

# New ways to think about enamel and dentine thickness in longitudinal tooth sections

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## Introduction

In 1985 Martin (1) described an objective way of measuring enamel thickness in longitudinal sections of primate teeth (see also 2). Average enamel thickness (AET) was calculated as the area of enamel (c) divided by the length of the enamel-dentine junction (e) (Fig. 1). This was further corrected for body size by scaling to the square root of the bi-cervical dentine cap area (b). Relative enamel thickness (RET) made it thus possible to compare enamel thickness between teeth in the same mouth and between the teeth of different taxa and has been used in a number of studies dealing with hominoid taxonomy, phylogeny, and paleodiet (e.g., 1, 3-10). The dentine as defined by

Martin (1) also includes pulp and dentine formed after crown completion during root growth.

In this study we asked how the area of dentine formed in the same time as enamel at crown completion compares with the enamel formed in a range of hominoid teeth. To that purpose, we added a new variable, the area of dentine formed at crown completion ( $d$ ), and calculated the average dentine thickness (ADT) as being the quotient of  $d$  divided by  $e$  (see Fig. 1). We asked how in longitudinal section does tooth size and shape influence ADT, and if ADT mirrors the pattern shown by AET. This should give new elements on the degree of developmental integration between enamel and dentine. Finally, we examined the variation in proportion of the pulp chamber within the dentine cap.

### Materials and methods

The sample includes histological and microCT longitudinal sections from 52 hominoid permanent maxillary and mandibular teeth, including 24 modern humans, 14 Neandertals, 5 chimpanzees (*Pan troglodytes*), 4 orangutans (*Pongo pygmaeus*), 3 *Proconsul nyanzae*, and single specimens from *Gorilla gorilla*, and *Hispanopithecus laietanus* (Table 1).

Bucco-lingual sections were physically or virtually extracted from the tooth record. For molars, mesial and distal sections were compiled to give the broadest possible picture of how ADT varies within the crown in this preliminary study. Virtual sections were generated from 3D models using Avizo 7 (VSG) following previously established sectioning protocols (10-12). Physically and virtually produced sections closely approximate one another (13), and therefore data were tabulated from both techniques.

The following variables were digitally measured or calculated using MPSAK 2.9 (in 14): the area of the enamel cap ( $c$ ; mm<sup>2</sup>), the bi-cervical dentine cap area ( $b$ ; mm<sup>2</sup>), the length of the enamel-dentine junction ( $e$ ; mm), the area of dentine formed at crown completion ( $d$ ; mm<sup>2</sup>), the area of pulp formed at crown completion ( $p = b-d$ ; mm<sup>2</sup>), the AET ( $c/e$ ; mm), the ADT ( $d/e$ ; mm), the enamel area as a percent of dentine area formed at crown completion ( $100 * c/d$ ), and the pulp area as a percent of Martin's dentine cap area ( $100 * p/b$ ).

Standard box and whisker plot revealing the interquartile range (25th-75th percentiles: boxes), 1.5 interquartile ranges (whiskers) and the median values (black line) were represented.

## Results and discussion

As previously described in a broader context (e.g., 10, 15-18), results show that AET increases from anterior to posterior teeth (trend in the modern human sample shown in Fig. 2). However ADT for the same teeth changes very little from anterior to posterior (Fig. 3). Even when this small sample of modern human teeth is supplemented with a varied selection of modern and fossil hominoid teeth, ADT between tooth types changes little from anterior to posterior (Fig. 4). This suggests that within hominoids, tooth shape has less effect on ADT than on AET and average odontoblast secretory rates are little different between tooth types.

With special reference to the first molars (M1), ADT does not exactly mirror AET (Figs. 5 and 6). For instance, orang-utans have enamel that more closely approaches Neandertals and modern humans in average enamel thickness than chimpanzees. But orang-utans have far greater ADT than either thin-enameled chimpanzees or thicker enameled Neandertals and modern humans. This demonstrates that ADT can vary independently of AET.

