources when examining taxonomic hypotheses. The data we provide in the SOM will be of utility in this respect.

In the majority of taxa there is a consistent trend for an increase in AET from the first to the third molar. This pattern may be related to increasing bite force mesiodistally along the tooth row (Macho and Berner, 1993; Schwartz, 2000), in conjunction with other morphological features such as zygomatic orientation, and mandibular size and shape and moralised premolars (Tobias, 1967; Rak 1983; Teaford and Ungar, 2000; Lucas, 2004; Smith et al., 2015). It has been proposed that changing trends in hominin enamel thickness, as reported here, could be an adaptation to resist an increasingly hard diet (Cerling et al., 2011; Rabenold and Pearson, 2011; Lucas et al., 2013) associated with masticatory stresses which lead to longitudinal fractures and tooth failure (Laden and Wrangham, 2005; Lucas et al., 2008; Smith et al., 2012b; Barani et al., 2011; Mahoney, 2013; Benazzi et al., 2013; Strait et al., 2013; Laird et al., 2016); culminating in *A. boisei* (Smith et al., 2015).

However, these stresses are not always directly correlated with diet (Schwartz, 2000; Martin, 2003; Lucas et al., 2013), and become more difficult to assess when there is evidence for food processing with tool use (Ungar, 1994; Fragaszy et al., 2004; Constantino et al., 2011; Zink et al., 2014; Harmand et al, et al, 2015). The heavy tooth wear observed in hominins (d'Incau et al., 2012; Lucas et al., 2013), suggests most species consumed abrasive diets throughout hominin evolution (Lucas et al., 1985; Vogel et al., 2008; Cerling et al., 2011; Rabenold and Pearson, 2011; Strait et al., 2013; Levin et al., 2015; Ungar et al., 2016) and increasing enamel thickness along the tooth row may have maintained masticatory function throughout life (King et al., 2005; Constantino et al., 2009, 2011; Lucas et al., 2013; Glowacka et al., 2016).

Our analysis of the regional distribution of enamel thickness across the crown is consistent with a previous study in non-human apes and humans (Kono, 2004) and with Skinner et al. (2015). Whereas mandibular molars tend to have relatively thicker enamel buccally, maxillary molars tend to have thicker enamel lingually. This is consistent with expectations of both load and attrition experienced by the 'functional' cusps in each jaw as they occlude (Schwartz, 2000; Benazzi et al., 2013). The relatively thick enamel of *Pongo* (compared to hominins and *Pan/Gorilla*) combined with a similar hominin-like pattern of enamel distribution across the tooth crown may indicate similar adaptations to hard or abrasive diets in *Pongo* (Kay, 1985; Martin et al., 2003; Smith et al., 2003; Taylor, 2006; Suwa et al., 2007; Olejniczak et al., 2008d). While this result for *Pongo* is consistent with the mandibular molar data (albeit with roughly equal buccal and lingual thickness), the results for *Gorilla* differ in showing relatively uniform distribution across the maxillary crown versus a much thicker buccal side in mandibular molars (but the sample size for *Gorilla* mandibular first molars was only two given difficulties in finding museum specimens with minimal first molar wear). Statistical comparisons of AET and RET at each molar position in the maxilla and mandible indicate general similarity in absolute and relative enamel thickness for most of the study taxa, however there are some exceptions. AET tends to overlap between maxillary and mandibular molars at each molar position in all taxa except modern humans. Specifically, AET in human maxillary molars tends to be thicker than their mandibular counterparts (reaching statistical significance in second and third molars). Examination of the crowns of the maxillary molar sample reveals a number of specimens with large

Carabelli's features, and this may contribute to this finding given that data is collected on a 2D plane of section that passes through this region of the crown. Figure 3b suggests a pattern of RET in which mandibular molars tend to have thicker enamel when scaled for dentine area in most of the study taxa (reaching statistical significance in some molar positions for *A. robustus* and *Pan*). However, as with AET modern humans are exceptional in have greater RET in maxillary molars at each position (being statistically significant at M2). There is some evidence that this pattern holds for Neanderthals (Olejniczak et al., 2008) and future studies of *Homo* specimens between 2.5 million years and 0.5 million years may highlight when this departure from the earlier hominin/non-human ape pattern first appeared.

