

Enamel Distribution in 3D: Is Enamel Thickness More Uneven in the Upper Second Molars of Durophagous Hominoids?

Distribution 3D de l'émail : la répartition de l'émail est-elle moins uniforme sur les secondes molaires supérieures des hominoides durophages ?

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Abstract Enamel thickness is not uniform across the dental crown of primates. It has been suggested that enamel distribution could be used in taxonomy or for ecological inferences. For instance, the thickness of molar enamel in mammals consuming hard food is expected to be uneven, despite differing reports on extant and extinct apes. Overall estimations of average and relative enamel thickness may mask the details of enamel distribution in complex teeth such as molars. Investigating enamel distribution and its purported relationship with ecology or phylogeny would require more detailed assessments. This paper aims to assess whether apes that consume hard foods on a regular basis, such as *Pongo pygmaeus*, can be characterized by the evenness or unevenness of enamel thickness. To do so, we combined topographic maps and distribution histograms of enamel thickness with cumulative profiles of its variation, or “pachymetric profiles”. We investigated a sample of 25 unworn hominoid upper second molars scanned by X-ray microtomography, and further compared this to a sample of 32 cercopithecines and colobines. Topographic maps show uniformly thin enamel for *Gorilla gorilla* and *Hylobates* sp., unevenly thin enamel for *Pan paniscus* and *Pan troglodytes*, and unevenly thick enamel for *Pongo pygmaeus*. The skewness of enamel distribution does not distinguish between ape species, but does separate apes from Old World monkeys. Contrary to previous reports on Old World monkeys, the slope of enamel thickness profiles, or pachymetric slope, does not predict the diet of extant apes. However, it does separate the *Pan* genus,

which is characterized by a higher pachymetric slope indicating more uneven enamel distribution compared to other apes. The uneven thickness of enamel distribution observed on topographic maps for *P. pygmaeus* is not supported by its low pachymetric slope, which instead indicates uniform enamel distribution. This discrepancy in the results obtained for *P. pygmaeus* can be interpreted as an evolutionary trade-off between fine-scale versus overall enamel distribution. On the one hand, unevenly thick enamel at a fine scale, combined with strongly decussated enamel as observed in *P. pygmaeus*, is expected to increase local resistance to crack propagation. On the other hand, uniformly thick enamel at the overall scale would improve the overall resilience of the enamel in coping with challenging food on a daily basis. Although understanding the effects of ecology on enamel distribution in apes requires further investigation, the results presented in this paper confirm the interest of enamel distribution for taxonomy and phylogeny.

Keywords Apes · Ecology · Enamel thickness · Pachymetric profiles · Phylogeny

Résumé L'épaisseur de l'émail n'est pas constante au sein de la couronne dentaire des primates. Il a été suggéré que la distribution de l'émail pouvait être utilisée en taxonomie ou pour faire des inférences écologiques. Par exemple, il est attendu que l'émail des molaires de mammifères consommant des aliments durs soit non uniformément épais, malgré des observations contradictoires chez les grands singes actuels et fossiles. Les variables estimant l'épaisseur de l'émail moyenne et relative peuvent dissimuler des variations plus subtiles dans la distribution de l'épaisseur de l'émail, notamment pour des dents complexes telles que les molaires. C'est pourquoi l'étude de la distribution de l'émail et ses possibles interactions avec l'écologie et la phylogénie peut nécessiter des estimateurs à la résolution plus fine. Cette étude a pour objectif de déterminer si les grands singes qui

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consomment des aliments plus résistants, comme *Pongo pygmaeus*, présentent un émail uniformément épais ou non uniformément épais. Pour ce faire, nous avons combiné les cartes topographiques et les histogrammes de distribution de l'épaisseur de l'émail avec les profils cumulés de la variation en épaisseur de l'émail, ou « profils pachymétriques ». Nous avons étudié un échantillon de 25 molaires supérieures non usées d'hominoïdes actuels, scannées par microtomographie à rayons X. Cet échantillon a ensuite été comparé à un échantillon de 32 cercopithèques et colobes. Les cartes topographiques indiquent que l'émail de *Gorilla gorilla* et d'*Hylobates* sp. est uniformément fin; que celui de *Pan paniscus* et *Pan troglodytes* est non uniformément fin; et que celui de *P. pygmaeus* est non uniformément épais. L'asymétrie de la distribution de l'émail ne permet pas de distinguer les grands singes entre eux, mais elle permet de les distinguer des singes de l'Ancien Monde. Contrairement à ce qui a pu être observé chez ces derniers, la pente des profils d'épaisseur de l'émail, ou pente pachymétrique, ne permet pas d'estimer le régime alimentaire des grands singes actuels. En revanche, elle permet de distinguer le genre *Pan*, dont la pente du profil pachymétrique est significativement plus grande que chez les autres grands singes, ce qui traduit une distribution moins uniforme. La distribution non uniforme observée sur les cartes topographiques n'est pas détectée chez *P. pygmaeus*, dont les profils pachymétriques ont une pente plus faible qui indique au contraire une distribution uniforme de l'émail. Les résultats contradictoires obtenus pour *P. pygmaeus* peuvent être interprétés comme un compromis évolutif entre la distribution fine de l'émail et sa distribution globale. D'une part, une distribution non uniforme à fine échelle, combinée à l'émail fortement décussé observé chez *P. pygmaeus*, augmenterait la résistance locale à la propagation des fractures de l'émail. D'autre part, un émail uniformément épais à une échelle plus globale augmenterait la résilience de la dent lorsqu'elle est confrontée à des aliments résistants quotidiennement. En résumé, comprendre l'influence de l'écologie sur la distribution de l'émail chez les grands singes nécessite de plus amples recherches. Cependant, l'ensemble des résultats obtenus confirme l'intérêt de la distribution de l'émail en taxonomie et en phylogénie.

