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Title: Enamel thickness trends in Plio-Pleistocene hominin mandibular molars

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Abstract: Enamel thickness continues to be an important morphological character in hominin systematics and is frequently invoked in dietary reconstructions of Plio-Pleistocene hominin taxa. However, to date, the majority of published data on molar enamel thickness of Pliocene and early Pleistocene hominins derive from naturally fractured random surfaces of a small number of specimens. In this study we systematically analyze enamel thickness in a large sample of Plio-Pleistocene fossil hominins (n = 99), extant hominoids (n=57), and modern humans (n=30). Based on analysis of 2D mesial planes of section derived from microtomography, we examine both average and relative enamel thickness, and the distribution of enamel across buccal, occlusal, and lingual components of mandibular molars. Our results confirm the trend for increasing enamel thickness during the Pliocene that culminates in the thick enamel of the robust Australopithecus species, and then decreases from early Homo to recent modern humans. All hominin taxa, and Pongo, share a regional average enamel thickness pattern of thick occlusal enamel and greater buccal than lingual enamel thickness. Pan is unique in exhibiting thinnest average enamel thickness in the occlusal basin. Statistical analysis indicates that among Pliocene hominins enamel thickness is a weak taxonomic discriminator. The data underlying these results are included as an appendix in the study.

We thank the editorial staff and the reviewers for their critical and helpful comments. Please find below a point by point explanation of how we addressed these comments with our revision.

Reviewers' comments:

AE Comments:
This is a very clean, easy to read manuscript that provides a thorough update to studies of enamel thickness in hominins. All three reviewers find the manuscript useful and praise its clarity, thoroughness, and brevity. However, the reviewers diverge in their opinions on how much revision is needed. Reviewer #3 finds the manuscript effectively acceptable as is, while the other two reviewers request some degree of revision. Reviewer #1 requests that the manuscript be revised with regard to "....inferences regarding the taxonomic valence and functional utility of enamel thickness..." Reviewer #2 focuses on the measurements of enamel thickness, and asks the authors especially to comment on why enamel is so thick in modern Homo, but not so in early Homo. The reviewer also offers some organizational suggestions.

The suggestions of the reviewers are certainly in the spirit of constructive advice, and should be relatively easy to manage. Given that the changes may involve extra analysis and an alteration in the primary thrust of the manuscript, I recommend that the authors revise the manuscript and reply to the reviewers comments. Pending the nature of the revisions, I suggest returning the ms to reviewer #1 if necessary.

Reviewer #1:
Overall, Skinner et al. provide a thorough and much needed compendium of enamel thickness in a range of early hominins, including early Homo. As such, it provides an extremely useful study that fills in the gap between good data available on hominoid enamel thickness and variation within species of Homo (i.e., Smith et al.). Examinations of this phenotype have a long history in both this field and this journal, and as such, topically it is appropriate for JHE. However, I do feel that in its current form, the ms tried to do too much, and in doing so, makes statements that may or may not be true; as there are not specific tests underlying such statements (see below), it leaves a reader not knowing how reliable these statements may be.

The one major drawback of this paper is the tension between being a wholly descriptive endeavor (and there's nothing wrong with that) and a series of inferential exercises (that would allow one to make specific statements about the taxonomic aspects of this feature) but are currently not present anywhere in the ms. I would strongly suggest that the ms be streamlined to focus on the descriptive part, as any inferences regarding the taxonomic valence and functional utility of enamel thickness are not tested, or hypotheses/predictions about these aspects stated explicitly. Engaging in the inferential part is essentially an exercise in making probabilistic statements, specifically about the likelihood that a species' phenotype (and variation therein) can confidently be distinguished from the range (and mean) expressed in other species. The authors do not do this - and again, that is okay - but instead conflate issues about degree of range overlap with probabilistic assessments of the taxonomic utility of that phenotype. So, statements such as "2D measurements of enamel thickness, which are commonly applied, are unreliable for definitive taxonomic distinction owing to the considerable overlap observed across taxa" (p. 15 l. 3-4) may be true. But as the authors know, two ranges can overlap quite

a bit but still be statistically - and thus by extension, perhaps biologically - different.

We thank the reviewer for this comment. We believe strongly that including the statistical analysis of enamel thickness differences between species is an important contribution of this paper, as enamel thickness is so often implicated in taxonomic hypotheses. Furthermore, the samples for some of the hominin taxa are almost complete (e.g., Au. africanus and A. robustus) and are unlikely to increase soon and this lends credence to our conclusions about the likely lack of significant difference between taxa (on average). However, we accept that we may have overstated our results and therefore we have re-written the relevant parts of the manuscript to more accurately reflect the strength/weaknesses of our results. We also have tried to clarify/separate the descriptive and inferential aspects of our results.

Additionally, given the effort of others to produce 3D measures of enamel volume for comparative purposes, it might be useful to explain why these authors feel a 2D assessment is sufficient. Furthermore, is there a reason to suspect that different conclusions regarding species ranges, means, etc., would be reached by extending this into three dimensions?

It would certainly be ideal to include 3D data for these taxa as the reviewer is correct that the overall picture of taxonomic, metameric and crown specific enamel thickness results would likely differ when the whole enamel crown is scaled against the whole dentine crown. We restricted our analysis to 2D in order to maximize sample size as it is very difficult to reconstruct the 3D enamel tissue that is missing from much of the study sample. In a 2D section there is a limited range of possibilities for how the missing enamel can be reconstructed. But in 3D this becomes theoretically and practically (e.g., warping the vertices of a 3D surface model) very difficult. Acknowledging that a 3D study would be an excellent next step we have edited the manuscript to more clearly justify our reporting of 2D data only and added to the discussion the fact that our results might differ if based on 3D data (and that this should be the topic of future studies of this material). Having said this we believe that the two approaches can be complimentary to each other and possible discrepancies could open new avenue for further research.

I also have a series of other small editorial comments:
Abstract:
Not sure that "implicated" is the correct word. Perhaps "invoked"?
Line 12: should read "early" not "Early" - that change should be made throughout the ms (e.g., p5, l. 7; p15, ls. 13, 15).

Both of these have been changed.

P4, l. 4 - "mandibular" not "lower." This may be minor, and the editors may feel differently, but I always thought that "upper" and "lower" were too colloquial, and that "maxillary" and "mandibular" seemed more appropriate. Plus (as in p5, l. 5, the authors use "mandibular"; they should pick one 'system' by which to indicate arcade and stick with that throughout the ms.

'lower' has now been changed to 'mandibular'

P4, l. 7 - what does "thin section mounted" mean?

This sentence has been re-worded for clarity: Ward and colleagues (2001) report linear measurements of 1.0 – 2.1mm based on ground thin-sections of naturally fractured (and thin-sectioned mounted) specimens…

Is it possible to use a term other than "opposite-side cusps"? Perhaps stick with the same theme and say "non-functional cusps" - though, admittedly, I hate those terms as all cusps are "functional" to some degree.
Opposite-side has been changed to 'adjacent'.

P5, l. 8 - remove comma after "as well as"

Done

P6, l.8 - why is it relevant to point out that the authors are avoiding the debate over the monophyly of the robust australopiths? Whether or not they represent a monophyletic clade does not influence whether or not enamel thickness patterning is a useful taxonomic discriminator.

This sentence has been removed.

P8, l. 7 - replace "we" with "was" - and I think the authors must provide more detailed information on how worn crowns were reconstructed. At the very least, a systematic methodology for doing so should be relayed. I appreciate the 'experiment' that they relay for Stw 308, but some readers would not characterize their measurement error of upwards of 5.2% as low, or acceptable. I am not suggesting that it isn't, I just think that there was likely some protocol that was followed that allowed the different researchers to reconstruct worn crowns, and that it is important for that protocol to be relayed in the Methods. And along those same lines, how much wear was tolerated; the authors use the phrase "partially worn" (p10, l. 1), but this could mean anything from slight wear to a high degree of cuspal wear, as in KNM-ER 1802 (Fig. 2). Can more information be provided on their tolerance for wear as a limiting factor in their sample composition?

We agree with the reviewer that our method and criteria for reconstructing missing enamel was lacking. We have now added the following to the methods section:

As can be seen in the SI figures, in the majority of cases this involved very minor additions of missing enamel over one or more cusp tips. In a small number of cases between one half and one third of the enamel cusp was reconstructed. Reconstruction was guided by reference to the outer enamel surface (to determine based on the presence of wear facets, where enamel was missing), the curvature of the enamel cap cross-section. Also, specimens which did not preserve an intact central occlusal basin (in cross-section) were removed as having preserved enamel on each side of a worn cusp is necessary for a reasonable estimation of missing enamel. Only in the thinly enameled apes (i.e., Gorilla and Pan) whose enamel distribution is quite uniform and whose dentine horns are relatively sharp, was it deemed acceptable to reconstruct missing tips of dentine horns.

We have also edited the text on p.10 to point out that the degree of applied artificial wear used for our test is at the extreme end compared to most of the study sample and in some sense this is a worst case scenario (e.g., thick enamelled taxon and marked wear) for a specimen that would have fit our criteria for reconstruction.

P10, l. 15 - should be singular, "hominin"; same for l. 17.

Done

P12, l. 21 - comma after "crown"

Done

P14, l. 21 - comma after "species." In fact, this first sentence of this section is a bit awkward and could do with it being broken into two sentences.

Split and reworded.

P15, l. 1 - "thick" not "think"
Here the authors state the 2D measures are not reliable for taxonomic purposes. So, are 3D measures better in this regard? Or is enamel thickness per se just not a useful tool for taxonomic discrimination? Please see my general comments above about the descriptive vs. the inferential.

Agreed. We have changed this sentence as follows:

Overall, the results of our analysis suggest that within the hominin clade, 2D measurements of enamel thickness may be unreliable for definitive taxonomic distinction. Specifically, the results of our statistical analysis can be used as a guide (taking into account sample size and variation within taxa) as to which taxonomic comparisons within the hominin clade are likely to yield informative taxonomic discrimination.

We feel that our current data, which are 2D, do not allows us to comment on whether 3D measures are better or not. We have still added a paragraph to this section of the discussion to address 3D vs 2D data.

If the authors insist on a probabilistic assessment of 'lack of taxonomic utility' than I would urge them to address that specifically within their analytical design. Furthermore, I would caution the authors that they should not discount the value of their particular phenotype for making taxonomically meaningful inferences, and then go ahead and use it anyway (for the isolated specimens).

I am not suggesting that the observations and explanations about enamel thickness variation laid out on p15 are unimportant. On the contrary, they are quite useful. Just that this whole section is at odds with the beginning of the Discussion as it is set against a backdrop relaying the taxonomic uselessness of enamel thickness.

Agreed. This section has been re-worded and our consideration of the utility of 2D enamel thickness more accurately reflects the results of our analysis (and is less pessimistic).

P15, l. 21 - "adaptation" should be plural

Done

P16, l. 5 - the use of the bridge "and a further increase in" in this sentence makes it somewhat confusing.

Reworded

p.16, l. 20. "Our results indicate that the majority of fossil hominins do exhibit greater enamel thickness buccally than lingually…" Of course they found that, the authors only examined mandibular molars, and this is a basic structural feature of most mammalian molars given the nature of the chewing cycle.

The phrase 'as expected' has been added to this sentence.

P16 -- I don't find the last section particularly strong; there are just some very broad statements attempting to link this phenotype to some broad notion of 'diet' or 'function'. In the first paragraph, they attribute the trend towards increasing enamel thickness to an increase in the incorporation of C4 foods. Fine. Then in the following paragraph, they link the same trend (at least for some australopiths) to an increase in the complexity of enamel surfaces. How so the authors envisage these two things (increasing C4 signal and increasing complexity of occlusal surfaces) as being linked? Are C4 foods (grasses, sedges, succulents, etc. - if you include CAM pathways foods) things that would leave a greater complexity signal? Or is it perhaps that increasing enamel thickness (i.e., global enamel thickness, as that is what AET assesses) is linked to increasing dietary breadth, which could manifest as an increase in a C4/CAM signal? As it stands, it is just not clear how the authors are linked two very different measures (isotopes and microwear textures) to the same trend in enamel thickness.

This section has been reorganized and expanded. In particular, the discussion of relevant isotopic data and microwear complexity has been split from the discussion of regional distribution of enamel. We have also attempted to clarify how current isotopic/microwear data are associated with the trends in enamel thickness found in our study.

One note about the tables:
Do the blank cells in Table 4 indicate a non-significant difference between taxa, or that sample sizes were too small to perform any statistical test? (I imagine the latter given the sample sizes by molar position listed in Table 1, right?)

All pairwise comparisons were calculated (even in the few cases with sample sizes of 1-2) and blank cells indicate non-significant results. This has now been clarified in the caption of Table 4.

Reviewer #2: This paper presents comprehensive quantification of enamel thickness for a comprehensive taxonomic sample of pre-homo fossil hominins, a limited sample of archaic homo, and with an adequate hominoid comparative sample.

I am not enough of an expert to verify the accuracy of your claim about most enamel thickness measurements being based on opportunistic fractures.

In your review of published data (page 3 line 19 and all of page 4) a summary table might help. You should include means given for the previous studies in addition to ranges.

We acknowledge that a summary table would be ideal, however, the lack of data at particular tooth positions for most taxa, the range of methods employed, and the opportunistic nature of the available data (i.e., some naturally fractured surfaces, some from ground thin sections) limits, in our view, the utility of a summary table in this case.

The methodological description is easy to follow and seems sound. I think it is okay that you visually reconstruct broken segments of the enamel surface in some cases to increase the sample size, because your error study confirms that its repeatable and not inaccurate. The inclusion of individual measurement data, images showing section location and actual cross-section used for measurements of most specimens is a very positive

feature of this work as it promotes incorporation of these data into future studies that wish to evaluate similar data collection methods on expanded samples. It also improves researchers' ability attempt to reproduce results if they desire.