An important caveat with regard to this comparison between maxillary and mandibular molars is the 2D nature of the data. Kono (2004) showed that 2D AET values are not an accurate estimator for whole crown AET in extant apes and humans. Olejniczak and colleagues (2008) demonstrated that 2D and 3D measures of enamel thickness can yield different results, with only 3D data highlighting a difference in dentine crown size (and associated measures of RET) between Neanderthals and modern humans. Such disparities will likely be increased in taxa, such as modern humans, that can exhibit marked reductions in the size and height cusps on the distal half of the tooth moving from first to third molars. Similarly, hominin taxa with a tendency towards mesiodistally expanded mandibular third molars, such as *A. robustus*, are likely to present different estimates of AET and RET between 2D and 3D data. While 3D distribution maps of enamel thickness are more frequently being included in studies of endostructural tooth crown morphology, effective means of statistically quantifying and comparing such distributions remain elusive (acknowledging also the difficulties in reconstructing partially worn crowns in 3D). However, a recent analytical approach (Zanolli et al., 2016) that combines Procrustes superimposition for consistent alignment and a projection of 3D of enamel distribution onto a 2D plane for statistical comparison could provide a means to leverage the taxonomic and functional morphological relevance of the enamel cap.

In conclusion, this study of maxillary molar 2D enamel thickness fills an important gap in published data about Plio-Pleistocene hominin teeth. It confirms recognized trends of enamel thickness differences through time in the hominin clade, the marked difference between hominins and non-human apes, and the derived nature of modern human enamel thickness. Measures of 2D enamel thickness remain an important, if somewhat simple, characteristic of hominin tooth morphology and the data we provide will be useful for alpha taxonomy of fragmentary/poorly preserved hominin teeth.

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Figure Captions

Figure 1. Box plots of average enamel thickness (left) and relative enamel thickness (right) for first, second and third maxillary molars for each taxon. There is a trend for increasing AET and RET through time in *Australopithecus*, *Homo* species exhibiting intermediate values and African apes having both absolutely and relatively thin enamel.

Figure 2. Patterns of regional average enamel thickness for the combined molar sample of each taxon. Fossil hominins, humans, and *Pongo* tend to exhibit the thickest enamel in the occlusal basin, while *Gorilla* and *Pan* exhibit the thickest enamel on the lingual tooth crown.

Figure 3. Boxplots of average enamel thickness (A) and relative enamel thickness (B) between maxillary and mandibular first, second, and third molars. Humans are unique in a tendency towards absolutely and relatively thicker maxillary than mandibular molars.

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Table 1. Composition of the study sample and mean and standard deviation (SD) of measured and calculated variables for each taxon and tooth position.