When expressed as a percent of dentine area formed at crown completion, enamel areas in modern human, Neandertal and chimpanzee M1s are not obviously different from one another, but orangutan M1s show lower values (Fig. 7). This indicates more clearly that within a tooth type, the amount of enamel formed with respect to dentine in the same time period is not tightly linked or integrated. One or other or both tissues can form variable amounts of average thickness independent of the other. Indeed, each may be adaptive in different ways.

When expressed as a percent of Martin's dentine cap area, the pulp area at crown completion is greater in chimpanzee M1s than in modern human, Neandertal, and orangutan M1s (Fig. 8). This might in part be because the pulp cavity within the crown of the tooth is positioned higher in teeth where the coronal dentine experiences less wear (19-21).

## Concluding remarks

These preliminary results show the relevance of measuring the area of dentine formed at crown completion to address paleobiological questions. ADT varies much less with tooth size and shape than AET from anterior to posterior in modern humans and among hominoids in general, and it does not consistently mirror AET, indicating that both tissues are not tightly linked during their development. Measuring the percent of enamel area formed with respect to the dentine area formed within the same time period is an alternative way of comparing relative enamel thickness between teeth. However the results need to be confirmed on larger ground and interpreted in the context of

rates of enamel and dentine formation during crown development. There remains also then the issue of finding sufficient numbers of tooth sections where dentine formation has not continued on as secondary dentine formation beyond the time of enamel (crown) completion. Alternatively, teeth where accentuated markings at the end of crown completion are also clearly reflected in the crown dentine are another means of defining ADT in fully formed teeth.

## Acknowledgments

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taxon	incisors	canines	pre molars	M1	M2	M3	Total
<b>modern humans</b>	4	2	3	7	6	2	24
<b>Neandertals</b>				14			14
<b><i>Pan troglodytes</i></b>				4	1		5
<b><i>Pongo pygmaeus</i></b>				4			4
<b><i>Proconsul nyanzae</i></b>				1	2		3
<b><i>Gorilla gorilla</i></b>				1			1
<b><i>Hispanopithecus laietanus</i></b>				1			1
<b>Total</b>	4	2	3	32	9	2	52

*M1: first molars; M2: second molars; M3: third molars*

Table 1. Composition of the hominoid maxillary and mandibular permanent tooth sample

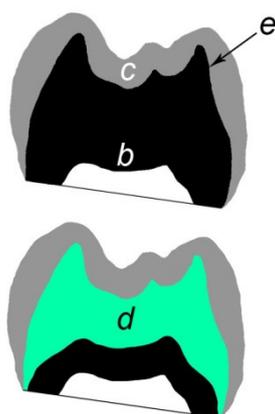


Figure 1. Sketch of a longitudinal section in a molar showing measurements used to determine average and relative enamel thicknesses, and average dentine thickness. Average enamel thickness (AET) scales the area of the enamel cap (*c*: in light gray) to the length of the enamel-dentine junction (*e*). Relative enamel thickness (RET) is calculated as the AET divided by the square root of the dentine and pulp area (*b*: dark+white). Average dentine thickness (ADT) scales the area of dentine formed at crown completion (*d*: green) to *e*.