One suggestion about enamel thickness evaluation… why not use a relative enamel thickness metric that is the square-root of enamel area divided by the length of the edj? This will give you a ratio that basically indicates whether the enamel cap looks more like a thin ribbon or a thick strap, which I think is what the human eye is gauging when it qualitatively makes an assessment about thickness. Your method for RET can be affected by additional un-investigated variables, like the shape of the EDJ. It is possible this different formulation of RET will even be somewhat independent of the presently used one as a result, and can be used in addition to it as a third way of evaluating enamel thickness.

Calculating relative enamel thickness as the square-root of enamel divided by the length of the EDJ is an interesting suggestion. However, we believe it is most appropriate to report measurements based on a protocol that is well established in the anthropological community. In our opinion, a comparison of the suggested approach and current methods would be best served by a more technically oriented paper (e.g., Benazzi et al., 2014) and is beyond the scope of this project.

The error studies are well-constructed and imbue confidence that methods are repeatable.

Analysis - when group sizes are less than 3, they should probably not be included in ANOVA's (eg Au. afarensis is represented by n=2 for m1, but included in ANOVA comparisons of Table 4).

We acknowledge that for the Kruskal-Wallis test across the whole sample the inclusion of taxa with n=2 are problematic, however, we would like to include them as they do indicate statistically significant differences between a number of pairwise comparisons that will be of interest to the anthropological community (e.g., that Homo sp indet differs significantly from modern humans).

Page 6, line 7-9: must be a more professional way of saying this.

This sentence has been removed.

Page 7, line 6: please provide a proper citation for Aviso software and include it in the bibliography

Following the JHE article Smith et al., 2012, we have changed this to Avizo (v6.3, FEI Inc.)

Page 7, line 14: I think it is confusing to call area of a 2D cross-section "surface area" just say "area" or "exposed-section area" If you say "surface area" some readers will confused thinking you are looking at the whole enamel surface and dentine surface

'surface' has been removed.

Page 13, lines 11-22 and page 14, lines 1-18: I think this discussion may be more appropriate in the introduction to help explain the motivation behind your methodology. You might consider citing Boyer (2008) who justified using a more subjective method of defining the portion of the tooth crown to be used for relief index calculation, with regard to the point that using the more objective approach (of Ungar and others in the

case of relief index) resulted in tooth orientations and measurements that were not broadly homologous for the sample at hand.

We thank the reviewer for this suggestion. As the main goal of the paper is to examine enamel thickness trends, rather than methodological issues, we would request to keep this topic in the discussion. We have now included Boyer (2008) in this section.

Page 15, lines 5-7 (as an example) - in this section you explain how certain variables they measured support or are consistent with a particular hypotheses, but say nothing about other, leaving the reader wondering. In the lines mentioned, you state that KNM WT-8556 falls in the range of Au africanus and Au afarensis in tooth size and AET. However, what about RET? Please at least mention that it is either outside the range - or inside but non-distinctive. Also this statement is vague - for the uninitiated, we don't know what your point is. Does this observation support an assignment to K. platyops or refute it? You don't actually tell us what your interpretation is. Apply the issue in this example to the other cases you mention in this section as well.

As also noted also by reviewer 1 we agree that this section was vague. We have added additional discussion of particular specimens and been specific about the implications of our results for each discussed specimen.

Page 16, lines 1-9 - would it be possible to do a correlation analysis on species mean enamel thickness and delta C13 values gleaned from the literature (like the Cerling papers?). It would be awesome if you could report a significant pearson correlation coefficient or something.

This is a great idea. Unfortunately, having consulted the supplementary information in Cerling et al., 2013 there is very little overlap in specimens (presumably because they were only given permission to destructively sample the less well preserved specimens). Only KNM-ER 1802B, 820 and 992, and KNM-WT 8556 were sampled. Therefore, we did not pursue this very interesting suggestion.

Coming to your conclusion, I think something is still missing from you analyses and discussion. You certainly demonstrate both relative and average enamel thickness increase through australopithecine evolution. But why is Homo sapiens so high and early homo so low in thickness?

We are slightly confused by this comment as our results state the opposite (i.e., recent Homo sapiens have thinner enamel than early Homo. We also refer to how are results for the Homo sp material from Omo is consistent with the findings of thick enamel in early Homo published by Smith et al., 2012.

Also it would still be nice to know how much of the AET variation is explained by tooth size versus RET. Couldn't you run a multiple regression with AET as the dependent variable and the other two as independents and comment on this more explicitly? If you showed that tooth size contributed substantially less to the variance, that would be interesting because you could argue that whatever dietary shifts happened put selective pressures on both absolute tooth size and on proportional enamel thickness. Winchester et al (2014) discuss increasing enamel thickness, tooth size, and hyspodonty as different strategies of achieving a similar goal - to put more enamel in the mouth and increase the "lifetime" of the tooth (and consequently its owner) in the face of an abrasive diet. So here you have an opportunity to comment on how much the evolutionary response for increasingly tough foods was expressed through tooth size increase versus proportional enamel thickness increase.

This is an interesting idea, however, we are not convinced of the statistical meaning of including RET as one of the independent variables as it is derived from AET (being simply the quotient of AET/SQRT of dentine area. We tried using tooth size and dentine area, however, even the latter is not independent from AET which is derived using EDJ length. For the purpose of this manuscript, and given the theoretical difficulties in finding a ethick measure that is not correlated with tooth size, we have chosen not pursue this line of investigation for the moment.

I also really think that RET as a ratio of sqrt(enamel area)/(edj length) will be a better reflector than (enamel area/dentine area).

See above

I did not check your bibliography for errors.

Overall good work.

Reviewer #3: This is a nice paper on enamel thickness. I found it clearly written and informative. The review of the topic is certainly of interest to JHE readers. I have only the most minor comments:
On page 4, perhaps the authors could explain linear measurements and radial linear measurements. I assume this is just taking a measurement of the exposed enamel, but I am not certain. Perhaps a figure could clarify?

R***adial thickness measurements are now explained in the text.***

On Page 5 I would refer to 'modern humans' as 'recent humans' just to be clear, since "modern" could include fossil H.s.

Done

On page 9, line 15 needs a comma after 'which'
Done

Also on page 9 the last full sentence (lines 21 and 22) is a bit awkward to read.

This sentence has been reworded.

Page 10, there is a type-o in line 1 (ordedr)

Corrected

Page 10 lines 14-15 - this sentence is difficult to read.

Reworded

Page 14, line 22 needs a comma after 'which'

Reworded

Other than these minor suggests I see no issues with publishing the manuscript as is.

Title: Enamel thickness trends in Plio-Pleistocene hominin mandibular molars

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Keywords: enamel, relative enamel thickness, average enamel thickness, *Australopithecus*, Paranthropus, *Homo*, microCT

Abstract

Enamel thickness continues to be an important morphological character in hominin systematics and is frequently invoked in dietary reconstructions of Plio-Pleistocene hominin taxa. However, to date, the majority of published data on molar enamel thickness of Pliocene and early Pleistocene hominins derive from naturally fractured random surfaces of a small number of specimens. In this study we systematically analyze enamel thickness in a large sample of Plio-Pleistocene fossil hominins (n = 99), extant hominoids (n=57), and modern humans (n=30). Based on analysis of 2D mesial planes of section derived from microtomography, we examine both average and relative enamel thickness, and the distribution of enamel across buccal, occlusal, and lingual components of mandibular molars. Our results confirm the trend for increasing enamel thickness during the Pliocene that culminates in the thick enamel of the robust *Australopithecus* species, and then decreases from early *Homo* to recent modern humans. All hominin taxa, and *Pongo*, share a regional average enamel thickness pattern of thick occlusal enamel and greater buccal than lingual enamel thickness. *Pan* is unique in exhibiting thinnest average enamel thickness in the occlusal basin. Statistical analysis indicates that among Pliocene hominins enamel thickness is a weak taxonomic discriminator. The data underlying these results are included as an appendix in the study.

Introduction

The thickness and distribution of enamel tissue across tooth crowns remains an important character in assessments of the taxonomy, phylogeny, and dietary reconstructions of fossil primates. Within the hominoid clade, over three decades of research has elucidated patterns of enamel thickness variation in fossil hominins (e.g., Martin, 1985; Beynon and Wood, 1986; Grine and Martin, 1988; Conroy, 1991; Macho and Thackeray, 1992; Schwartz et al., 1998; Brunet et al., 2002, 2005; Olejniczak and Grine, 2005; Smith et al., 2006b; White et al., 2006; Olejniczak et al., 2008a/b; Smith et al., 2009a/b, 2012a), fossil hominoids (e.g., Martin et al., 2003; Smith et al., 2003, Olejniczak et al., 2008c), and extant hominoids (Molnar and Gantt, 1977; Gantt, 1986; Grine, 1991; Schwartz, 2000; Kono, 2004; Tafforeau, 2004; Smith et al., 2005, 2006a; Kono and Suwa, 2008; Olejniczak et al., 2008d; Smith et al., 2012b). Many of these studies dating to the last decade have utilized microtomography to systematically produce homologous mesial planes of section in molars, which has led to more rigorous taxonomic comparisons (see review in Smith et al., 2012a). However, due to inherent practical and methodological difficulties in producing microtomographic scans of their dentitions, systematic analysis has not been conducted on the majority of otherwise extensively investigated Pliocene hominin taxa. In this contribution we fill in this gap for many species of the genus *Australopithecus* and complement the extensive review recently published by Smith and colleagues (2012a) for Pleistocene *Homo*.

To date the majority of reported enamel thickness values for Pliocene hominins derive from linear measurements taken on naturally cracked surfaces of molars. For example, White and colleagues (1994) report linear measurements of *Ardipithecus* (*Ar.*) *ramidus* molars ranging from 1.1-1.2mm and for *Australopithecus* (*Au.*) *afarensis* of 1.4-2.0mm. Based on microtomography,

Suwa and colleagues (2009) reported *Ar. ramidus* as having enamel thickness greater than *Pan* but thinner than later *Australopithecus*. Johanson and colleagues (1982) and White and colleagues (2000) report linear dimensions for various *Au. afarensis* specimens but do not report any measurements for mandibular molars. In the initial publication of the *Au. anamensis* specimens, linear measurements of upper and mandibular molars ranged between 1.5 and 2.0mm (Leakey et al., 1995). Ward and colleagues (2001) report linear measurements of 1.0 – 2.1mm based on ground thin-sections of naturally fractured (and thin-sectioned mounted) specimens (upper molar KNM-ER 30748 and mandibular molar KNM-ER 30749) in the occlusal basin, cusp tip and lingual and buccal walls. The *Au. anamensis* finds from Asa Issie exhibit radial (i.e., measured not in a mesial plane of section but rather along a trajectory running perpendicular from the dentine surface to the enamel surface) linear measurements of 1.7 – 2.3mm for functional cusps (i.e., buccal cusps on mandibular molars and lingual cusps on upper molars) and 1.3 – 2.0mm for adjacent cusps (White et al., 2006). Haile-Selassie and colleagues (2010) assessed enamel thickness in the Woranso-Mille material from naturally fractured molars and concluded that the range (1.5-2.1mm) falls within the range of reported measurements for *Au. afarensis, Au. anamensis* and *Au. africanus*. In their analysis of crown formation times Lacruz and Ramirez Rozzi (2010) report linear enamel thickness measurements of 1.95mm (AL 333-52), 2.13mm (AL 366-1), and 1.71mm (Omo L2-79). Examining *Au. africanus* specimens, Grine and Martin (1988) report average enamel thickness values of 1.81mm (Stw 284; now referred to as Stw 280) and 1.78mm (Stw 402), and relative enamel thickness values of 21.27 (Stw 280) and 23.06 (Stw 402). Macho and Thackeray (1992) used medical CT to examine the regional distribution of enamel thickness across the crowns of *Au. robustus*, *Au. africanus*, and *Homo* sp. maxillary molars finding considerable overlap

between taxa in many regions of the crown. Finally, Olejniczak and colleagues (2008b) published data on *Au. africanus* and *Au. robustus* from South Africa, expanding their analysis to 3D enamel distribution across the crown. Collectively, however, the limited sample size, limited assessment of enamel thickness (i.e., often linear measurements), and variation in location of measurement result in a poor characterization of enamel thickness variation along the molar row in Pliocene hominins.

Using microtomography and controlled mesial planes of section in mandibular molars, we analyze enamel thickness to assess taxonomic differences in mandibular molar crowns of *Au. anamensis*, *Au. afarensis*, *Au. africanus*, *Au. boisei*, *Au. robustus*, and specimens of early *Homo*. We compare these results to samples of *Pan*, *Gorilla*, and *Pongo*, as well as a sample of recent humans. The goals of this study are to: 1) analyze enamel thickness variation among Plio-Pleistocene hominins using a 2D mesial plane of section; 2) characterize the distribution of lingual, occlusal and buccal enamel among hominin taxa; 3) assess the reliability of taxonomic discrimination based on enamel thickness measured in a 2D section; 4) evaluate the affinity of taxonomically ambiguous specimens based on their enamel thickness values; and 5) provide molar-specific enamel thickness measurements for extant apes and fossil hominins for use by other researchers.

Materials

The study sample consists of mandibular molars (n = 186) belonging to both extant hominoids and fossil hominins and is detailed in full in Appendix 1. The number of first, second and third molars of each taxon is listed in Table 1. This sample is the largest compiled to date for a

systematic analysis of enamel thickness in Plio-Pleistocene hominins of Africa. Molars either derive from mandibles or are isolated specimens. In the case of the latter, the justification for assigning a molar to a particular position is also noted. Specimens were chosen for study that exhibited no evidence of known pathology. Given that sex is unknown for the majority of fossil specimens it was not incorporated into our analysis as a variable.