Mots clés Écologie · Épaisseur de l'émail · Grands singes · Phylogénie · Profils pachymétriques

Introduction

The multifactor origins of enamel thickness

Because of its widely accepted taxonomic and phylogenetic value, enamel thickness is an important measurement in

anthropology [1]. But because thicker enamel lessens deformation due to strain, thus improving resistance to tooth fracture, enamel thickness is also influenced by natural selection and may thus inform about the ecology of our extinct relatives [2]. Average enamel thickness (AET) seems to correlate with life expectancy in anthropoid primates [3]. Different estimates of relative enamel thickness (RET) have been made on the teeth of primates to infer diet and physical properties of food, mostly its hardness [1,4,5] and abrasiveness [6,7,8]. Thicker enamel could have also been selected in some extinct primates as a morphological response to the consumption of tough foods such as tubers or sedges [9,10].

Besides phylogeny and natural selection, enamel thickness is affected by physiological, developmental or environmental factors [11], which may explain regional differences reported within the same genus [12]. Ultimately, thick enamel could result from a wide array of factors, and it may be necessary to combine AET or RET with other enamel features such as its distribution in order to interpret enamel thickness.

Enamel distribution as an estimator of tooth function?

While AET and RET are convenient overall estimators of enamel thickness, enamel is usually not evenly distributed over the tooth surface. This is especially true for complex teeth such as premolars and molars, which have multiple cusps with different ranges of enamel thickness. For instance, in hominoids, enamel is significantly thicker on the upper molar lingual cusps and on the lower molar buccal cusps, which undergo more stress during mastication and have consequently been termed “functional cusps” [13-15]. In primates in general, function may play a major role in enamel distribution and it has been suggested that enamel distribution could be used to infer either the phylogeny or the ecology of extinct species, for instance when no differences in AET or RET have been observed [14,16]. Regarding ecological inferences, two different hypotheses have been put forward.

First, Lucas et al. [2] expected the enamel of mammals consuming hard food to be unevenly thick i.e., thicker at the molar cusp tips before they start wearing out. Their hypothesis is based on the assumption that unevenly distributed enamel would increase its resistance by inhibiting the extension of cracks where hard food comes into contact with the outer enamel surface. Conversely, evenly distributed enamel would promote the extension of cracks and make the molars more sensitive to challenging hard food. They also predicted that enamel decussation i.e., crossed sets of enamel prisms that increase resistance to crack propagation [17,18], would be found throughout the enamel cap in consumers of hard food.

In contrast, Olejniczak et al. observed on topographic maps of lower molar enamel thickness that *Gigantopithecus blacki*

and, to a lesser extent, *Pongo pygmaeus* were characterized by more evenly thick enamel than extant African apes, resulting in broader and flatter occlusal surfaces in *G. Blacki* and *P. pygmaeus* [19]. Since *P. pygmaeus* is a consumer of hard and tough foods [20], they subsequently hypothesized that more uniformly thick enamel, combined with short dentine horn height, might be explained by “hyper-masticatory” adaptation. However, this hypothesis is yet to be compared with the predictions of Lucas et al.[2].

Measuring enamel distribution

Most studies investigating enamel distribution are based on qualitative observations, either from three-dimensional (3D) topographic maps [19] or from two-dimensional (2D) sections that can be located on mesial, distal, lingual or buccal sections [21], at regular intervals along the molar row [22] or along the complete dental row [23]. From such 2D sections, enamel distribution can be quantified using linear measurements, for instance the minimum enamel thickness of the occlusal fovea or the maximum thickness of the lateral surface [16]. Assuming that enamel growth time is known, linear measurements can even be used to compute the daily enamel growth rate for different enamel regions [24]. Alternatively, enamel distribution can be measured by comparing AET and RET [21,22], lateral AET and lateral RET [25], relative enamel content [27] or relative enamel area [26] between slices made at different locations of the enamel crown.