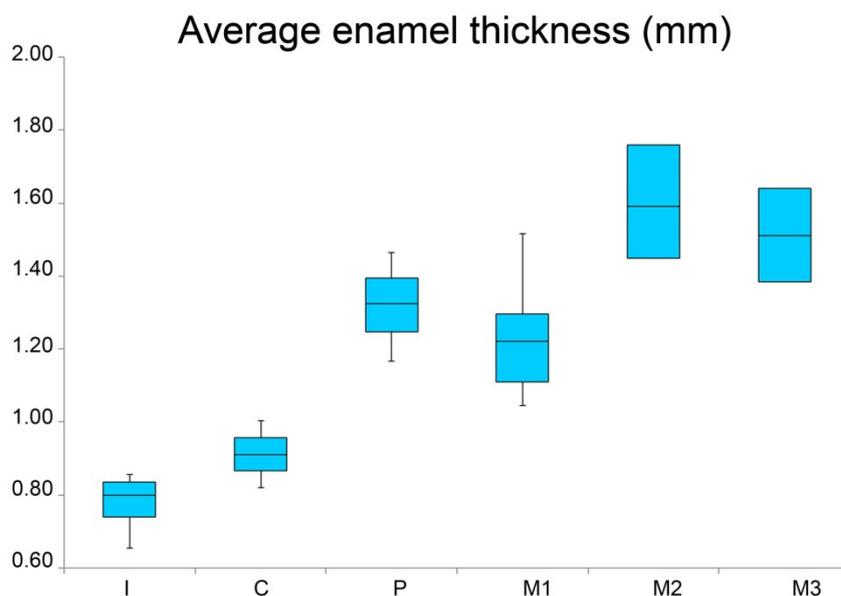


Figure 2. Average enamel thickness (*c/e*; mm) in modern human permanent teeth. I: incisors; C: canines; P: premolars; M1: first molars; M2: second molars; M3: third molars. *N* = 24.

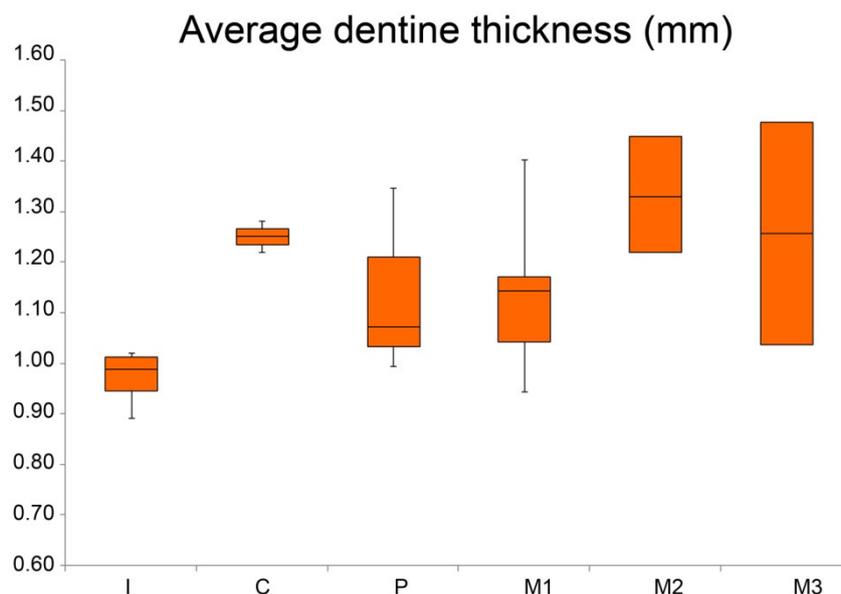


Figure 3. Average dentine thickness (d/e; mm) in modern human permanent teeth. I: incisors; C: canines; P: premolars; M1: first molars; M2: second molars; M3: third molars. N = 24.