Hominoid taxa include *Pongo* sp., *Gorilla* sp., *Pan paniscus* and *Pan troglodytes* ssp. Due to the small sample sizes for some molar positions no species delineation was made for *Pongo* and *Gorilla* and no subspecies delineation for *Pan troglodytes*. The Plio-Pleistocene hominin taxa include *Au*. *anamensis*, *Au*. *afarensis*, *Au*. *africanus*, *Au*. *aethiopicus*, *Au*. *boisei*, *Au*. *robustus*, *Homo* sp. indet., *H*. *erectus*, and modern *H*. *sapiens*. A number of specimens of uncertain taxonomic affinity were also analyzed and their taxonomic affinity assessed based on their measured enamel thickness values.

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 for Natural History (ZMB), Berlin, Germany; the Senckenberg Research Institute (SMF), Frankfurt, Germany; the Royal Museum for Central Africa (MRAC), Terverun, Belgium; and the Max Planck Institute for Evolutionary Anthropology (MPI), Leipzig, Germany. The modern human sample derives from the Leipzig University Anatomical Collection (ULAC), Leipzig, Germany; the “Francisc J. Rainer” Anthropology Institute (R), Bucharest, Romania; and the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

Methods

To obtain a 2D mesial plane of section each molar was non-destructively imaged using computed tomography (using either a BIR Actis 300/225 FP or SkyScan 1172 microtomographic scanner) with a resultant isometric voxel size of 15-65 μm^3. The CT data set of each specimen was rotated manually in Avizo (v6.3, FEI Inc.) into anatomical position. Next, a plane was placed perpendicular to the occlusal plane and passing through the tip of the protoconid dentine horn. This plane was then rotated to pass through the tip of the metaconid dentine horn. This slice image was then saved in TIFF format (Figure 1). Benazzi and colleagues (2014) have outlined a methodology to produce repeatable 2D planes of section. This methodology was not adopted for this study because it is difficult to apply to many of the fragmentary hominin teeth used in this study whose cervical line is not preserved (and see Discussion).

Four variables were measured on each mesial section using ImageJ (v1.47, NIH): area of the enamel cap (mm^2), area of the coronal dentine crown (mm^2) delimited by a line drawn between the most cervical enamel extensions, length of the enamel-dentine junction, or EDJ (mm), and bi-cervical diameter (mm) also measured between the most cervical enamel extensions. These measurements are listed for each specimen in Appendix 1. In order to assess regional differences in enamel thickness buccolingually across the tooth crown the mesial crown section was divided into lingual, occlusal and buccal components. This division was accomplished in ImageJ by connecting the tip of each dentine horn to the corresponding tip of the cusp at the outer enamel surface. Figure 1 illustrates the measurement locations.

Figure 1 here

The Supplementary Information contains figures of the majority of hominin specimens measured as well as a sample of extant hominoids and modern humans, illustrating the location of the plane of section and the delineation of the enamel and dentine components of the section. This is particularly important as it allows researchers to assess our placement of the plane of section. In a number of cases, and particularly in the fossil hominin sample, missing enamel over cusp tips was reconstructed in the mesial section. As can be seen in the SI figures, in the majority of cases this involved very minor additions of missing enamel over one or more cusp tips. In a small number of cases between one half and one third of the enamel cusp was reconstructed. Reconstruction was guided by reference to the outer enamel surface (to determine based on the presence of wear facets, where enamel was missing), the curvature of the enamel cap cross-section. Also, specimens which did not preserve an intact central occlusal basin (in cross-section) were removed as having preserved enamel on each side of a worn cusp is necessary for a reasonable estimation of missing enamel. Only in the thinly enameled apes (i.e., *Gorilla* and *Pan*) whose enamel distribution is quite uniform and whose dentine horns are relatively sharp, was it deemed acceptable to reconstruct missing tips of dentine horns. While this reconstruction of missing enamel introduces a subjective component into our analysis, it is worthwhile for characterization of enamel thickness trends within the hominin clade as the number of absolutely unworn hominin teeth is very small. In almost all cases a researcher can evaluate our reconstruction of each specimen in the supplementary material and since we provide all of the raw data, they are able to drop specimens from the sample and re-calculate sample statistics for their own purposes.

Quantitative analyses

We calculated two standard measures of enamel thickness following well established protocols (Martin, 1985; Olejniczak et al., 2008a). Average enamel thickness (AET) was calculated as the area of the enamel cap divided by the length of the EDJ. This yields the average straight line distance from the EDJ to the enamel surface in millimeters. Relative enamel thickness (RET) was calculated as AET divided by the square root of dentine area and multiplied by 100. This yields a scale-free value of enamel thickness that allows comparisons between taxa of differing tooth/body size. For the assessment of regional variation in AET across the tooth crown we divided the surface area of the enamel for each region by its corresponding EDJ length. Plots of the log of AET against the log of dentine area were used to illustrate the relationship between AET and tooth size and to visualize the placement of specimens of uncertain taxonomic affinity. Significant differences in AET and RET between the study taxa were assessed in SPSS 20 using a Kruskal-Wallis Test with posthoc pairwise comparisons.

Intraobserver error in AET and RET was assessed by MMS and CG each repeating the complete processing sequence (including rotation and mesial section derivation) for two specimens 10 times each, over a period of three months. Interobserver error rates (calculated as the difference in the measurement of MMS and CG divided by the average of their measurements) were 2.4% (AET) and 3.56% (RET) for a modern human specimen and 0.6% (AET) and 1.66% (RET) for an *Au. robustus* specimen. Intraobserver error (calculated as the average deviation from the mean of 10 measurements of a modern human specimen) was 1.3% (AET) and 1.4% (RET) for MMS and 0.9% (AET) and 1.1% (RET) for CG. These values are considered acceptable and establish the repeatability of the protocol. We also compared our measurements of particular specimens with

1 those from a previous study (Olejniczak et al., 2008a) and noted mean differences of between 3.1
2 – 7.1%. In most cases, variation is due to differences in locating the bi-cervical line, which can
3 affect RET in particular due to the marked effect of changes in coronal dentine surface area.
4 We also tested the potential impact of the inclusion of partially worn teeth by artificially
5 wearing one of the unworn thick-enameled hominin teeth (STW 308) and blindly reconstructing
6 the missing enamel (Supplementary Figure 1). This reconstruction was conducted five times on
7 different occasions. The range of measured enamel area was 40.1-43.0mm, resulting in a range of
8 calculated AET of 1.81-1.94mm. This results in a difference in AET of 1.0-5.2%. Given the high
9 degree of applied artificial wear (that is at the extreme end relative to the majority of specimens in
10 the study sample) in this thick enameled specimen this test is essentially the worst case scenario
11 for a specimen that would have fit our criteria for reconstruction, and this level of error supports
12 the inclusion of partially worn specimens in the analysis in order to supplement sample size and
13 improve the characterization of enamel thickness in fossil hominin species.
14
15 **Results**
16 Figure 2 presents a selection of second molars from the majority of the study taxa.
17 Additionally, Supplementary Figures 2-19 illustrate 2D planes of section, measured enamel and
18 dentine area, and the position of the plane of section for all hominin molars and the majority of
19 the extant comparative sample. Table 2 lists the mean and standard deviation calculated for each
20 of the four measured variables, AET, and RET for each taxon at each molar position. Table 3 lists
21 the values of measured variables for the specimens of unknown taxonomic affiliation. Table 4 lists
22 the results of the Kruskal-Wallis posthoc pairwise comparisons for AET and RET among the study

taxa at each molar position. Although across the study taxa all tests of AET and RET are highly significant ($p = <0.001$), pairwise comparisons reveal that this result is driven primarily by significant differences between the extant apes (*Pan*, *Gorilla*, *Pongo,* and recent humans) on the one hand, and the thick enameled *Australopithecus* species on the other. Within fossil hominin first molars, only *Au. anamensis* is significantly thinner in AET than *Au. robustus*. Within fossil hominin second molars, *Au. anamensis* is significantly thinner than both *Au. boisei* and *Au. robustus* in AET and RET. Additionally, second molars of *Au. africanus* are significantly thinner than *Au. robustus* in RET. For third molars, *Au. anamensis* is significantly thinner than both *Au. boisei* and *Au. robustus* in AET and thinner than *Au. robustus* in RET. *Au. boisei* third molars are significantly thicker than *H. erectus* in AET.

Figure 2 here

Table 2 here

Table 3 here

Figure 3 presents box plots of AET across the study sample. There is a clear trend of increasing AET from *Au. anamensis* to *Au. africanus* and a general increase in AET from first to third molars in these taxa. *Au. boisei* and *Au. robustus* exhibit the highest AET values, with the second molar being the thickest on average in *Au. robustus*. AET in *Homo* sp. is comparable with *Au. africanus* and then there is a marked decrease in *H. erectus* and then modern humans. Of the extant apes, *Pongo* presents the thickest AET at each molar position and *Pan* the thinnest (with *Gorilla* intermediate). Figure 4 presents box plots of RET across the study sample and highlights a broadly similar trend of increasing thickness in *Australopithecus*, followed by a decrease in *Homo*. As RET is essentially scaled by tooth size there is greater overlap with large toothed taxa, such as

Au. africanus, being more similar to *Au. anamensis* in RET, than AET. Similarly, the position of *Gorilla* and *Pan* shifts as the former's enamel thickness is relatively smaller than the latter's after scaling for tooth size.

Figure 3 here

Figure 4 here

Table 4 here

Table 5 lists the mean and standard deviation of buccal, occlusal, and lingual measurements of AET for each of the study taxa. Figure 5 illustrates the pattern of regional variation in a combined molar sample for each taxon. The majority of study taxa present a consistent regional distribution with AET concentrated in the occlusal basin and a slight dominance of the buccal side over the lingual side. *Gorilla* is unique in presenting thickest AET buccally (and decreasing from occlusal to lingual), while *Pan* possesses thinnest enamel in the occlusal basin.

Figure 5 here

Table 5 here

Figures 6-8 present bivariate plots of the log of AET against the log of dentine area for first second and third molars, respectively. In essence, this is a visual representation of RET. Generally, the distribution of taxa is consistent in first, second and third molars with *Gorilla* being characterized by thin enamel covering a large dentine core. Although broadly overlapping in tooth size, *Au. boisei* and *Au. robustus* exhibit thicker AET than *Au. africanus*. In second and third molars, *Au. afarensis* tends to exhibit relatively thicker AET than *Au. anamensis*. *Pan* is consistently positioned and exhibits thin enamel over its relatively small molars. With regard to the first molar specimens of uncertain taxonomic affinity (Table 3), KNM-WT 8556 falls within the range of *Au.*

africanus and close to *Au. afarensis*. Omo K7-19 has thick AET similar to *Homo* sp. and *Au. robustus*, while Omo L26-1g sits between the convex hulls of *Au. robustus* and *Au. africanus*. Second molars L28-31 and L795-1 have relatively thick AET for the size of their dentine crown and fall in proximity to a cluster of *Au. robustus*, *Au. boisei,* and *Au. aethiopicus*. Finally, L28-30 exhibits thick AET for its size, while Omo 75s-16 falls near modern humans and *H. erectus*.

Figure 6 here

Figure 7 here

Figure 8 here

Discussion

Defining and quantifying enamel thickness

Since the first analyses of naturally fractured tooth crowns, the definition of enamel thickness and the way it is measured have been in flux and varied substantially from one author to another. As a consequence, though enamel thickness has frequently been used to interpret taxonomy and diet in hominin fossils, methods used to quantify it have been less than satisfactory in many cases. Researchers depended, short of other options, on naturally fractured surfaces where the plane of breakage is random, resulting in non-comparable metric data. Also enamel thickness data were not necessarily derived from the same cusps, tooth type or sides of the teeth, questioning the biological homology of the measured data. None the less, recently developed imaging and visualization methods have resulted in more systematic assessments of enamel thickness variation (e.g., Schwartz et al., 2000; Kono, 2004; Tafforeau, 2004; Kono and Suwa, 2008; Olejniczak et al., 2008a). These non-invasive techniques offer a multitude of possibilities to

quantify enamel distribution across the tooth or in particular regions of the tooth crown, and allow for collecting and combing data on large fossil data sets.

Benazzi et al (2014) have published a revised CT-based methodology, the goal of which is to remove as much subjectivity in defining a mesial plane of section as possible. This method focuses on the cervix as a means of defining a basal plane from which a perpendicular plane can be derived and placed at the intersection of particular dentine horns. Their methodology is an important step forward in developing published data that can be used by other researchers, however, it can be challenging to apply the method to fragmentary fossil teeth. In particular, partial crowns may preserve a mesial section but lack the distal portion of the cervix. In order to include such specimens they would have to be oriented manually, albeit virtually, as is done in this study. Also, when cervical enamel is missing (which is quite common in fossil specimens) these regions of the cervix will have to be estimated.

There are also many examples of fossil/modern teeth whose pattern of enamel extension around the circumference of the crown (and by consequence the cervix) is abnormal or results in the creation of a plane of section that is not biologically homologous. Also, the approach of Olejniczak (2006) that uses a plane fit to three dentine horns can result in the measurement of non-homologous planes of section due to variation in relative dentine horn height (which should not be directly associated with enamel thickness). If the theoretical basis of the 2D plane of section is to capture functionally and/or developmentally (sensu Butler, 1956) relevant enamel thickness values associated with occlusion (and thus perpendicular to the occlusal plane), then the cervix cannot always be relied upon to produce this plane. We would caution that in the absence of a critical evaluation of the plane produced, systematic variation can be introduced in enamel

thickness measurements that exceeds normal levels of inter- and intraobserver error. Thus, we stress the importance of biological homology as a defining principle in developing measurement protocols (see also Boyer, 2008). Future studies should test the comparability of the method outlined by Benazzi et al (2014) and a basal plane oriented manually (as was done in this study). If it is found to result in acceptably small differences in measured AET and RET, then researchers can be confident in combing manually oriented specimens when it is necessary to do so to produce an homologous plane of section.