Enamel distribution can also be quantified in 3D using AET and RET on well-defined dental regions of the enamel cap, such as the occlusal fovea versus the lateral surface, or the cuspal region versus the cervical region [16,28]. However, delimiting dental regions at a finer scale can be highly subjective. Alternatively, enamel distribution can be assessed from 3D models (in fact polygonal meshes) of the outer enamel surface (OES) and of the underlying enamel dentine junction (EDJ). In this case, the enamel thickness corresponds to the shortest normal distance from the OES to the EDJ surface [29]. In a later study, Thiery et al. [30] used within-model variation of this enamel-dentine distance to quantify enamel distribution in upper second molars of extant anthropoids. They reported a more uneven enamel distribution in Old World monkeys consuming hard food. This study is an extension of the Thiery *et al.* study [30] using the same methods.

Objectives

The aim of this study was to investigate whether the enamel of upper second molars in hard food specialist hominoids is uniformly thick, as suggested by the results of Olejniczak et al. [20] or unevenly thick, as predicted by Lucas et al. [2]. To do

so, we combined qualitative assessments from topographic maps of enamel distribution with quantitative assessments from within-model (intramesh) variations in enamel-dentine distance, as described by Guy et al. [29,30]. Since *Pongo pygmaeus* consumes more challenging hard food than other apes [20,32], the thickness of its enamel is expected to be more uneven [2,30].

Methods

Material

We collected 57 upper second molars from the following institutions: the University of Poitiers PALEVOPRIM collections, France, the Muséum national d’Histoire naturelle in Paris, France, the Royal Museum of Central Africa in Tervuren, Belgium and the Senckenberg Museum in Frankfurt, Germany (Table S1). We included 25 teeth of apes (Hominoidea), as well as 32 teeth of Old World monkeys (Cercopithecoidea) for extra-group comparison. No living animal was involved in this work, and no animal was killed specifically for this study. Only juvenile specimens and sub-adults were selected, so that the enamel was minimally worn *i.e.*, score of 1-2 using Scott’s dental wear scoring system [33].

Acquisition of Dental 3D Meshes

In order to investigate enamel thickness without damaging valuable museum specimens of juvenile primates, the teeth were scanned using high-resolution X-ray micro-computed tomography (HR- μ CT) at the Microtomography Centre in Poitiers, France. The scans were acquired using an EasyTom HR-microtomograph. Isovoxel resolution ranged from 15 to 30 μ m depending on tooth size. The resulting array of 2D slices was stacked to build 3D reconstructions of the teeth, which were segmented using Avizo following Guy *et al* [29,35]. We extracted models (polygonal 3D meshes) from both OES and EDJ. Using Geomagic Studio, these models were re-tessellated to 55,000 triangles of normalized area, which removed scaling effects on triangle geometry [34].

Following Guy et al. [35], the OES and EDJ surfaces were paired together and their orientation was standardized. Both OES and EDJ models were cropped occlusally *i.e.*, we retained only the occlusal basins and discarded the polygons below a plane parallel to the occlusal plane (xy) and passing through the lowermost point of (i), the enamel occlusal fovea and (ii), the dentine occlusal fovea.

Enamel-dentine distance and thickness maps

Following Guy et al. [29], enamel-dentine distances (EDD) were computed as the shortest Euclidean distance to the EDJ

surface. All computations were made in R 3.3.0 [36]. Surfaces were opened out as 3D meshes, and from the resulting array of polygon-based values, topographic maps of enamel thickness were plotted using the Rvcg package [37] (Fig. 1A). It is worth noting that our EDD maps are very

similar to Kono et al.'s thickness maps or *T-maps*, which picture the minimum distance to EDJ from OES pixels [15,16]. Both 3D AET and 3D RET values have already been published in another paper, so they are not reported here [30].