Taxon	*n*	Enamel Area (mm2)	SD	Dentine Area (mm2)	SD	EDJ[a] Length (mm)	SD	AET (mm)	SD	RET	SD	BCD (mm)	SD
First molar													
A. anamensis	0	-	-	-	-	-	-	-	-	-	-	-	-
A. afarensis	0	-	-	-	-	-	-	-	-	-	-	-	-
A. africanus	5	30.9	1.7	52.0	8.9	23.2	1.3	1.3	0.1	18.7	2.1	12.5	1.3
A. robustus	6	41.3	7.8	56.2	10.2	23.6	2.3	1.8	0.2	23.4	2.8	11.9	1.6
A. boisei	3	46.9	9.3	57.6	9.3	22.0	1.3	2.1	0.4	28.3	6.5	14.1	0.7
Homo sp.	4	36.2	5.0	46.4	7.5	21.7	1.5	1.7	0.3	25.0	5.5	12.4	0.5
Homo sapiens	10	23.2	2.4	41.1	2.3	20.7	1.3	1.1	0.1	17.7	1.6	10.6	0.6
Gorilla	2	27.3	3.3	81.2	4.3	29.9	0.7	0.9	0.1	10.1	1.2	13.6	0.6
Pan	8	13.0	2.0	36.1	4.9	19.7	1.3	0.7	0.1	11.0	0.9	9.6	0.8
Pongo	4	18.5	3.9	37.2	8.4	19.8	1.4	0.9	0.2	15.2	1.3	10.2	1.2
Second molar													
A. anamensis	2	24.5	1.1	42.5	8.6	20.3	1.7	1.2	0.0	18.8	2.6	14.0	0.5
A. afarensis	1	30.7	-	42.7	-	19.8	-	1.6	-	23.7	-	14.2	-
A. africanus	9	40.1	4.4	56.2	8.7	23.3	1.7	1.7	0.3	23.3	4.0	15.2	1.3
A. robustus	6	49.8	6.6	60.6	4.9	23.3	0.9	2.1	0.3	27.5	3.5	14.6	1.2
A. boisei	1	47.5	-	51.9	-	20.6	-	2.3	-	32.0	-	14.3	-
Homo sp.	2	25.1	3.3	36.7	7.2	18.9	1.5	1.4	0.1	22.6	2.2	10.6	0.8
Homo sapiens	10	24.6	3.3	36.2	7.0	18.6	1.7	1.4	0.2	22.8	3.2	10.3	1.2
Gorilla	7	29.7	6.1	96.6	17.5	31.4	3.0	0.9	0.2	9.7	2.0	15.3	1.6
Pan	7	15.3	3.8	37.8	9.4	20.6	2.7	0.7	0.1	12.1	1.4	9.6	1.2
Pongo	3	22.2	4.1	44.5	6.1	20.3	1.0	1.1	0.2	16.5	3.3	11.6	0.4
Third molar													
A. anamensis	1	34.7	-	51.8	-	21.1	-	1.6	-	22.8	-	13.5	-
A. afarensis	3	31.0	1.7	52.0	8.9	23.2	1.3	1.3	0.1	18.7	2.1	12.5	1.3
A. africanus	6	48.8	9.0	67.2	13.8	24.7	2.0	2.0	0.3	24.2	2.8	13.6	2.0
A. robustus	5	46.9	9.3	57.6	9.3	22.0	1.3	2.1	0.4	28.3	6.5	14.1	0.7
A. boisei	4	36.2	5.0	46.4	7.5	21.7	1.5	1.7	0.3	25.0	5.5	12.4	0.5
Homo sp.	4	25.4	5.0	34.5	10.3	17.1	2.9	1.5	0.2	25.7	3.3	9.5	1.6
Homo sapiens	9	25.9	5.5	34.8	10.9	17.3	3.0	1.5	0.2	26.1	5.0	9.8	1.5
Gorilla	8	30.5	4.5	84.0	12.4	29.0	1.9	1.0	0.1	11.5	1.3	13.7	1.4
Pan	3	14.0	2.0	30.8	7.4	19.0	1.1	0.7	0.1	13.4	0.9	8.4	0.3
Pongo	6	20.8	1.9	35.7	9.0	18.4	1.9	1.1	0.9	19.4	3.1	10.7	0.8

[a] Abbreviations: EDJ – enamel-dentine junction, AET – average enamel thickness, RET – relative enamel thickness, BCD – bi-cervical diameter.

Table 2. Pairwise comparisons of AET (bottom left) and RET (top right) between the study taxa (p-values in bold are significant ≤ 0.05 and shaded cells are non-human ape comparisons).