Enamel thickness and its role in taxonomic determination

Enamel thickness has been widely used to diagnose hominin species. In particular, the geochronologically earliest ones are expected to possess at least moderately thicker enamel compared to that of extant African great apes, while 'robust' australopiths are characterized as having very thick enamel. Overall, the results of our analysis suggest that within the hominin clade, 2D measurements of enamel thickness may be unreliable for definitive taxonomic distinction. Specifically, the results of our statistical analysis can be used as a guide (taking into account sample size and variation within taxa) as to which taxonomic comparisons within the hominin clade are likely to yield informative taxonomic discrimination. And the database of individual measurements we provide can be used to statistically test particular taxonomic hypotheses or determine whether enamel thickness can be used to inform the affinity of newly discovered/measured specimens. Acknowledging these potential shortcomings, AET and RET values do offer some insight into the affinity of taxonomically uncertain specimens. KNM-WT 8556 has been attributed to *Kenyanthropus platyops* (Leakey et al., 2001) and *Au. africanus* (Brown et

al., 2001). AET and tooth size (based on dentine surface area) of the mandibular first molar are within the range of *Au. africanus* and in the vicinity of *Au. afarensis* in (Fig. 6). The RET value of 21.79 for this specimen is within the range of *Au. africanus* and within one standard deviation of the mean of *Au. afarensis*. Unfortunately, until enamel thickness values in a sample of mandibular first molars of *K. platyops* are published it is unlikely that enamel thickness can be used as a primary criterion for the taxonomic affinity of this specimen. Omo K7-1969-19 is similar in size, AET, and RET to KNM-ER 1802 and DNH 67 and would be consistent with a classification to *Homo* sp. (but see Leakey et al., 2012 for a discussion of the taxonomic affinity of KNM-ER 1802). L26-1g was attributed to *Au. africanus* by Howell and colleagues (1987) and has AET and RET values that align it with *Au. afarensis* and/or *Homo* sp. L28-30 (M2) and L28-31 (M3) are attributed to *Homo* sp. by Suwa (1996). Both present AET and RET values similar to *Au. boisei* but over a relatively small dentine crown, which would be consistent with the recent finding of high AET values in early *Homo* by Smith and colleagues (2012a). Omo 75s-16 has relatively low AET and moderately high RET, suggesting that while it may be early *Homo* (Suwa pers communication) it is different from other potential early *Homo* specimens such as L28-30. An important possibility for further clarifying the taxonomic status of these specimens from West Turkana, Kenya and Omo, Ethiopia will be an analysis of enamel thickness in the sample of ~3Ma teeth from Lomekwi, Kenya (Brown et al., 2001; Leakey et al., 2001).

An increasing number of studies are examining dental tissue proportions in 3D (e.g., Kono, 2004; Olejniczak et al., 2008a/b; Kono and Suwa, 2008; Suwa et al., 2009; Benazzi et al., 2014; Zanolli et al., 2014) and it is clear that taxonomic differences in molar crown shape (e.g., being mesiodistally wider or narrower) will result in differences in AET and RET between 2D mesial plane

of section and 3D whole crown calculations (Olejniczak et al., 2008a). As there are tooth crown shape differences between Pliocene hominins it will be necessary to determine whether the patterns of statistically significant differences (and lack thereof in some pairwise comparisons) found in this study, hold for 3D analyses of these specimens. However, it should be noted that reconstructing missing enamel in 3D (due to fragmentation of the enamel cap around the cervix, missing portions of the enamel cap, and the difficulty of reconstructing the original outer enamel surface) can be extremely difficult and sample sizes may drop precipitously for many hominin taxa. Additional analyses of crown and/or EDJ morphology may further elucidate the taxonomic affinity of these specimens (Skinner et al., 2008a/b, 2009).

Dietary adaptation and enamel thickness

Enamel thickness has also been the basis for interpreting hominoid/hominin dietary adaptations (e.g., Kay, 1981; Dumont, 1995; Shimizu, 2002; Vogel et al., 2008; Smith et al., 2012b). As such, thick enamel is commonly associated with the consumption of hard (Constantino et al., 2009; 2011) and/or abrasive (Rabenold and Pearson, 2011) grass-based food material. Recent results from isotopic and microwear research (see review in Sponheimer et al., 2013), have created favorable conditions for testing these longstanding hypotheses. Isotopic studies of dental enamel (e.g., Wynn et al., 2013; Cerling et al., 2013) demonstrate an increase in C4 consumption from *Au. anamensis* to *Au. afarensis,* and an additional increase in C4 consumption from *Au. aethiopicus* and *Au. boisei*. Our results suggest that this increase in C4 consumption by hominins is associated with a concomitant increase in enamel thickness; however, whether increased enamel thickness is related to abrasion resistance (Rabenold and Pearson, 2011) or fracture resistance

(Constantino et al., 2009, 2011; Strait et al., 2013) continues to be debated. Ungar and Sponheimer (2011) analyzed microwear texture of Plio-Pleistocene hominins and found a decrease in complexity from *Au. anamensis*, to *Au. afarensis*, to *Au. boisei* that could correlate to an increase in the need to shear tough foods (such as C4 grasses). Thus, for these taxa in East Africa there is an associated change from greater complexity, lower C4 isotopic signatures and thinner enamel in *Au. anamensis*, to reduced complexity, higher C4 isotopic signatures and thicker enamel in *Au. boisei*. However, a similar trend across Pliocene hominins is complicated by the findings of Ungar and Sponheimer (2011) of relatively high microwear complexity and relatively high C3 plant consumption found by in *Au. robustus* (which also overlaps somewhat with the patterns in *H. erectus*). Since *Au. robustus* has similarly high AET/RET values as *Au. boisei*, our results support the hypothesis that thick enamel in *Au. robustus* (and possibly early *Homo*) cannot be attributed to similar selective pressures (Ungar and Sponheimer, 2011; Sponheimer et al., 2013). Delezene and colleagues (2013) analyzed microwear texture of *Au. afarensis* and *Au. africanus* premolars and molars and found an increase in complexity (a proxy for hard-object feeding) from premolars to molars within each species. Future analyses should explore whether the microwear pattern along the tooth row (premolars to molars) is also matched in enamel thickness distribution.

In his analysis of enamel thickness distribution in mesial sections of hominoid upper molars, Schwartz (2000) noted a strong taxonomic signal and a relationship between differential enamel distribution and diet. A number of studies have highlighted the influence of differential distribution of enamel across the crown and tooth function (Macho and Thackeray, 1992; Shimizu, 2002; Kono, 2004; Kono and Suwa, 2008). Our results indicate that the majority of fossil hominins, as expected, do exhibit greater enamel thickness buccally than lingually. However, unexpectedly,

the thickest enamel is usually found occlusally. Thus, any variation in diet associated with changes in isotopic chemistry, microwear, tooth size, does not seem to be associated with variation in differential distribution of enamel buccolingually across the crown. Future studies should consider more detailed mapping of the 3D distribution of enamel across the crown (e.g., Kono, 2004; Olejniczak et al., 2008) and correlations with primary facet orientation and position (Kullmer et al., 2009). Ultimately, these studies can be expanded to using FE models to test the interaction of enamel thickness, dentine crown morphology, and tooth wear on tooth function (e.g., Benazzi et al., 2011, 2013).

Conclusion

In this study we report on 2D mesial plane of section enamel thickness values in Pliocene and early Pleistocene fossil hominins and non-human large ape mandibular molars. Our findings confirm a general trend for increasing enamel thickness throughout the Pliocene *Australopithecus* species culminating in *Au. boisei*. The majority of hominin and non-human large ape species exhibit thickest enamel in the occlusal basin, less thick buccally and thinnest lingually. *Gorilla* exhibits the thinnest enamel relative to its tooth crown size and has thickest enamel buccally. *Pan* species are unique in exhibiting the thinnest enamel occlusally. While there is considerable overlap in average and relative enamel thickness values among hominins of similar geochronological age, enamel thickness retains the potential to be a useful taxonomic indicator for particular genera and time periods.

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Figure captions

Figure 1. Illustration of protocol used to collect enamel thickness data. Top left shows a surface model of a mandibular first molar with a red line indicating the location of the 2D plane of section. Top right shows the 2D plane of section for this specimen upon which measurements were collected. Bottom right shows the surface area of the enamel cap (yellow) and the dentine (blue). Bottom left shows the bi-cervical diameter measurement (red line), the enamel-dentine junction length measurement (white line), and the black lines delimit the lingual, occlusal and buccal regions used to measure the distribution of enamel across the crown.

Figure 2. Selection of mandibular second molars of the study sample. The red line indicates slice position and the segmented enamel and dentine image is overlaid on original slice to show areas corrected for missing enamel. White scale bar = 5mm.

Figure 3. Box plots of average enamel thickness values for each taxon.

Figure 4. Box plots of relative enamel thickness values for each taxon.

Figure 5. Patterns of regional (buccal, occlusal, lingual) average enamel thickness for the combined molar sample of each taxon. Hominins and *Pongo* tend to exhibit thickest enamel in the occlusal basin, while *Gorilla* and *Pan* exhibit thickest enamel on the lateral tooth crown.

Figure 6. Plot of AET (log) against dentine surface area (log) for the first molar. Specimens of uncertain taxonomic affinity are marked with stars.

Figure 7. Plot of AET (log) against dentine surface area (log) for the second molar. Specimens of uncertain taxonomic affinity are marked with stars.

Figure 8. Plot of AET (log) against dentine surface area (log) for the third molar. Specimens of uncertain taxonomic affinity are marked with stars.

Supplementary figure captions

Supplementary Figure 1. Example of estimation of worn enamel in a 2D mesial section. The unworn crown of STW 308 (top left) was artificially worn (top right) to remove a substantial proportion of enamel (much greater than in most of the study specimens). The original segmentation of enamel and dentine tissue (bottom left) can be compared to the blind estimation of the original enamel (bottom right). Note that there is only a 2.2% difference in the calculated average enamel thickness between the original and reconstructed specimen.

Supplementary Figure 1. *Au. anamensis* M1 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 3. *Au. anamensis* M2 and M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 4. *Au. afarensis* M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 5. *Au. africanus* M1 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 6. *Au. africanus* M2 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 7. *Au. africanus* M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 8. *Au. boisei* M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 9. *Au. robustus* M1 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 10. *Au. robustus* M2 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 11. *Au. robustus* M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 12. *H. erectus* M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 13. *Homo sp.* M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 14. Modern *Homo sapiens* selection of the M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 15. *Pan troglodytes* (MPI sample) M1 – M3 - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 16. *Pan troglodytes* (ZMB sample) M1 – M3 - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 17. *Pan paniscus* M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 18. *Gorilla* M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Supplementary Figure 19. *Pongo* selection of the M1 – M3 sample - mesial planes of section and their location for each specimen. White scale bar = 5mm.

Table 1. Composition of the study sample[1]

Taxon	M1	M2	M3	Total
Pongo	9	8	3	20
Gorilla	2	5	6	13
Pan paniscus	3	5	0	8
Pan troglodytes	6	7	3	16
Australopithecus anamensis	6	4	3	13
Australopithecus afarensis	2	4	2	8
Australopithecus africanus	9	13	12	34
Australopithecus aethiopicus	0	2	1	3
Australopithecus boisei	0	4	3	7
Australopithecus robustus	6	8	10	24
Homo sp. indet.	2	2	0	4
Homo erectus	1	3	2	6
Homo sapiens	8	15	7	30
Total	54	80	52	186

1. Not including specimens of uncertain taxonomic affinity listed in Table 4.

Table 2. Mean and standard deviation of selected measured variables for each taxon and tooth position.