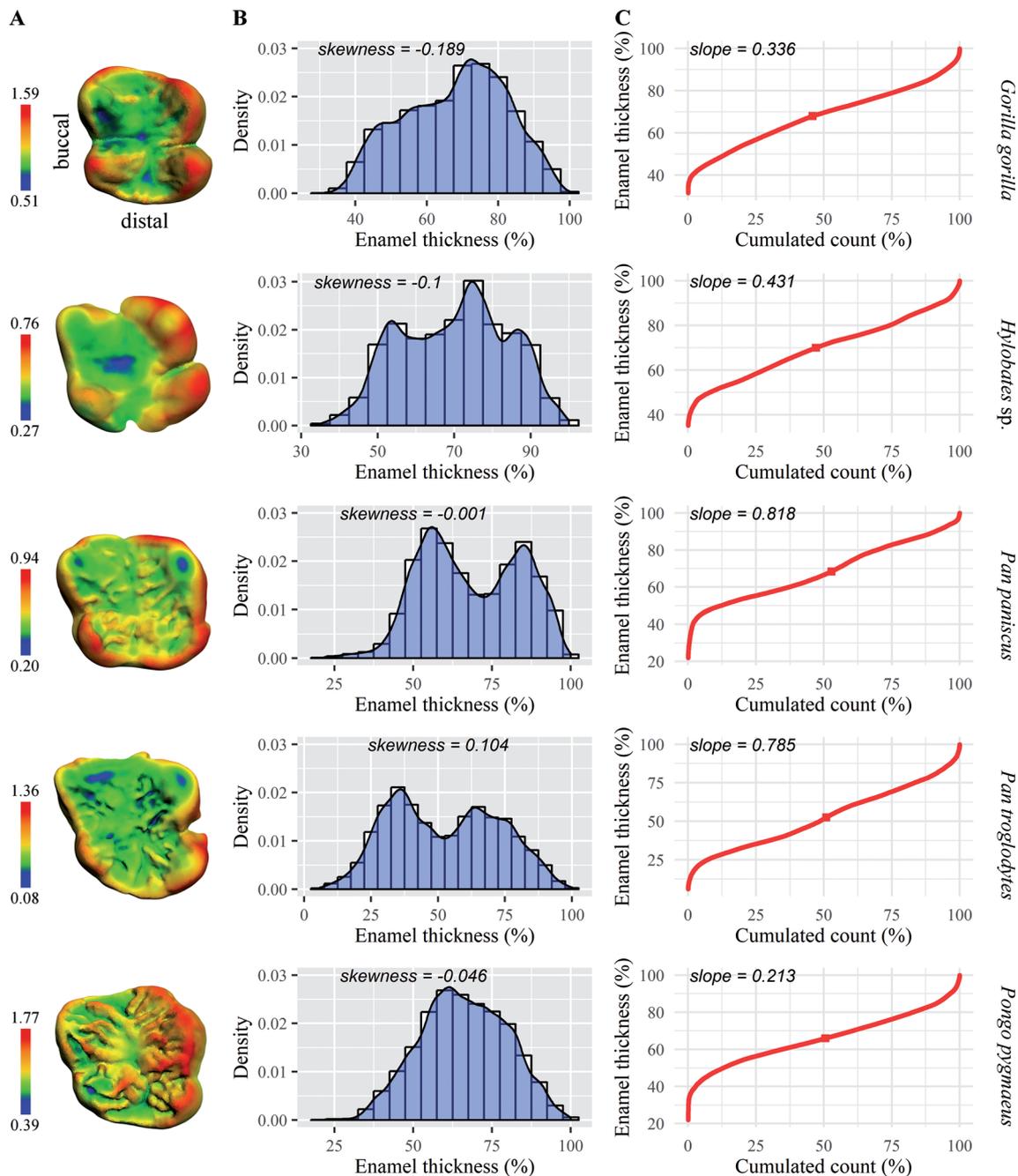


Fig. 1 Enamel distribution on the second upper molars of five extant ape species. The dental surfaces were cropped above the lowermost point of the occlusal surface. A: topographic maps of enamel-dentine distance (EDD), in mm; B: histograms of EDD distribution and density curves; C: pachymetric profiles. The red square corresponds to average enamel thickness / *Distribution de l'émail de la deuxième molaire supérieure de cinq espèces actuelles de grands singes. Les surfaces dentaires ont été recadrées au-dessus du point le plus bas de la surface occlusale. A : carte topographique de la distance émail-dentine (EDD) en mm ; B : histogrammes de la distribution d'EDD et des courbes de densité ; profilé pachymétrique. Les carrés rouges correspondent à l'épaisseur moyenne de l'émail*

Within-model distribution of enamel-dentine distance

For every 3D tooth model, the range of EDD values was used to plot distribution histograms (Fig. 1B; Fig. S2). Two kinds of information could be retrieved from these figures. First, the major distribution modes were isolated. Second, we computed Pearson's skewness of the EDD distribution curves. Skewness is an estimation of a distribution's asymmetry: the skewness of a perfectly symmetrical distribution is zero, a negative value usually indicates asymmetry towards higher values and a positive value indicates asymmetry towards lower values. The higher the absolute skewness, the more asymmetrical the distribution of EDD values will be. The reverse is not true, however, because low skewness might also be due to a long tail somewhat compensated by a short but strong tail on the other side of the distribution curve.