First Molar	*A. ana*	*A. afar*	*A. afri*	*A. rob*	*A. boi*	*Homo* sp.	*Homo sap.*	*Gorilla*	*Pan*	*Pongo*
A. ana		-	-	-	-	-	-	-		-
A. afar	-		-	-	-	-	-	-	-	-
A. afri	-	-		0.265	0.131	0.249	0.681	0.065	**0.025**	0.404
A. rob	-	-	0.222		0.546	0.880	**0.041**	**0.007**	**<0.001**	0.056
A. boi	-	-	0.095	0.497		0.667	**0.035**	**0.004**	**<0.001**	**0.030**
Homo sp.	-	-	0.322	0.907	0.467		0.103	**0.007**	**0.001**	0.060
Homo sap.	-	-	0.195	**0.009**	**0.009**	0.053		0.064	**0.010**	0.372
Gorilla	-	-	0.415	0.082	**0.037**	0.120	0.473		0.736	0.255
Pan	-	-	**0.0012**	**<0.001**	**<0.001**	**0.001**	**0.016**	0.345		0.240
Pongo	-	-	0.309	**0.028**	**0.013**	0.057	0.474	0.223	1.000	
Second Molar										
A. ana		0.607	0.506	.0186	0.212	0.464	0.343	0.089	0.290	0.718
A. afar	0.700		0.917	0.677	0.525	0.798	0.877	0.062	0.167	0.406
A. afri	0.281	0.726		0.288	0.338	0.795	0.990	**<0.001**	**0.007**	0.202
A. rob	0.079	0.374	0.263		0.677	0.175	0.214	**<0.001**	**0.001**	**0.046**
A. boi	0.137	0.340	0.353	0.718		0.259	0.282	**0.007**	**0.026**	0.107
Homo sp.	0.216	0.532	0.613	0.811	0.633		0.868	**0.009**	**0.050**	0.250
Homo sap.	0.603	0.714	0.113	**0.014**	0.133	0.159		**<0.001**	**0.004**	0.74
Gorilla	0.529	0.361	**0.008**	**0.000**	**0.029**	**0.030**	0.059		0.336	0.135
Pan	0.174	0.144	**0.000**	**0.000**	**0.006**	**0.004**	**0.003**	0.274		0.452
Pongo	0.889	0.603	0.146	**0.027**	0.091	0.135	0.274	0.163	0.585	
Third Molar										
A. ana		0.489	0.833	0.888	0.369	0.302	0.564	0.164	0.348	0.616
A. afar	0.604		0.420	0.378	0.787	0.641	0.454	**0.001**	**0.021**	0.058
A. afri	0.413	0.87		0.902	0.229	0.215	0.751	**0.002**	0.064	0.182
A. rob	0.408	0.673	0.970		0.205	0.136	0.453	**0.004**	0.090	0.251
A. boi	0.221	0.313	0.453	0.491		0.832	0.322	**<0.001**	**0.006**	**0.017**
Homo sp.	0.311	0.484	0.699	0.735	0.785		0.343	**<0.001**	**0.003**	**0.009**
Homo sap.	0.920	0.169	**0.045**	0.086	**0.019**	0.156		**<0.001**	0.140	**0.028**
Gorilla	0.468	**0.043**	**0.002**	**0.003**	**<0.001**	**<0.001**	**0.030**		0.563	0.084
Pan	0.236	**0.016**	**0.001**	**0.002**	**0.006**	**0.003**	0.155	0.376		0.444
Pongo	0.663	0.130	**0.019**	**0.023**	**0.004**	**0.0013**	0.129	0.579	0.204	

*Light shading indicates comparisons between hominins and extant non-human apes. Blank cells indicate non-significant results. In bold are results with a significant difference between taxa.

Table 3. Regional AET measurements (mean and standard deviation) for the combined maxillary molar sample of each taxon.

Taxon	*n*	Lingual	SD	Occlusal	SD	Buccal	SD
A. anamensis	3	1.2	0.37	1.26	0.71	0.97	0.31
A. afarensis	4	1.65	0.18	1.99	0.12	1.36	0.32
A. africanus	20	1.74	0.29	1.75	0.36	1.29	0.27
A. robustus	17	1.93	0.26	2.09	0.38	1.58	0.35
A. boisei	8	2.41	0.51	2.59	0.58	1.90	0.4
Homo sp.	10	1.90	0.32	2.09	0.33	1.51	0.29
Homo sapiens	29	1.29	0.33	1.43	0.31	1.22	0.18
Gorilla	17	0.99	0.23	0.9	0.17	0.93	0.12
Pan	18	0.75	0.17	0.62	0.08	0.65	0.12
Pongo	13	1.08	0.31	1.11	0.21	0.92	0.18

Table 4. Intraspecific pairwise comparisons[a] of AET and RET between mandibular and maxillary molars by molar position.

Taxon	AET M1	AET M2	AET M3	RET M1	RET M2	RET M3
A. africanus	ns	ns	ns	ns	ns	ns
A. robustus	ns	ns	ns	ns	ns	0.028
Homo sapiens	ns (0.06)	0.005	0.034	ns	0.037	ns
Gorilla	ns	ns	ns	ns	ns	ns
Pan	ns	ns	ns	0.008	0.54	ns
Pongo	ns	ns	ns	ns	ns	ns

[a] Kruskal-Wallis with posthoc pairwise comparisons.