Taxon	Tooth	N	Enamel Area (mm^2)	SD	Dentine Area (mm^2)	SD	EDJ Length (mm)	SD	BCD (mm)	SD	AET (mm)	SD	RET	SD
Pongo	M1	9	19.64	5.40	42.21	9.00	20.21	1.78	9.56	1.12	0.96	0.18	14.79	1.70
Gorilla	M1	2	23.94	1.12	76.27	4.01	27.96	1.34	12.77	0.16	0.86	0.08	9.84	1.19
Pan	M1	9	12.89	2.00	29.79	3.64	18.01	0.94	7.67	0.40	0.71	0.09	13.08	1.33
A. anamensis	M1	6	19.79	2.52	28.70	5.37	17.72	1.42	9.93	0.61	1.12	0.13	21.21	3.88
A. afarensis	M1	2	25.25	1.35	43.01	5.19	19.80	1.50	11.37	0.23	1.28	0.03	19.53	1.62
A. africanus	M1	9	29.10	3.52	43.41	9.21	20.81	2.01	11.04	0.92	1.40	0.16	21.67	3.97
A. aethiopicus	M1	0	-	-	-	-	-	-	-	-	-	-	-	-
A. boisei	M1	0	-	-	-	-	-	-	-	-	-	-	-	-
A. robustus	M1	6	39.53	4.59	47.46	10.15	21.56	2.03	11.64	0.86	1.84	0.18	27.10	4.12
H. sp. indet.	M1	2	33.35	0.95	34.33	2.83	19.24	1.21	11.66	1.87	1.73	0.07	29.61	2.35
H. erectus	M1	1	23.06	-	36.28	-	19.55	-	10.28	-	1.18	-	19.59	-
H. sapiens	M1	8	18.50	2.84	33.65	3.60	19.29	1.20	8.66	0.53	0.96	0.10	16.47	1.14
Pongo	M2	8	23.65	2.31	46.52	4.65	20.54	1.00	10.56	1.01	1.16	0.14	17.05	2.58
Gorilla	M2	5	30.10	4.55	82.84	13.54	29.91	1.74	14.00	0.91	1.00	0.12	11.10	1.33
Pan	M2	12	13.73	2.11	30.04	4.52	18.21	0.85	7.93	0.88	0.75	0.11	13.82	2.02
A. anamensis	M2	4	24.61	1.94	46.27	4.52	20.52	0.70	12.50	0.43	1.20	0.10	17.69	1.75
A. afarensis	M2	4	27.41	4.50	36.23	7.23	18.08	1.48	11.74	0.70	1.51	0.20	25.33	3.62
A. africanus	M2	13	36.66	5.12	51.84	9.92	22.13	1.82	13.08	1.29	1.66	0.21	23.27	3.30
A. aethiopicus	M2	2	50.52	3.15	66.77	6.30	23.73	1.46	13.86	1.31	2.13	0.00	26.09	1.21
A. boisei	M2	4	46.18	15.74	50.93	14.87	21.63	2.89	13.63	2.36	2.11	0.50	29.58	5.17
A. robustus	M2	8	44.47	5.46	49.14	9.57	20.71	1.79	12.76	1.21	2.15	0.21	31.09	4.54
H. sp. indet.	M2	3	31.66	6.12	37.95	6.47	20.09	1.49	11.76	1.34	1.57	0.24	25.54	2.74
H. erectus	M2	3	27.39	3.95	35.80	3.46	18.90	0.76	11.67	0.08	1.45	0.15	24.15	1.34
H. sapiens	M2	15	20.73	2.56	33.62	5.67	18.44	1.49	9.11	0.76	1.12	0.10	19.56	2.27
Pongo	M3	3	20.08	2.06	34.30	10.55	17.99	2.42	9.17	0.95	1.13	0.21	20.05	5.94
Gorilla	M3	6	26.55	3.43	65.66	6.76	26.49	1.24	13.35	0.98	1.01	0.14	12.43	1.73
Pan	M3	3	14.69	1.93	31.79	0.88	19.22	0.65	7.91	0.66	0.76	0.08	13.53	1.27
A. anamensis	M3	3	26.30	3.91	39.37	3.91	19.22	0.90	12.14	1.01	1.37	0.17	21.79	2.32
A. afarensis	M3	2	28.78	0.52	39.35	0.78	18.65	0.16	11.83	1.70	1.54	0.01	24.61	0.47
A. africanus	M3	11	41.08	3.99	55.71	9.53	22.93	1.87	13.63	1.32	1.79	0.16	24.33	3.32
A. aethiopicus	M3	1	57.47	-	73.35	-	25.79	-	15.49	-	2.23	-	26.02	-
A. boisei	M3	3	57.32	7.13	59.15	14.39	22.37	1.87	14.16	1.10	2.56	0.18	33.67	3.74
A. robustus	M3	10	43.43	3.34	52.57	5.25	21.63	0.93	13.21	1.15	2.01	0.17	27.86	3.10
H. sp. indet.	M3	0	-	-	-	-	-	-	-	-	-	-	-	-
H. erectus	M3	2	25.24	1.94	35.47	4.22	18.54	0.62	10.75	0.91	1.37	0.15	23.05	3.90
H. sapiens	M3	7	21.60	4.55	31.27	7.59	17.49	2.14	8.65	1.43	1.23	0.19	22.36	3.82

Notes

Table 3. Enamel thickness values for specimens with uncertain taxonomic affinity

Accession	Current taxon	Citation	Tooth	Basis[1]	Citation	Enamel Area (mm^2)	Dentine Area (mm^2)	EDJ Length (mm)	BCD[2] (mm)	AET[3]	RET[4]
KNM-WT 8556	*A. afarensis*	A	LM1	1	A	27.74	41.38	19.79	11.61	1.40	21.79
Omo K7-1969-19	*Homo* sp.	D	LM1	3	B	38.60	35.89	21.02	11.58	1.84	30.65
L26-1g	*A.* aff. *africanus*	E	RM1	3	B	34.29	50.82	21.78	11.77	1.57	22.09
L28-31	*Homo* sp.	B	RM2	3	B	44.45	36.41	19.29	9.77	2.30	38.18
Omo 75s-1969-16	*Homo* sp.	C	RM3	3	C	26.24	30.46	18.06	10.77	1.45	26.32
L28-30	*Homo* sp.	B	RM3	3	B	41.02	36.11	17.99	10.49	2.28	37.94
L795-1	Hominin	B	RM2	3	B	51.70	63.66	24.21	14.82	2.14	26.76

Notes:

1. Basis – 1 = molar in jaw or from associated dentition, 2 = molar position based on morphology and possible association with other teeth, 3 = molar position is best estimation based on morphology; 2. BCD = bi-cervical diameter; 3. AET = average enamel thickness; 4. RET = relative enamel thickness

Citations: A – Brown et al., 2001; B – Suwa, 1996; C – Suwa pers. comm; D – Alemseged pers. comm; E – Howell et al. 1987

Table 4. Molar enamel thickness comparison (AET bottom/RET top). Kruskal-Wallis with posthoc pairwise comparisons. Light shading indicates comparisons between hominins and extant non-human apes. Blank cells indicate non-significant results.

Taxon	*Pongo*	*Gorilla*	*Pan*	*Au. anam.*	*Au. afar.*	*Au. afric.*	*Au. boisei*	*Au. rob.*	*H.* sp. indet.	*H. erectus*	*H. sapiens*
First molars											
Pongo				0.013	0.003		-	<0.001	0.004		
Gorilla				0.005	0.031	0.003	-	<0.001			
Pan				0.001	0.031	<0.001	-	<0.001	<0.001		
Au. anamensis			0.003				-				
Au. afarensis		0.012					-				
Au. africanus	0.006	0.035	<0.001				-				0.047
Au. boisei	-	-	-	-	-	-					
Au. robustus	<0.001	0.005	<0.001	0.025							0.005
H. sp. indet.	0.013	0.022	<0.001								0.021
H. erectus											
H. sapiens			0.044		0.012			0.001	0.018		
Second molars											
Pongo					0.024	0.018	0.003	<0.001	0.026		
Gorilla					<0.001	<0.001	<0.001	<0.001	0.001	0.007	0.005
Pan	0.015				0.001	<0.001	<0.001	<0.001	0.001	0.015	0.007
Au. anamensis			0.032				0.014	0.002			
Au. afarensis		0.029	0.001								
Au. africanus	0.011	0.001	<0.001					0.040			
Au. boisei	0.011	0.001	<0.001	0.043							0.017
Au. robustus	<0.001	<0.001	<0.001	0.007							<0.001
H. sp. indet.		0.030	0.001								
H. erectus			0.013								
H. sapiens			0.016			<0.001	0.002	<0.001			
Third molars											
Pongo							0.013	0.036	-		
Gorilla					0.045	0.001	<0.001	<0.001	-		0.026
Pan						0.020	<0.001	0.001	-		
Au. anamensis							0.020		-		
Au. afarensis									-		
Au. africanus	0.029	0.001	0.001						-		
Au. boisei	0.002	<0.001	<0.001	0.015					-		0.011
Au. robustus	0.003	<0.001	<0.001	0.030					-		0.025
H. sp. indet.	-	-	-	-	-	-	-	-			
H. erectus							0.027				
H. sapiens						0.011	0.001	<0.001			

Note: *Australopithecus aethiopicus* specimens not included in statistical tests due to small sample size. A hyphen indicates no molars of that position for that taxon.

Table 5. Regional average enamel thickness measurements for the combined molar sample.

Taxon	N	Buccal	SD	Occlusal	SD	Lingual	SD
Pongo	20	1.02	0.17	1.15	0.27	1.02	0.13
Gorilla	13	1.05	0.12	0.99	0.20	0.88	0.10
Pan	24	0.79	0.11	0.67	0.09	0.78	0.13
A. anamensis	13	1.23	0.23	1.27	0.20	1.11	0.15
A. afarensis	8	1.43	0.25	1.59	0.26	1.36	0.13
A. africanus	34	1.62	0.21	1.77	0.31	1.50	0.21
A. boisei	7	2.15	0.48	2.57	0.52	2.14	0.38
A. robustus	24	1.93	0.26	2.27	0.27	1.80	0.21
H. sp. indet.	4	1.76	0.23	1.82	0.24	1.58	0.17
H. erectus	6	1.32	0.06	1.49	0.22	1.28	0.20
H. sapiens	30	1.09	0.17	1.18	0.22	1.05	0.12

Note: *Australopithecus aethiopicus* not included in regional AET analysis due to small sample size (n = 3).

Appendix A. Measured variables for study sample

Accession	Taxon	Tooth	Basis[1]	Citation	Enamel Area (mm^2)	Dentine Area (mm^2)	EDJ Length (mm)	BCD[2] (mm)	AET[3]	RET[4]
AL145-35	*A. afarensis*	LM1	1	A	26.17	46.68	20.85	11.53	1.26	18.37
AL333w-1a	*A. afarensis*	LM1	1	A	24.28	39.34	18.78	11.21	1.29	20.61
AL128-23	*A. afarensis*	RM2	1	A	20.66	29.68	16.37	11.18	1.26	23.17
AL145-35	*A. afarensis*	LM2	1	A	29.81	46.48	20.12	12.09	1.48	21.73
AL241-14	*A. afarensis*	LM2	3	A	29.35	33.35	17.87	12.56	1.64	28.44
AL333w-1a	*A. afarensis*	LM2	1	A	27.65	35.39	17.93	11.14	1.54	25.92
AL400-1a	*A. afarensis*	RM3	1	A	29.14	38.80	18.85	10.63	1.55	24.82
AL333w-32	*A. afarensis*	RM3	2	A	28.37	39.90	18.65	13.03	1.52	24.08
STW421B	*A. africanus*	LM1	2	B	30.70	58.83	23.72	12.34	1.29	16.87
STS9	*A. africanus*	RM1	3	N	34.82	40.34	19.56	11.66	1.78	28.03
Taung1	*A. africanus*	LM1	1	C	28.32	42.90	21.94	11.71	1.29	19.71
STW327	*A. africanus*	LM1	1	B	29.63	49.77	20.80	11.55	1.42	20.19
STW151	*A. africanus*	RM1	1	D	28.87	32.41	19.20	9.80	1.50	26.41
STW106	*A. africanus*	RM1	1	B	20.35	36.00	18.67	10.56	1.09	18.17
STW123a	*A. africanus*	RM1	1	B	31.75	37.45	18.96	10.86	1.67	27.36
STW309a	*A. africanus*	RM1	1	B	32.56	53.09	23.77	12.04	1.37	18.80
STW246	*A. africanus*	LM1	2	B	29.62	46.15	21.22	10.77	1.40	20.55
STS24	*A. africanus*	RM1	1	E	29.11	34.07	18.99	9.81	1.53	26.26
STW3	*A. africanus*	LM2	2	B	40.98	46.55	21.43	12.89	1.91	28.03
STW412B	*A. africanus*	LM2	2	B	25.31	42.86	20.52	11.83	1.23	18.84
STW327	*A. africanus*	LM2	1	B	43.22	61.57	23.12	13.96	1.87	23.83
MLD2	*A. africanus*	RM2	1	Z	36.84	52.71	22.70	14.43	1.62	22.35
STW498c	*A. africanus*	LM2	1	B	37.64	76.41	26.40	14.69	1.43	16.31
STW404	*A. africanus*	RM2	1	B	33.00	44.89	19.60	11.78	1.68	25.13
STW61	*A. africanus*	RM2	2	B	35.12	43.53	21.23	13.31	1.65	25.08
STW555	*A. africanus*	LM2	2	B	31.33	50.19	23.53	11.18	1.33	18.80
STW109	*A. africanus*	RM2	1	B	38.61	51.70	22.41	14.89	1.72	23.96
STW537(269)	*A. africanus*	RM2	1	B	41.75	53.19	23.24	14.03	1.80	24.63
STW308	*A. africanus*	RM2	1	B	40.90	50.42	22.11	13.28	1.85	26.05
STW133	*A. africanus*	LM2	2	B	42.87	61.50	22.94	13.20	1.87	23.83
STW213	*A. africanus*	LM2	1	B	33.92	44.63	21.39	11.78	1.59	23.74
STW529(532)	*A. africanus*	LM3	1	B	42.55	47.54	21.48	12.75	1.98	28.73
STW 560B	*A. africanus*	LM3	1	B	38.78	59.64	23.10	14.14	1.68	21.74
STW498c	*A. africanus*	LM3	1	B	46.64	69.26	26.79	14.75	1.74	20.92
STW384	*A. africanus*	RM3	1	B	42.95	72.46	24.98	15.41	1.72	20.20
STW14	*A. africanus*	RM3	1	B	43.16	56.74	22.45	12.84	1.92	25.52
STW404	*A. africanus*	RM3	1	B	39.40	51.70	21.27	11.97	1.85	25.76
STW109	*A. africanus*	RM3	1	B	42.98	51.03	22.21	14.83	1.94	27.09
STW520	*A. africanus*	RM3	2	B	31.33	48.53	22.25	12.65	1.41	20.22
STW586	*A. africanus*	LM3	1	B	37.73	41.50	20.44	11.59	1.85	28.66
STW280(278)	*A. africanus*	RM3	1	B	41.65	60.69	25.1	15.28	1.66	21.30
STW537	*A. africanus*	RM3	1	B	44.73	62.91	24.80	14.47	1.80	22.74
KNM-ER 20422	*A. anamensis*	LM1	3	F	21.24	31.12	18.37	10.44	1.16	20.73
KNM-ER 30201	*A. anamensis*	LM1	3	G	17.69	24.80	15.61	9.30	1.13	22.76
KNM-ER 35232	*A. anamensis*	LM1	3	G	24.21	28.06	18.34	10.32	1.32	24.92
KNM-KP 31728	*A. anamensis*	LM1	3	G	18.26	20.46	15.70	9.20	1.16	25.71
KNM-KP 31712J	*A. anamensis*	RM1	1	G	17.90	33.11	17.56	9.73	1.02	17.72
KNM-KP 34725R	*A. anamensis*	RM1	1	G	19.06	34.66	19.55	10.60	0.97	16.56
KNM-ER 35233	*A. anamensis*	LM2	3	G	22.39	43.76	20.25	11.93	1.11	16.71
KNM-KP 29286	*A. anamensis*	LM2	1	G	24.13	41.52	21.03	12.72	1.15	17.80