Pachymetric profiles

Cumulative profiles of enamel thickness, or "pachymetric profiles" [30] (from the Greek *pachys*-/παχύς- "thick" and *métron*-/μέτρον "a measure"), are meant to represent the rate of change in the thickness of an object and draw on the cumulative profiles of ground elevation (hypsometric profiles) used in traditional topography [31], with EDD replacing elevation. These profiles are built from EDD (in percentage of maximum EDD) plotted against the accumulated polygon count for each EDD value (as a percentage of the total number of polygons) (Fig. 1C).

The pachymetric slope is defined as the average slope of the pachymetric profile at average EDD. It is an estimate of the unevenness of enamel thickness: the steeper the slope, the more abrupt the thickness profile, and the less gradual the change in enamel thickness [30].

Results

Topographic maps

Occlusal enamel was found to be thinner than lateral enamel in *Gorilla gorilla*, *Hylobates* sp, *Pan paniscus* and *Pan troglodytes*, although it was especially marked in the genus *Pan*. Topographic maps of upper second molars show that the enamel of the occlusal fovea is evenly thin in *G. gorilla* and *Hylobates* sp, with relatively thicker enamel on the buccal side. (Fig.1A; Fig. S2). Several *G. gorilla* teeth have thinner enamel on the protocone tip, although this might result from slight apical wear (Fig. S2). Both *P. paniscus* and *P. troglodytes* have an unevenly thin enamel distribution on the occlusal surface, which is characterized by local thickening in the enamel crenulations and by a thinner protocone tip, but again this might result from slight apical wear

(Fig. 1A; see also Kono 2004). The upper second molars of *Pongo pygmaeus* have unevenly thick enamel, characterized by local thickening not only on enamel crenulations, but also on the protocone and hypocone tips (Fig. 1A).

Within-model enamel distribution

Most *P. paniscus* and *P. troglodytes* specimens have a clear bimodal and sometimes multimodal EDD distribution (Fig. 1B; Fig. S2). In contrast, the second mode is less marked or completely absent in *G. gorilla* and *P. pygmaeus* specimens. No difference in distribution asymmetry could be detected between hominoid species (Kruskal-Wallis chi-squared = 3.872, df = 3, p-value = 0.275). Skewness scores for hominoids are close to zero and never below -0.50 (Fig. 2). In contrast, Old World monkeys have skewness scores as low as -1.25 (Fig. 3).

Pachymetric slope

The hard food specialist *P. pygmaeus* and the soft but tough food specialist *G. gorilla* have similar pachymetric slopes (Fig. 2). In contrast, both *P. paniscus* and *P. troglodytes* have significantly higher pachymetric slope scores (Wilcoxon rank sum test, W = 145, p-value < 0,001). Moreover, for a given skewness of EDD distribution, panines always have a steeper pachymetric slope and therefore a more uneven enamel distribution than any other extant ape (Fig. 2).

Discussion

Using topographic maps of EDD, we observed that the crenulations on the surface of *Pongo pygmaeus* upper second

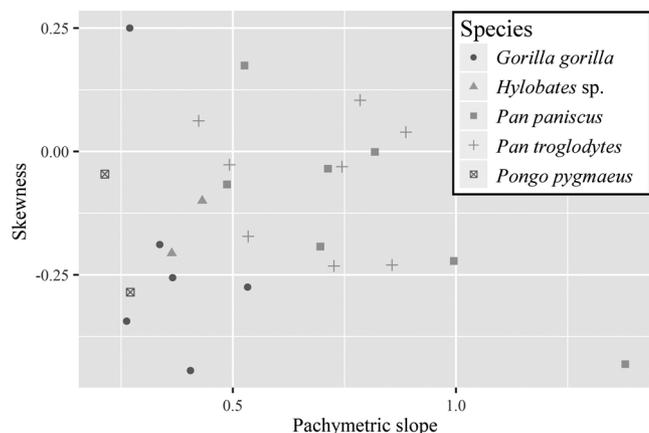


Fig. 2 Skewness of EDD distribution versus pachymetric slope in apes. Both variables are dimensionless / *Asymétrie de la distribution de l'EDD comparée aux pentes pachymétriques chez les grands singes. Les deux variables n'ont pas de dimension*