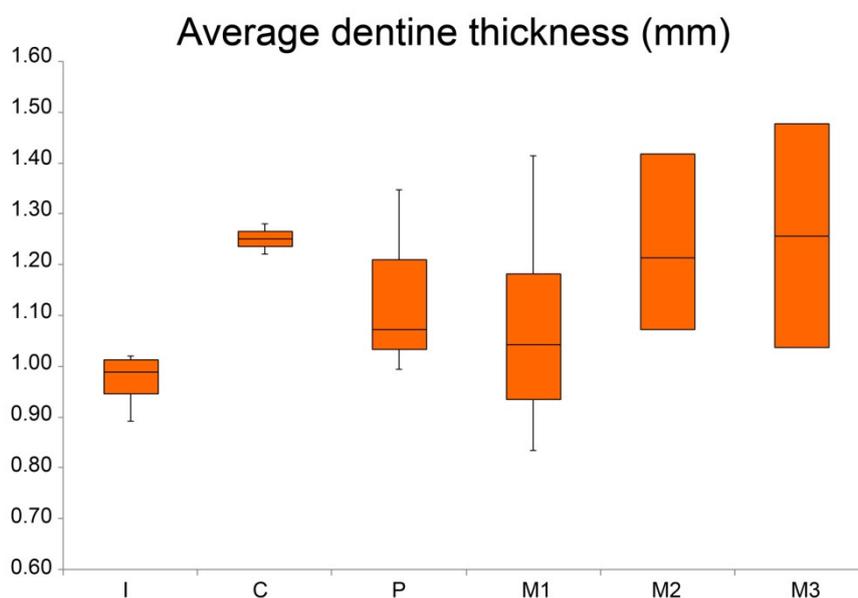


Figure 4. Average dentine thickness (d/e; mm) in modern humans, Neandertals, *Pan troglodytes*, *Pongo pygmaeus*, *Proconsul nyanzae*, *Gorilla gorilla*, and *Hispanopithecus laietanus* permanent teeth. I: incisors; C: canines; P: premolars; M1: first molars; M2: second molars; M3: third molars. N = 52.

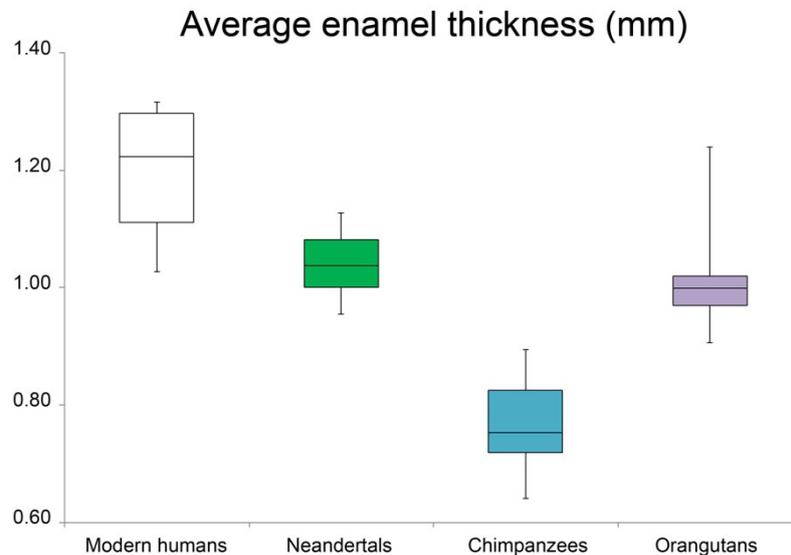


Figure 5. Average enamel thickness (c/e; mm) in modern human ( $N = 7$ ), Neandertal ( $N = 14$ ), chimpanzee ( $N = 4$ ), and orangutan ( $N = 4$ ) permanent first molars.

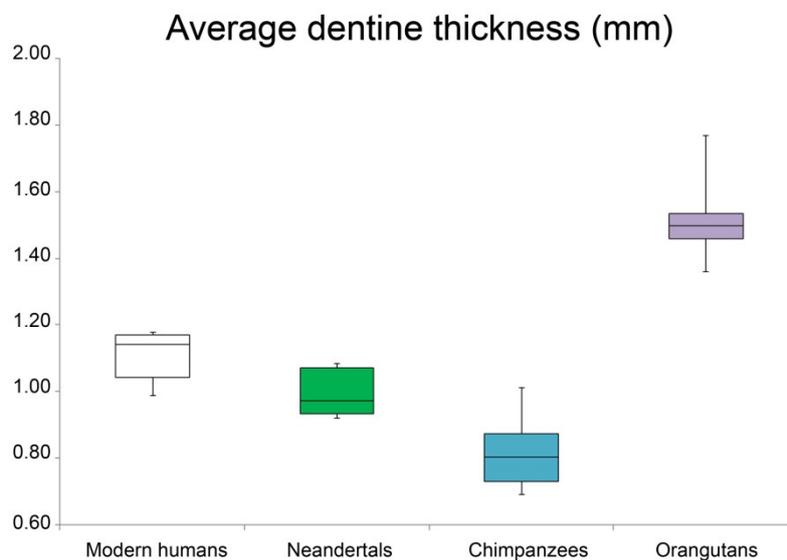


Figure 6. Average dentine thickness (d/e; mm) in modern human ( $N = 7$ ), Neandertal ( $N = 14$ ), chimpanzee ( $N = 4$ ), and orangutan ( $N = 4$ ) permanent first molars.