KNM-KP 34725T	*A. anamensis*	LM2	1	G	26.99	48.16	20.30	12.43	1.33	19.16
KNM-KP 30500D	*A. anamensis*	RM2	1	G	24.53	51.64	18.77	12.91	1.31	18.19
KNM-ER 20428	*A. anamensis*	LM3	3	F	30.13	43.76	20.11	13.00	1.50	22.65
KNM-KP 29281	*A. anamensis*	LM3	1	G	22.30	38.09	19.15	11.03	1.16	18.87
KNM-KP 29286	*A. anamensis*	LM3	1	G	25.51	36.25	19.01	12.40	1.34	22.29
ZMB 31435	*Gorilla* sp.	LM1	1	H	24.32	73.43	29.10	12.66	0.84	9.75
ZMB 83546	*Gorilla* sp.	LM1	1	H	22.91	79.11	29.04	12.88	0.79	8.87
ZMB 30940	*Gorilla* sp.	RM2	1	H	26.49	90.23	31.74	13.78	0.83	8.79
ZMB 31435	*Gorilla* sp.	LM2	1	H	32.29	75.72	30.30	12.92	1.07	12.25
ZMB 83546	*Gorilla* sp.	LM2	1	H	36.65	103.03	29.60	15.41	1.24	12.20
ZMB 83581	*Gorilla* sp.	RM2	1	H	24.89	70.27	28.62	14.18	0.87	10.37
SMF 45713	*Gorilla* sp.	RM2	1	H	29.28	74.94	28.98	13.72	1.01	11.67
ZMB 30940	*Gorilla* sp.	RM3	1	H	25.49	75.36	29.18	13.63	0.87	10.06
ZMB 30941	*Gorilla* sp.	RM3	1	H	25.14	69.32	26.92	14.37	0.93	11.22
ZMB 31277	*Gorilla* sp.	LM3	1	H	31.16	68.10	26.16	14.13	1.19	14.43
ZMB 31435	*Gorilla* sp.	LM3	1	H	30.19	63.27	26.72	11.69	1.13	14.20
ZMB 31626	*Gorilla* sp.	RM3	1	H	24.95	62.03	25.31	12.82	0.99	12.52
ZMB 83581	*Gorilla* sp.	RM3	1	H	21.98	55.86	25.22	13.44	0.87	11.66
R123	*Homo sapiens*	LM1	1	M	15.78	32.18	19.27	9.12	0.82	14.44
R1101 1498	*Homo sapiens*	LM1	1	M	23.61	43.09	20.74	8.13	1.14	17.34
R1140 899	*Homo sapiens*	RM1	1	M	16.14	32.02	18.01	8.73	0.90	15.83
R1989 1382	*Homo sapiens*	LM1	1	M	25.50	41.53	21.00	9.31	1.21	18.84
R2602 1673	*Homo sapiens*	LM1	1	M	20.42	38.39	21.15	8.91	0.97	15.58
Belgian93a	*Homo sapiens*	LM1	2	I	24.10	38.41	21.16	8.58	1.14	18.38
Beligian129a	*Homo sapiens*	LM1	2	I	18.11	31.33	19.04	7.57	0.95	16.99
BelgianA31	*Homo sapiens*	RM1	2	I	19.50	36.52	19.71	8.64	0.99	16.38
102 I151	*Homo sapiens*	LM1	1	M	16.76	31.39	18.76	8.44	0.89	15.95
R123	*Homo sapiens*	LM2	1	M	15.86	28.67	18.50	8.90	0.86	16.01
R186	*Homo sapiens*	RM2	1	M	19.27	29.92	17.38	9.78	1.11	20.27
R258 144	*Homo sapiens*	RM2	1	M	20.39	34.86	19.29	8.36	1.06	17.90
R690 1372	*Homo sapiens*	RM2	1	M	21.45	37.16	19.98	8.88	1.07	17.61
R913 759	*Homo sapiens*	RM2	1	M	21.49	32.01	18.18	9.41	1.18	20.89
R1101 1498	*Homo sapiens*	LM2	1	M	16.42	28.96	18.79	9.32	0.87	16.24
R1234	*Homo sapiens*	LM2	1	M	19.77	32.74	18.11	8.94	1.09	19.08
R1345 1006	*Homo sapiens*	LM2	1	M	17.32	23.12	15.65	8.16	1.11	23.02
R1639 1186	*Homo sapiens*	LM2	1	M	19.35	33.11	18.65	7.79	1.04	18.03
R2433 1156	*Homo sapiens*	LM2	1	M	23.61	41.57	20.76	9.57	1.14	17.64
ULAC 58	*Homo sapiens*	LM2	1	L	22.55	36.32	19.09	10.37	1.18	19.60
ULAC 607	*Homo sapiens*	RM2	1	L	20.51	33.63	18.22	10.15	1.13	19.40
Belgian41a	*Homo sapiens*	RM2	2	I	21.66	26.80	16.88	9.29	1.28	24.79
Belgian100f	*Homo sapiens*	LM2	2	I	18.21	29.84	17.44	9.59	1.04	19.11
R463	*Homo sapiens*	LM3	1	M	18.84	30.36	18.54	8.28	1.02	18.44
R556	*Homo sapiens*	RM3	1	M	17.19	23.87	16.40	8.41	1.05	21.46
R605 1185	*Homo sapiens*	LM3	1	M	18.66	33.88	18.39	8.69	1.01	17.44
R1586 2425	*Homo sapiens*	LM3	1	M	18.91	26.07	16.12	8.15	1.17	22.98
R2540 1650	*Homo sapiens*	RM3	1	M	21.19	26.03	15.18	6.93	1.40	27.37
ULAC 799-27	*Homo sapiens*	LM3	1	L	28.30	46.36	21.25	11.61	1.33	19.56
M132	*Homo sapiens*	LM3	?	J	27.76	32.30	18.28	8.50	1.52	26.72
MRAC 29026	*Pan paniscus*	RM1	1	K	9.39	22.09	16.47	7.00	0.57	12.13
MRAC 84036M11	*Pan paniscus*	LM1	1	K	12.39	28.36	18.55	7.54	0.67	12.54
MRAC 29030	*Pan paniscus*	RM1	1	K	10.28	27.72	17.68	7.49	0.58	11.05
MRAC 22908	*Pan paniscus*	LM2	1	K	10.04	25.83	17.39	6.60	0.58	11.36
MRAC 29030	*Pan paniscus*	LM2	1	K	13.64	27.27	18.12	7.44	0.75	14.42
MRAC 29055	*Pan paniscus*	LM2	1	K	13.39	28.83	18.45	8.05	0.73	13.51
MRAC 84036M11	*Pan paniscus*	LM2	1	K	14.45	27.93	18.50	7.61	0.78	14.78
MRAC 84036M03	*Pan paniscus*	LM2	1	K	13.05	21.14	16.35	7.77	0.80	17.36
ZMB 0A16207	*Pan troglodytes*	LM1	1	H	12.56	30.80	18.29	7.38	0.69	12.37
ZMB 20811	*Pan troglodytes*	RM1	1	H	13.41	33.11	18.05	7.92	0.74	12.92

ZMB 32356	*Pan troglodytes*	RM1	1	H	14.37	28.93	18.36	7.41	0.78	14.55
ZMB 35526	*Pan troglodytes*	RM1	1	H	13.73	33.34	19.56	8.15	0.70	12.15
ZMB 83623	*Pan troglodytes*	LM1	1	H	15.17	30.10	17.86	8.08	0.85	15.48
ZMB 30847	*Pan troglodytes*	LM2	1	H	14.76	32.08	19.00	7.54	0.78	13.72
ZMB 31279	*Pan troglodytes*	RM2	1	H	11.93	29.60	17.58	7.63	0.68	12.48
ZMB 72844	*Pan troglodytes*	RM2	1	H	13.60	32.16	18.76	9.03	0.72	12.78
ZMB 83661	*Pan troglodytes*	RM2	1	H	10.74	29.91	18.58	6.65	0.58	10.57
ZMB 83655	*Pan troglodytes*	LM3	1	H	16.93	32.81	19.82	7.23	0.85	14.91
MPI 13437	*Pan troglodytes*	RM1	1	J	14.83	33.63	19.60	8.08	0.76	13.04
MPI 13433	*Pan troglodytes*	RM2	1	J	16.58	31.31	17.69	9.05	0.94	16.75
MPI 13437	*Pan troglodytes*	RM2	1	J	17.17	37.89	19.36	9.13	0.89	14.41
MPI 11800	*Pan troglodytes*	RM2	1	J	15.12	36.55	19.74	8.63	0.77	12.67
MPI 11800	*Pan troglodytes*	LM3	1	J	13.76	31.30	18.54	7.96	0.74	13.26
MPI 11779	*Pan troglodytes*	RM3	1	J	13.58	31.26	21.16	8.48	0.64	11.48
ZMB 6954	*Pongo* sp.	LM1	1	H	22.58	39.90	20.03	8.19	1.13	17.85
ZMB 6957	*Pongo* sp.	RM1	1	H	15.27	34.63	19.35	8.46	0.79	13.41
ZMB 6987	*Pongo* sp.	RM1	1	H	17.90	40.77	19.81	9.16	0.90	14.15
ZMB 30946	*Pongo* sp.	RM1	1	H	32.10	62.09	24.56	11.55	1.31	16.59
ZMB 67173	*Pongo* sp.	RM1	1	H	18.79	39.93	19.34	9.04	0.97	15.37
SMF 1113	*Pongo* sp.	LM1	1	H	13.35	30.46	17.62	8.78	0.76	13.73
SMF 1577	*Pongo* sp.	RM1	1	H	19.46	47.58	22.65	10.74	0.86	12.46
SMF 2654	*Pongo* sp.	LM1	1	H	16.76	39.42	19.69	10.01	0.85	13.56
SMF 38296	*Pongo* sp.	LM1	1	H	19.68	45.10	20.76	10.18	0.95	14.12
ZMB 6954	*Pongo* sp.	LM2	1	H	25.82	44.17	19.53	9.65	1.32	19.89
ZMB 6957	*Pongo* sp.	RM2	1	H	23.92	37.09	19.41	9.29	1.23	20.24
SMF 1117	*Pongo* sp.	RM2	1	H	22.99	45.03	20.34	11.21	1.13	16.85
SMF 2639	*Pongo* sp.	LM2	1	H	19.09	50.45	21.42	10.13	0.89	12.55
SMF 15837	*Pongo* sp.	RM2	1	H	22.17	48.89	22.32	9.90	0.99	14.20
SMF 38296	*Pongo* sp.	LM2	1	H	25.32	32.34	20.94	12.19	1.21	21.26
SMF 59140	*Pongo* sp.	RM2	1	H	23.65	49.09	21.52	10.52	1.10	15.69
SMF 59142	*Pongo* sp.	LM2	1	H	25.34	51.66	21.11	11.59	1.20	16.70
ZMB 6957	*Pongo* sp.	RM3	1	H	22.42	28.76	17.36	8.22	1.29	24.09
ZMB 83515	*Pongo* sp.	LM3	1	H	18.83	46.46	21.19	10.11	0.89	13.03
ZMB 12209	*Pongo* sp.	RM3	1	H	18.86	27.67	16.19	9.19	1.16	22.15
KNM-ER 820	*Homo erectus*	RM1	1	P	23.06	36.28	19.55	10.28	1.18	19.59
KNM-BK 67	*Homo erectus*	RM2	1	Q	25.75	30.51	18.55	10.25	1.39	25.13
KNM-ER 992A	*Homo erectus*	RM2	1	P	24.56	33.35	18.76	11.61	1.31	22.67
KNM-ER 1507	*Homo erectus*	LM2	1	P	29.98	38.25	19.40	11.72	1.55	24.99
KNM-BK 67	*Homo erectus*	RM3	1	P	26.41	32.48	17.89	10.10	1.48	25.89
KNM-ER 992A	*Homo erectus*	RM3	1	P	23.89	38.45	19.10	11.39	1.25	20.17
DNH 67	*Homo* sp. indet.	RM1	2	O	33.43	33.04	18.08	9.87	1.85	32.18
KNM-ER 1802	*Homo* sp. indet.	RM1	1	P	33.65	36.51	20.20	11.32	1.67	27.57
KNM-ER 1802	*Homo* sp. indet.	RM2	1	P	34.85	37.05	20.07	12.52	1.74	28.53
KNM-ER 1506A	*Homo* sp. indet.	RM2	1	P	30.88	41.12	21.31	12.24	1.45	22.60
L62-17	*A. aethiopicus*	RM2	3	N	48.06	62.32	22.62	12.93	2.12	26.92
L157-35	*A. aethiopicus*	LM2	3	N	52.53	71.23	24.62	14.78	2.13	25.28
OmoF22-1b	*A. aethiopicus*	RM3	2	N	57.04	73.35	25.81	15.49	2.21	25.80
KMN-ER 1820	*A. boisei*	LM1	1	P	51.24	53.53	24.37	12.93	2.10	28.74
L427-7	*A. boisei*	LM1	1	N	51.38	46.59	20.54	12.81	2.50	36.65
Omo47-1973-1500	*A. boisei*	RM1	3	N	36.05	46.45	21.31	13.72	1.69	24.82
KNM-ER 3230	*A. boisei*	LM1	1	P	65.00	72.45	25.89	16.80	2.51	29.50
KNM-ER 15930	*A. boisei*	LM1	1	R	31.23	38.22	18.93	11.19	1.65	26.69
L628-3	*A. boisei*	LM1	3	N	63.04	75.26	23.98	14.30	2.63	30.30
KNM-ER 3230	*A. boisei*	RM1	1	P	59.65	54.59	21.93	15.19	2.72	36.81
KNM-ER 15930	*A. boisei*	LM1	1	R	49.37	47.59	20.72	13.00	2.38	34.53
DNH60B	*A. robustus*	RM1	1	O	31.62	31.62	18.61	10.80	1.70	30.22
SK3974	*A. robustus*	RM1	2	S	39.92	41.17	18.99	10.39	2.10	32.76
SK6	*A. robustus*	RM1	1	S	31.15	53.22	21.73	12.46	1.43	19.65