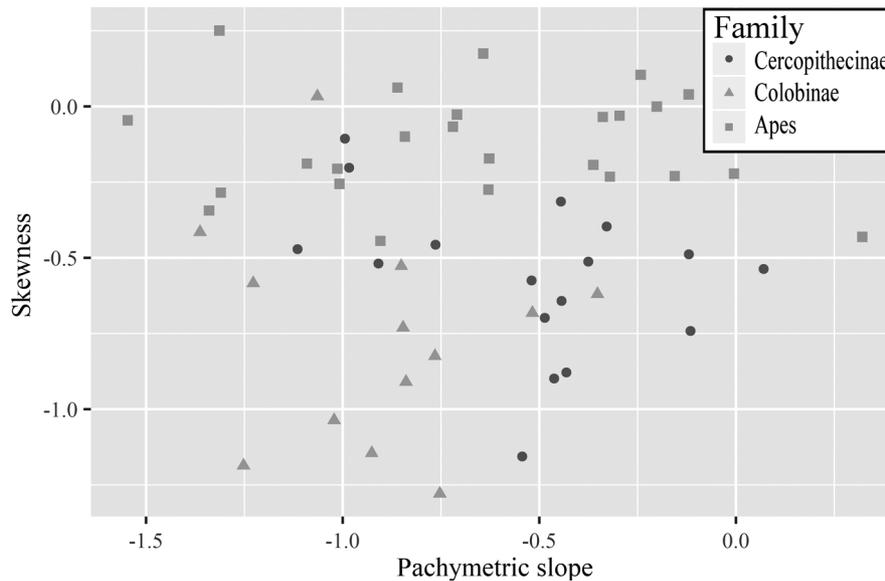


Fig. 3 Skewness of EDD distribution versus pachymetric slope in apes and Old World monkeys combined. Both variables are dimensionless / *Asymétrie de la distribution de l'EDD comparée aux pentes pachymétriques chez les singes de l'ancien monde et les grands singes combinés. Les deux variables n'ont pas de dimension*

molars result in uneven enamel thickness (Fig. 1A; Fig. S2). The enamel is locally thicker on the edge of the crenulations and at the tip of the functional cusps i.e., the protocone and the hypocone. To a lesser extent, this is also the case for the crenulated molars of *P. paniscus* and *P. troglodytes* (Fig. 1; Fig. S2). These observations contrast with the results of Olejniczak et al. [19] and tend to support the hypothesis of Lucas et al., who expected enamel to be unevenly thick in primates consuming hard food, such as *P. pygmaeus* [2]. Together with data on the enamel microstructure, which suggest that enamel decussation is more marked in *P. pygmaeus* than in any other extant ape [38], the predictions of Lucas et al. match what is observed in hominoids.

Nevertheless, this qualitative observation is not supported by the quantitative measurements reported in this paper, especially the slope of the cumulative enamel thickness profile (pachymetric slope). The upper second molars of *P. pygmaeus* are indeed characterized by a relatively low pachymetric slope, comparable to that of the upper second molars of the soft but tough food consumer *Gorilla gorilla* (Fig. 1C). This contradicts our expectations, as the pachymetric slope was significantly steeper for the hard food consuming species of Old World monkeys [30]. In contrast, the upper second molars of *P. paniscus* and *P. troglodytes* were characterized by steep pachymetric slopes, which probably result from unevenly thin occlusal enamel (Fig. 1C). These observations support the hypothesis of Olejniczak et al., who expected the enamel of *P. pygmaeus* to be more uniformly thick than in other apes [19].

These contrasting results can be explained by the fact that fine morphological details of enamel distribution, which are observable on thickness maps (Fig. 1A; Fig. S2), are concealed in the overall value calculated from pachymetric profiles (Fig. 1C; Fig. S2). This could result from an adaptive trade-off between better resistance to small-scale crack propagation, as suggested by Lucas et al. [2] and a large, thickly enamelled occlusal surface which is resilient to repetitive chewing of challenging food, as suggested by Olejniczak et al. [19]. However, it is not clear whether this trade-off might be linked to enamel crenulations or not. While crenulations of the enamel are observed in many seed-eating primates, their adaptive function is still in debate [39,20].

Because our sample is limited to unworn upper second molars, several questions remain unanswered. One the one hand, it is not known whether the methods presented here would produce the same results when applied to other tooth positions i.e., third molars, first molars and premolars. In hominoids, enamel thickness tends to increase along the dental row, but the putative effect of this gradient on enamel distribution is unknown [23,40]. On the other hand, there might be differences in enamel distribution between upper and lower molars. Furthermore, the hypothesis of unevenly thick enamel in hominoids adapted to hyper-mastication was formulated not from upper molars, but from lower molars [19].

In addition, enamel distribution is expected to be strongly affected by dental wear. We predict that the removal of occlusal enamel would increase the influence of the thick,

unworn lateral enamel on the distribution curves (Fig. 1A), resulting in greater asymmetry of EDD distribution and a steeper pachymetric slope as the tooth wears down. Most specimens of extinct hominoids are characterized by dental wear, and investigating the distribution of enamel across different wear stages may be a useful addition to other approaches, for example on lateral enamel [25].