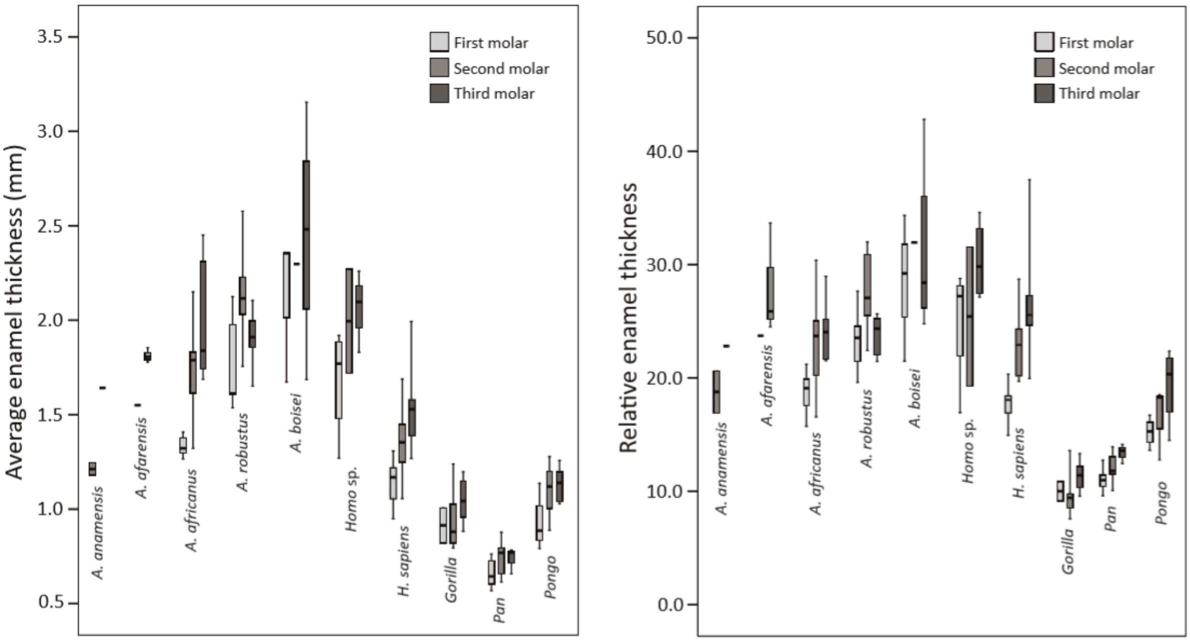

Figure 1

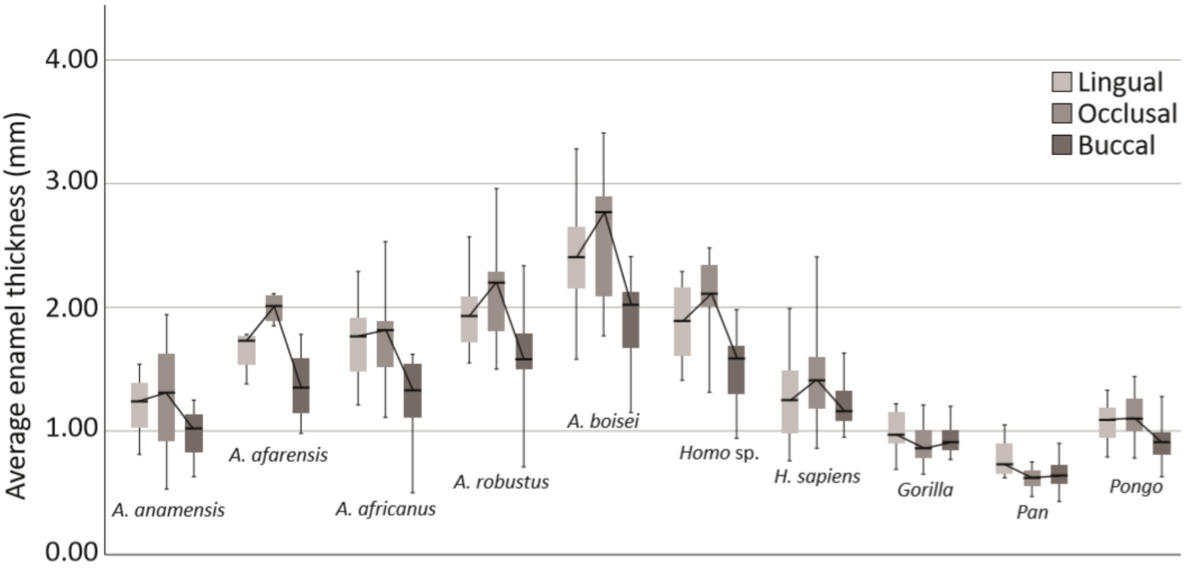

Figure 2

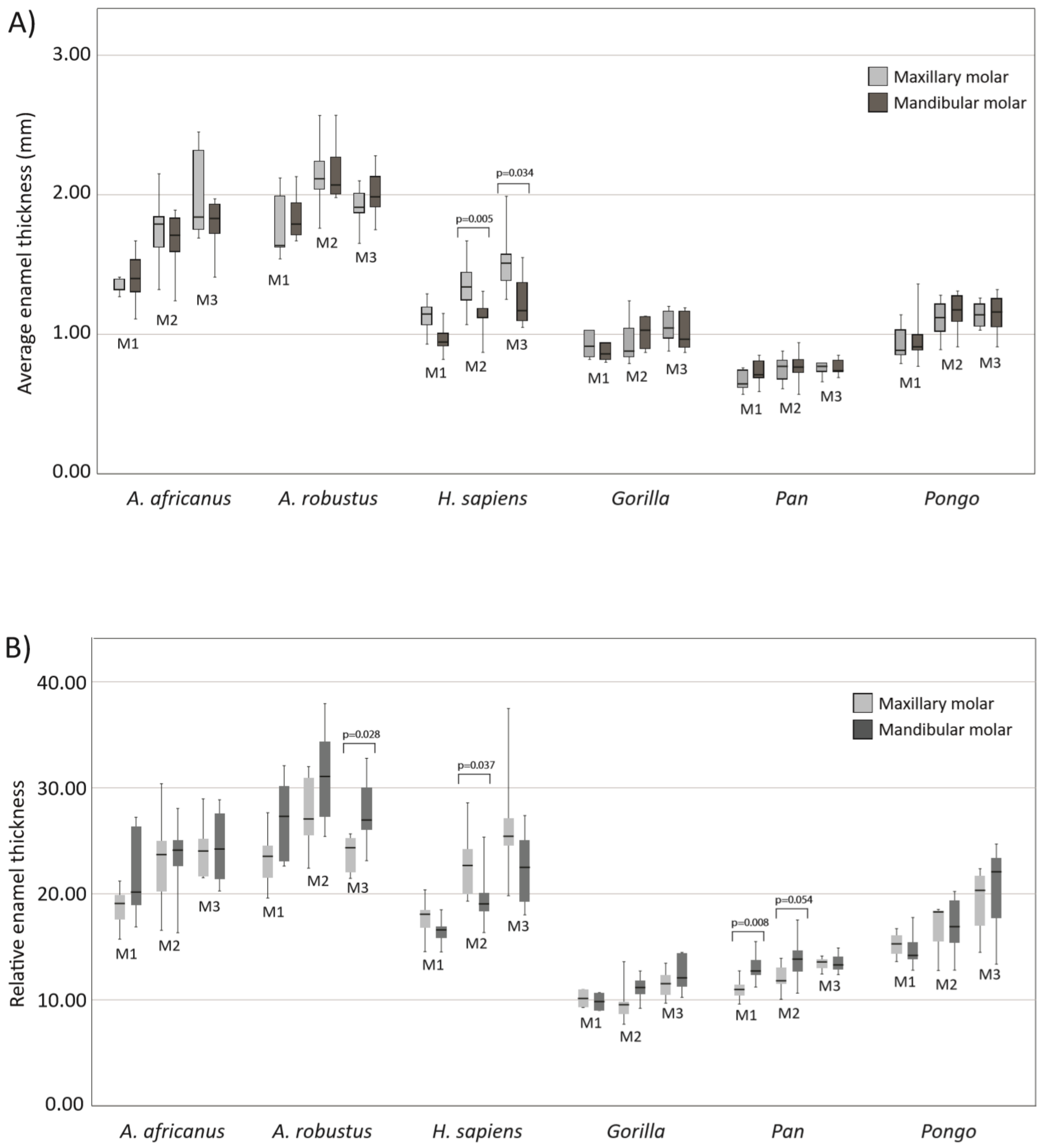
A)
Average enamel thickness (mm)
3.00
2.00
1.00
0.00
Maxillary molar
Mandibular molar
M1
M2
M3
p=0.005
p=0.034
A. africanus
A. robustus
H. sapiens
Gorilla
Pan
Pongo
B)
Relative enamel thickness
40.00
30.00
20.00
10.00
0.00
Maxillary molar
Mandibular molar
M1
M2
M3
p=0.028
p=0.037
p=0.008
p=0.054
A. africanus
A. robustus
H. sapiens
Gorilla
Pan
Pongo

Figure 3