SK61	*A. robustus*	RM1	1	S	44.23	57.72	23.94	12.80	1.85	24.32
SK62	*A. robustus*	LM1	1	S	43.62	43.95	20.76	10.89	2.10	31.69
SK 63	*A. robustus*	RM1	1	S	38.67	41.58	20.15	10.99	1.92	29.77
SK(826b)828	*A. robustus*	LM1	2	S	40.79	55.35	24.27	12.01	1.68	22.59
DNH60C	*A. robustus*	RM1	1	O	38.93	32.92	17.98	11.77	2.17	37.74
SK6	*A. robustus*	LM1	1	S	49.42	54.13	21.655	14.17	2.28	31.02
SKW5	*A. robustus*	LM2	1	T	43.46	49.06	20.56	12.40	2.11	30.18
SKX4446	*A. robustus*	RM2	1	T	45.40	61.11	23.34	14.31	1.95	24.88
SK1587a	*A. robustus*	LM2	1	S	36.03	37.86	18.34	10.81	1.96	31.93
SK25	*A. robustus*	RM2	1	S	53.23	49.06	21.11	12.11	2.52	36.00
SK843.846a	*A. robustus*	LM2	1	S	42.51	51.00	21.09	13.03	2.02	28.22
SK1	*A. robustus*	LM2	2	S	45.20	58.01	23.13	13.44	1.95	25.66
SK6	*A. robustus*	LM3	1	S	48.99	48.18	21.94	13.91	2.23	32.18
SK23	*A. robustus*	LM3	1	S	42.52	51.97	22.40	12.71	1.90	26.33
SKW5	*A. robustus*	RM3	1	T	45.34	49.44	20.46	12.49	2.22	31.51
SK843.846a	*A. robustus*	LM3	1	S	45.70	53.76	22.22	11.40	2.06	28.06
SK75	*A. robustus*	RM3	2	S	44.86	54.85	22.47	13.13	2.00	26.96
SK81	*A. robustus*	LM3	1	S	42.28	54.77	21.93	12.64	1.93	26.04
SKX10643	*A. robustus*	RM3	2	U	39.96	43.56	20.48	12.47	1.95	29.56
SKX5014	*A. robustus*	RM3	2	T	38.94	57.27	22.64	14.06	1.72	22.73
TM1600	*A. robustus*	LM3	1	V	38.70	49.56	21.41	13.75	1.81	25.67
SK851	*A. robustus*	RM3	3	S	45.97	62.33	23.37	15.55	1.97	24.92
KNM-WT 8556	Uncertain	RM1	3	W	27.74	41.38	19.79	1.40	21.79	11.61
OmoK7-1969-19	Uncertain	LM1	3	X	38.60	35.89	21.02	1.84	30.65	11.58
OmoL26-1g	Uncertain	RM1	3	N	34.29	50.82	21.78	1.57	22.09	11.77
L795-1	Uncertain	RM2	3	N	51.70	63.66	24.21	2.14	26.76	14.82
L28-31	Uncertain	RM2	3	Y	44.45	36.41	19.29	2.30	38.18	9.77
Omo75s-1969-16	Uncertain	RM3	3	N	26.24	30.46	18.06	1.45	26.32	10.77
L28-30	Uncertain	RM3	3	N	41.02	36.11	17.99	2.28	37.94	10.49

Notes:

1. Basis – 1 = molar in jaw or from associated dentition, 2 = molar position based on morphology and possible association with other teeth, 3 = molar position is best estimation based on morphology
2. BCD = bi-cervical diameter
3. AET = average enamel thickness
4. RET = relative enamel thickness

Citations: A – Johanson et al., 1982 ; B – Moggi-Cecchi et al., 2006; C – Dart, 1925; D – Mogg-Cecchi et al., 1998 ; E – Grine, 1981; F - Coffing et al., 1994; G – Ward et al., 2001 ; H – ZMB records ; I – Michel Toussaint pers. Comm ; J – MPI-EVA records ; K – MRAC records ; L – ULAC records; M – FJR records; N – Suwa, 1996; O – Moggi-Cecchi et al., 2010; P – Wood, 1991; Q – Leakey et al., 1969; R – Leakey and Walker, 1988; S – Brain, 1981; T – Grine, 2004; U – De Ruiter, 2001; V – Thackeray et al., 2001; W – Brown et al., 2001; X – Alemseged personal communication; Y – Howell et al., 1987; Z – Dart, 1948.

Figure 1

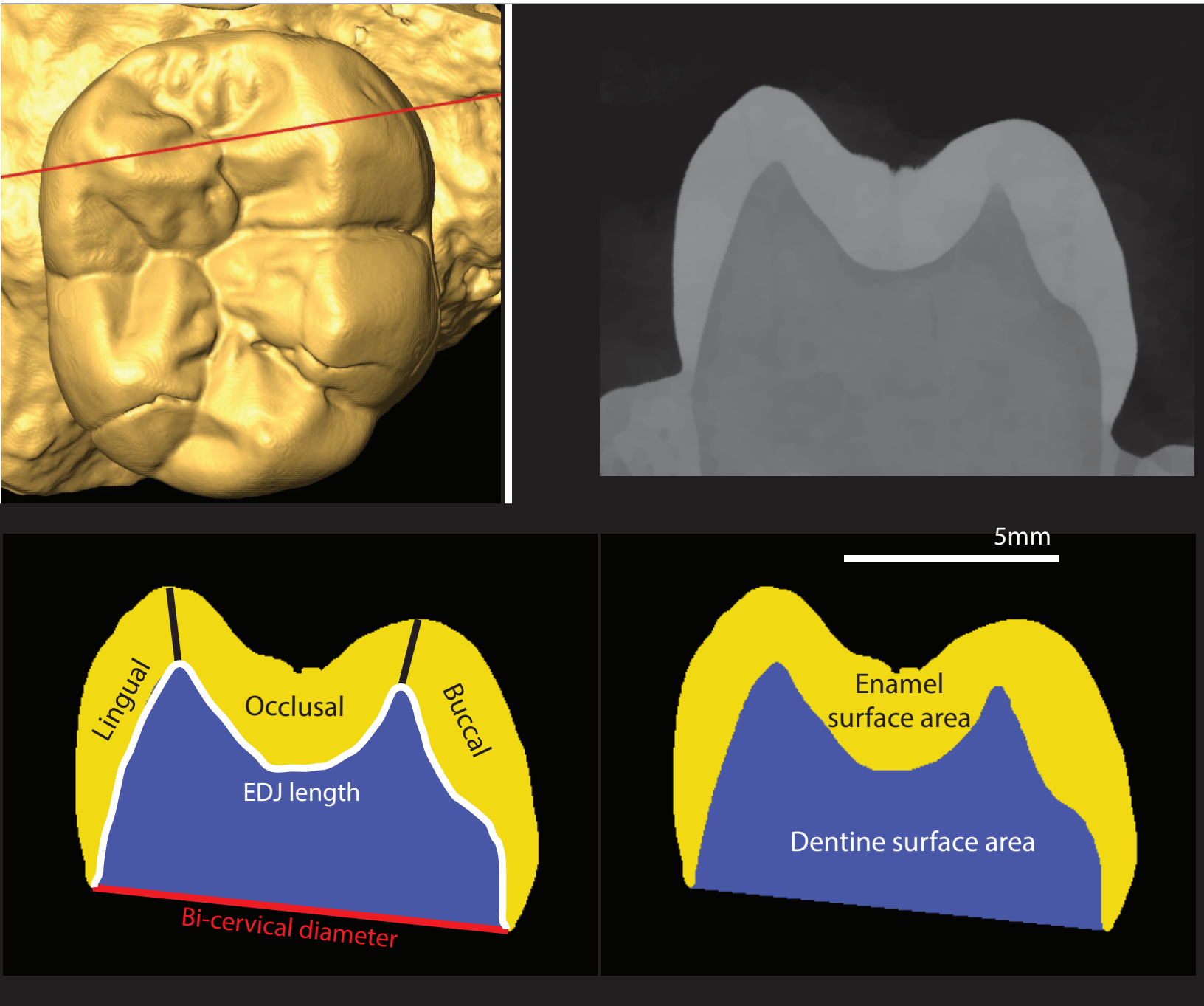
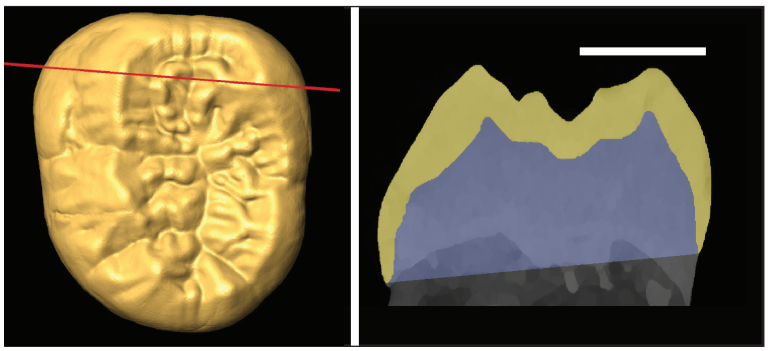
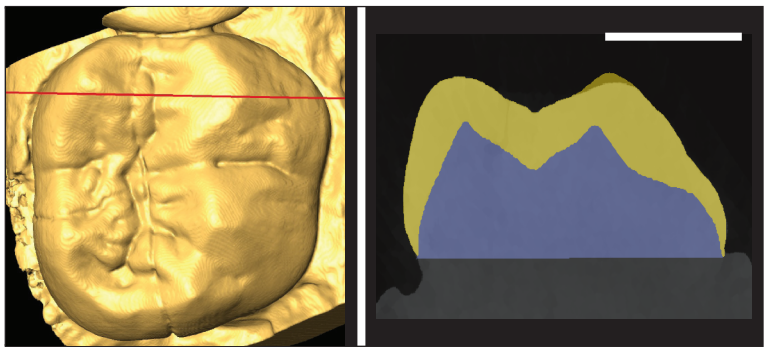

Lingual
Occlusal
Buccal
EDJ length
Bi-cervical diameter
5mm
Enamel
surface area
Dentine surface area