Another factor that was not taken into account here is sexual dimorphism, especially in *P. pygmaeus*. Female orangutans have significantly higher AET and RET scores than males in both *P. pygmaeus* and *P. abelli* [40]. While this difference has been related to a significantly larger dentine core in males, a larger EDJ surface may also affect enamel distribution. Both specimens of *P. pygmaeus* used in this study are subadults, but their RET scores fall outside the range for males, suggesting that they could be females [40,30]. Including male specimens in future comparisons would help to understand how enamel distribution in *P. pygmaeus* is affected by sexual dimorphism and by dentine core size in general.

This study nevertheless shows that enamel distribution requires further investigation as it may convey both ecological and phylogenetic information. As regards the latter, one unexpected result was the difference in EDD distribution skewness between Old World monkeys and apes (Fig. 3). This result is unlikely to reflect more asymmetrical molars in Old World monkeys because the range of pachymetric profiles is actually wider in apes [30]. However, EDD skewness is close to zero in apes whereas it is almost entirely negative in Old World monkeys. This indicates that the EDD asymmetry shifts towards high EDD values in Old World monkeys. In apes however, this asymmetry may come from lower EDD values as well, as seen in the unevenly thin enamel of *P. paniscus* and *P. troglodytes* (Fig. 1A-B).

Another important phylogenetic application that emerges from this study is the identification of extinct hominoids from their enamel distribution. Several authors have proposed differences in enamel distribution as diagnostic features [9, 14, 19]. In this study, extant panines were characterized by steeper pachymetric slopes compared to other extant apes. We also observed that the enamel of the occlusal fovea is visibly thinner than lateral enamel, but this feature has been related to the ripe fruit dependent diet of the genus *Pan* [16,28,41]. Nevertheless, we suggest that a highly uneven enamel distribution in upper second molars, combined with thin occlusal enamel, could be diagnostic of the genus *Pan*. Fossil panines would therefore be expected to have a steep pachymetric slope, at least for unworn upper second molars [42]. This is consistent with evidence that genes involved in the regulation of enamel secretion underwent stronger selection in the genus *Pan* than in other extant apes [43].

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Conflict of interest: The authors do not have any conflict of interest to declare.

References

- Martin L (1985) Significance of enamel thickness in hominoid evolution. *Nature*, 314(6008):260–3
- Lucas PW, Constantino P, Wood B, Lawn B (2008) Dental enamel as a dietary indicator in mammals. *BioEssays*, 30(4):374–85
- Pampush JD, Duque AC, Burrows BR, et al (2013) Homoplasy and thick enamel in primates. *J Hum Evol*, 64(3):216–24
- Kay RF (1981) The nut-crackers – a new theory of the adaptations of the Ramapithecinae. *Am J Phys Anthropol*, 55(2):141–51
- Daegling DJ, McGraw WS, Ungar PS, et al (2011) Hard-Object Feeding in Sooty Mangabeys (*Cercocebus atys*) and Interpretation of Early Hominin Feeding Ecology. *PLoS ONE*, 6(8), e23095
- Maas MC (1991) Enamel structure and microwear: An experimental study of the response of enamel to shearing force. *Am J Phys Anthropol*, 85(1):31–49
- Teaford MF, Maas MC, Simons EL (1996) Dental microwear and microstructure in early oligocene primates from the Fayum, Egypt: Implications for diet. *Am J Phys Anthropol*, 101(4):527–43
- Rabenold D, Pearson OM (2011) Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. *PLoS ONE*, 6(12): e28379
- Olejniczak AJ, Smith TM, Skinner MM, et al (2008) Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus*. *Biol Lett*, 4(4):406–10
- Ungar PS, Hlusko LJ (2016) The evolutionary path of least resistance. *Science*, 353(6294):29–30
- Żądzińska E, Kurek M, Borowska-Strugińska B, et al (2013) The effect of the season of birth and of selected maternal factors on linear enamel thickness in modern human deciduous incisors. *Arch Oral Biol*, 58(8):951–63
- Kato A, Tang N, Borries C, et al (2014) Intra- and interspecific variation in macaque molar enamel thickness. *Am J Phys Anthropol*, 155(3):447–59
- Macho GA, Berner ME (1993) Enamel thickness of human maxillary molars reconsidered. *Am J Phys Anthropol*, 92(2):189–200