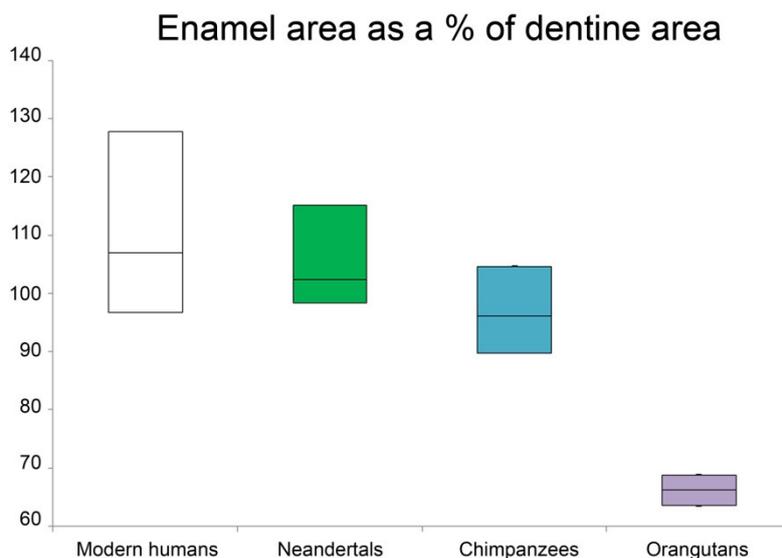


Figure 7. Enamel area as a percent of dentine area formed at crown completion ( $100 * c/d$ ) in modern human ( $N = 7$ ), Neandertal ( $N = 14$ ), chimpanzee ( $N = 4$ ), and orangutan ( $N = 4$ ) permanent first molars.

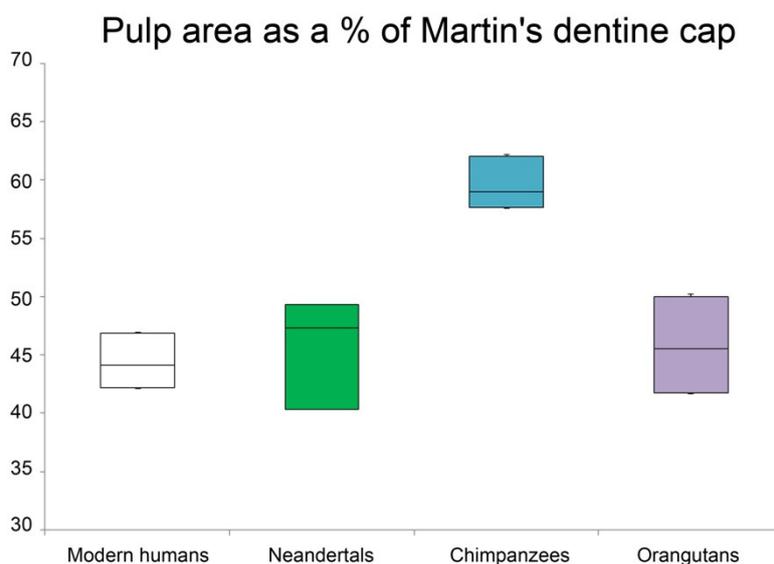


Figure 8. Pulp area at crown completion as a percent of Martin's dentine cap area ( $100 * p/b$ ) in modern human ( $N = 7$ ), Neandertal ( $N = 14$ ), chimpanzee ( $N = 4$ ), and orangutan ( $N = 4$ ) permanent first molars.