14. Schwartz GT (2000) Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *Am J Phys Anthropol*, 111(2):221–24
15. Kono RT, Suwa G, Tanijiri T (2002) A three-dimensional analysis of enamel distribution patterns in human permanent first molars. *Arch Oral Biol*, 47(12):867–75
16. Kono RT (2004) Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. *Anthropol Sci*, 112(2):121–46
17. Koenigswald W, Rensberger JM, Pretzschner HU (1987) Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature*, 328(6126):150–152
18. Bajaj D, Arola DD (2009) On the R-curve behavior of human tooth enamel. *Biomaterials*, 30(23-24):4037–46
19. Olejniczak AJ, Smith TM, Wang W, et al (2008). Molar enamel thickness and dentine horn height in *Gigantopithecus blacki*. *Am J Phys Anthropol*, 135(1):85–91
20. Vogel ER, van Woerden JT, Lucas PW, et al (2008) Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *J Hum Evol*, 55(1):60–74
21. Macchiarelli R, Mazurier A, Illerhaus B, Zanolli C (2009) *Ouranopithecus macedoniensis* (Mammalia, Primates, Hominoidea): virtual reconstruction and 3D analysis of a juvenile mandibular dentition (RPI-82 and RPI-83). *Geodiversitas*, 31(4):851–63
22. Smith TM, Olejniczak AJ, Martin LB, Reid DJ (2005) Variation in hominoid molar enamel thickness. *J Hum Evol*, 48(6):575–92
23. Smith TM, Olejniczak AJ, Reh S, et al (2008) Brief communication: Enamel thickness trends in the dental arcade of humans and chimpanzees. *Am J Phys Anthropol*, 136(2):237–41
24. Zanolli C, Dean C, Rook L, et al (2016) Enamel thickness and enamel growth in *Oreopithecus*: Combining microtomographic and histological evidence. *CR Palevol*, 15(1):209–26
25. Zanolli C, Bayle P, Bondioli L, et al (2017) Is the deciduous/permanent molar enamel thickness ratio a taxon-specific indicator in extant and extinct hominids? *CR Palevol*, 16(5):702–14
26. Englisch LM, Kostrzewa K, Kopke S, et al (2017) Uneven distribution of enamel, dentine and cementum in cheek teeth of domestic horses (*Equus caballus*): A micro computed tomography study. *PLOS ONE*, 12(8):e0183220
27. Winkler DE, Kaiser TM (2015) Structural Morphology of Molars in Large Mammalian Herbivores: Enamel Content Varies between Tooth Positions. *PLOS ONE*, 10(8):e0135716
28. Kono RT, Suwa G (2008) Enamel Distribution Patterns of Extant Human and Hominoid Molars: Occlusal versus lateral enamel thickness. *Bull Natl Mus Nat Sci, Ser D*, 34:1–9
29. Guy F, Gouvard F, Boistel R, et al (2013) Prospective in (primate) dental analysis through tooth 3D topographical quantification. *PLoS ONE*, 8(6):e66142
30. Thiery G, Lazzari V, Ramdarshan A, Guy F (2017) Beyond the map: enamel distribution characterized from 3D dental topography. *Front Physiol*, 8:524
31. Strahler AN (1952) Hypsometric (area-altitude) analysis of erosional topography. *GSA Bulletin*, 63(11):1117–42
32. Lucas PW, Gaskins JT, Lowrey TK, et al (2012) Evolutionary optimization of material properties of a tropical seed. *J Roy Soc Interface*, 9(66):34–42
33. Scott EC (1979) Dental wear scoring technique. *American Journal of Physical Anthropology*, 51(2):213–17
34. Lazzari V, Guy F (2014) Quantitative three-dimensional topography in taxonomy applied to the dental morphology of catarrhines. *Bull Mém Soc Anthropol Paris*, 26(3–4):140–6
35. Guy F, Lazzari V, Gilissen E, Thiery G (2015) To what extent is primate second molar enamel occlusal morphology shaped by the enamel-dentine junction? *PLoS ONE*, 10(9):e0138802
36. R Core Team (2016) R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing
37. Schlager S (2017) Morpho and Rvcg – Shape Analysis in R. In: Zheng G, Li S, Székely G (eds), *Statistical Shape and Deformation Analysis*. Academic Press, pp 217–56
38. Macho GA, Jiang Y, Spears IR (2003) Enamel microstructure—a truly three-dimensional structure. *J Hum Evol*, 45(1):81–90
39. Lucas PW, Teaford MF (1994) Functional morphology of colobine teeth. In: Davies G, Oates J (eds) *Colobine monkeys: their ecology, behaviour and evolution*. Cambridge, Cambridge University Press, pp 173–203
40. Smith TM, Kupczik K, Machanda Z, et al (2012) Enamel thickness in Bornean and Sumatran orangutan dentitions. *Am J Phys Anthropol*, 147(3):417–26
41. Suwa G, Kono RT, Simpson SW, et al (2009) Paleobiological Implications of the *Ardipithecus ramidus* Dentition. *Science*, 326(69):94–9
42. McBrearty S, Jablonski NG (2005) First fossil chimpanzee. *Nature*, 437(7055):105–8
43. Horvath JE, Ramchandran GL, Fedrigo O, et al (2014) Genetic Comparisons Yield Insight into the Evolution of Enamel Thickness during Human Evolution. *J Hum Evol* 73:75–87