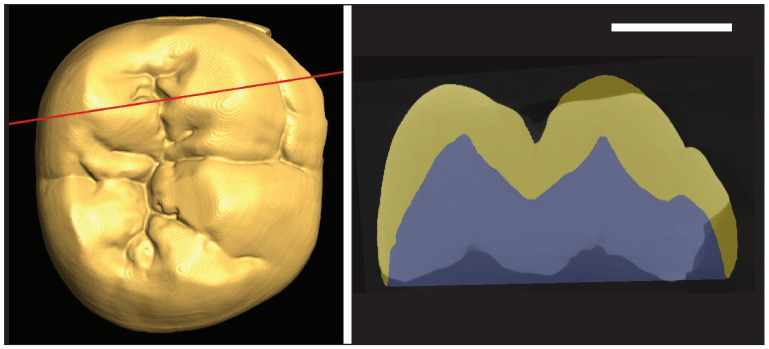
Figure 2



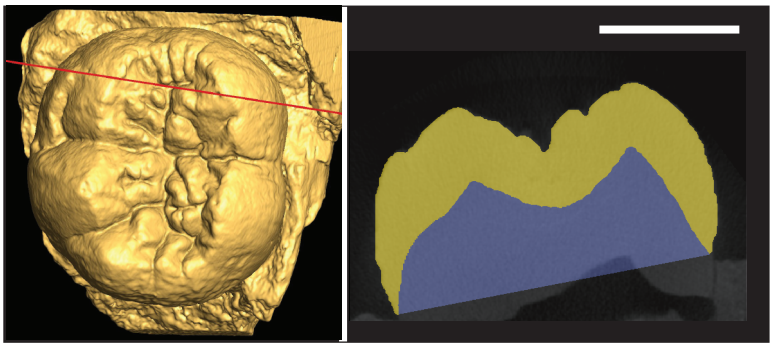
Au. anamensis - KNM-ER 34725T LM2



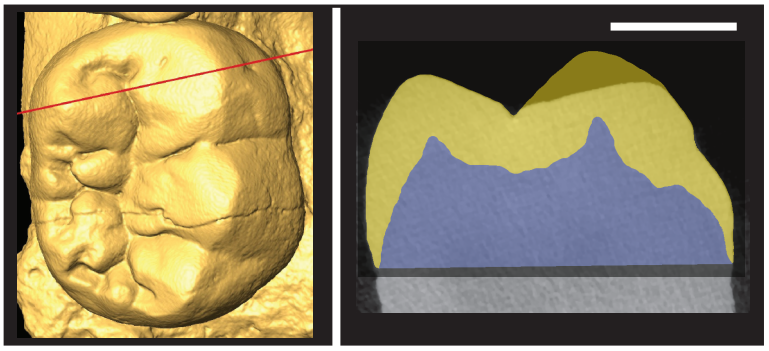
Au. afarensis - AL128-23 RM2



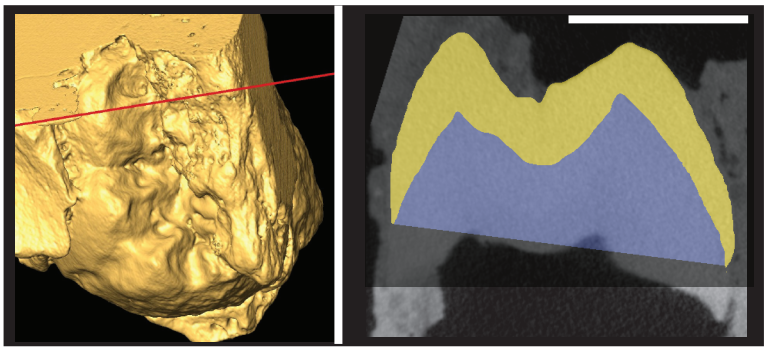
Au. africanus - STW537 RM2



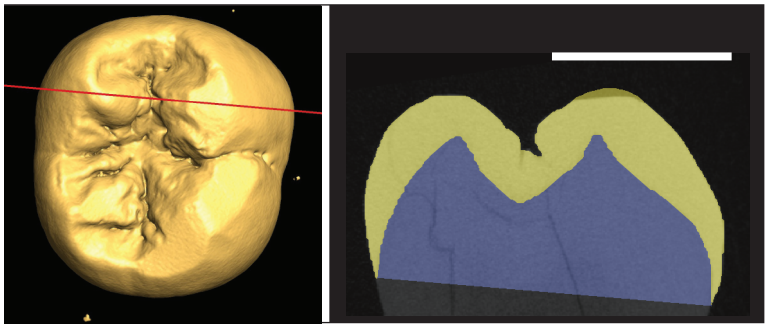
Au. boisei - L427-7 LM2



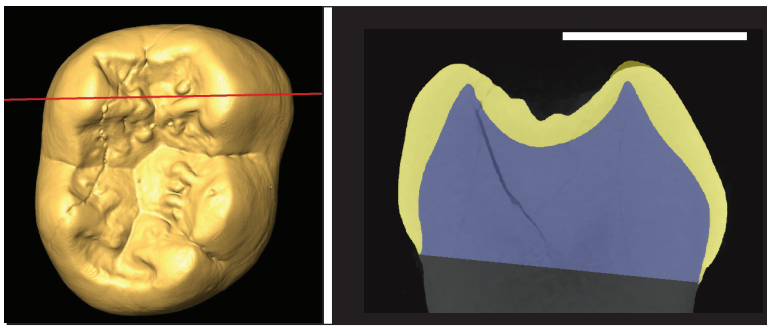
Homo sp indet - KNM-ER 1802 RM2



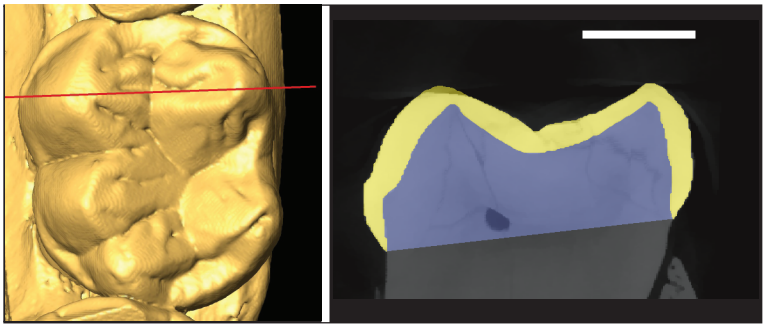
Homo erectus - KNM-ER 1507 LM2



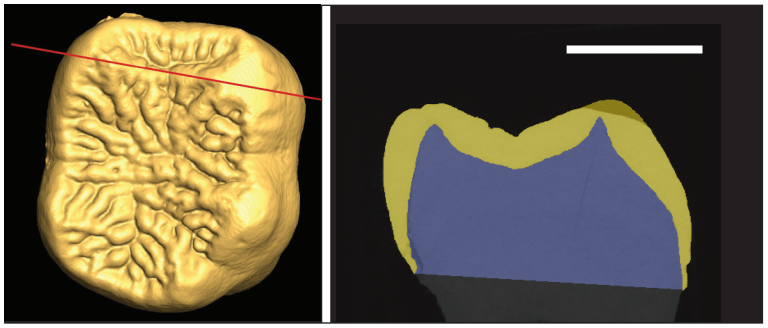
Homo sapiens - R913-759 RM2



Pan troglodytes - ZMB 31279 RM2



Gorilla sp. - ZMB 31435 LM2



Pongo sp. - SMF 15837 RM2

Figure 3

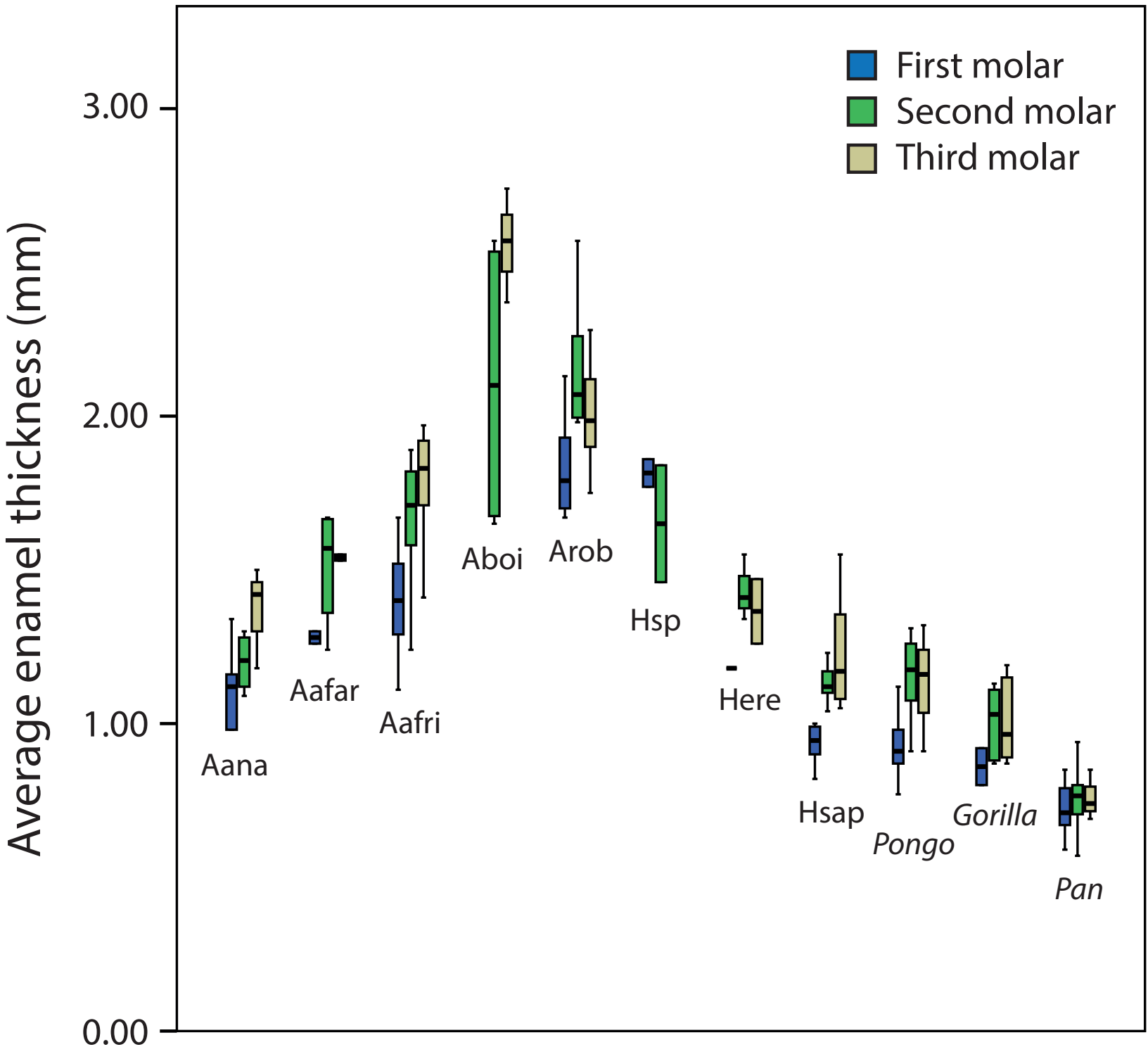

First molar
Second molar
Third molar
Average enamel thickness (mm)
3.00
2.00
1.00
0.00
Aana
Aafar
Aafri
Aboi
Arob
Hsp
Here
Hsap
Pongo
Gorilla
Pan

Figure 4

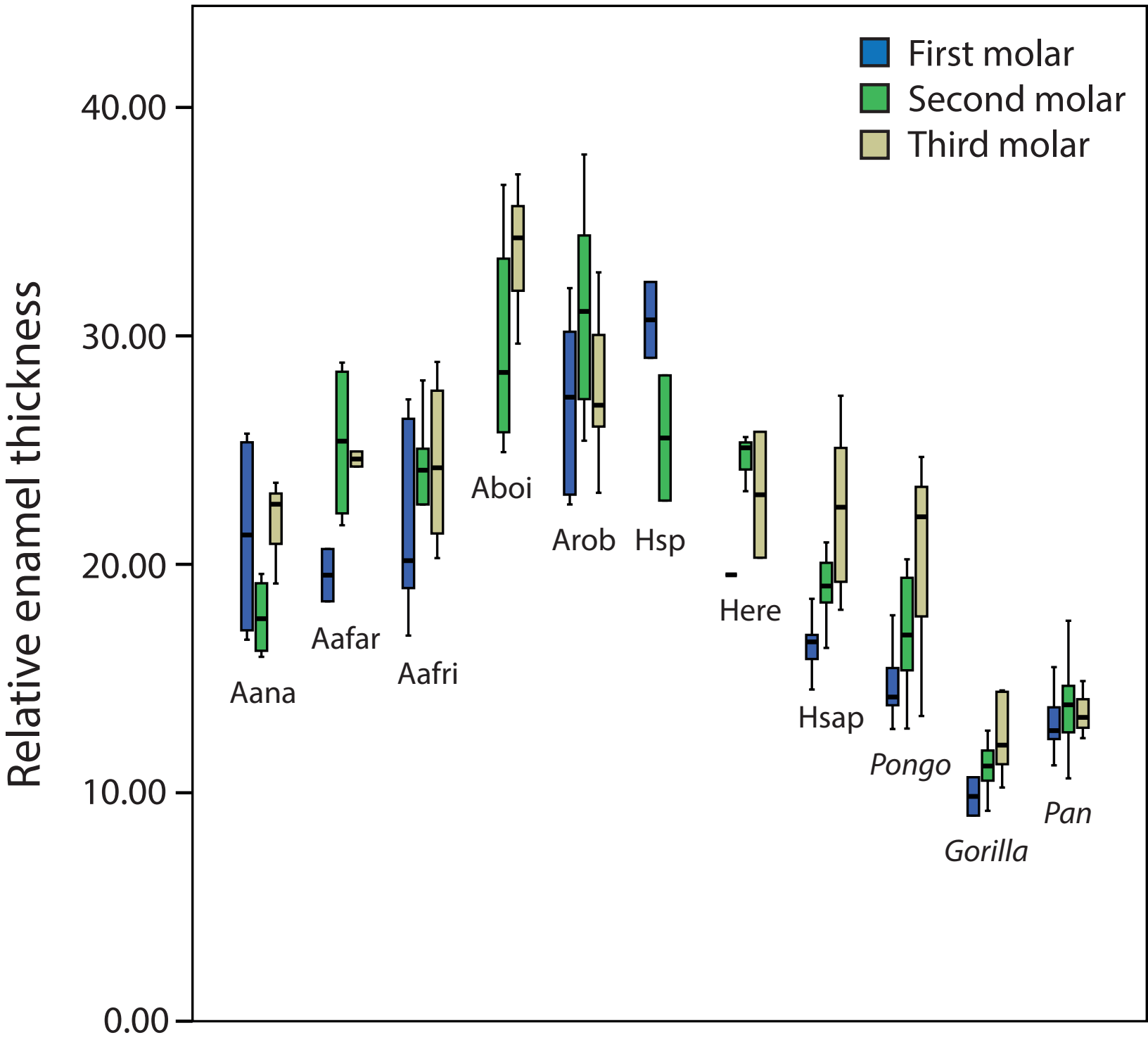

First molar
Second molar
Third molar
Relative enamel thickness
40.00
30.00
20.00
10.00
0.00
Aana
Aafar
Aafri
Aboi
Arob
Hsp
Here
Hsap
Pongo
Gorilla
Pan

Figure 5

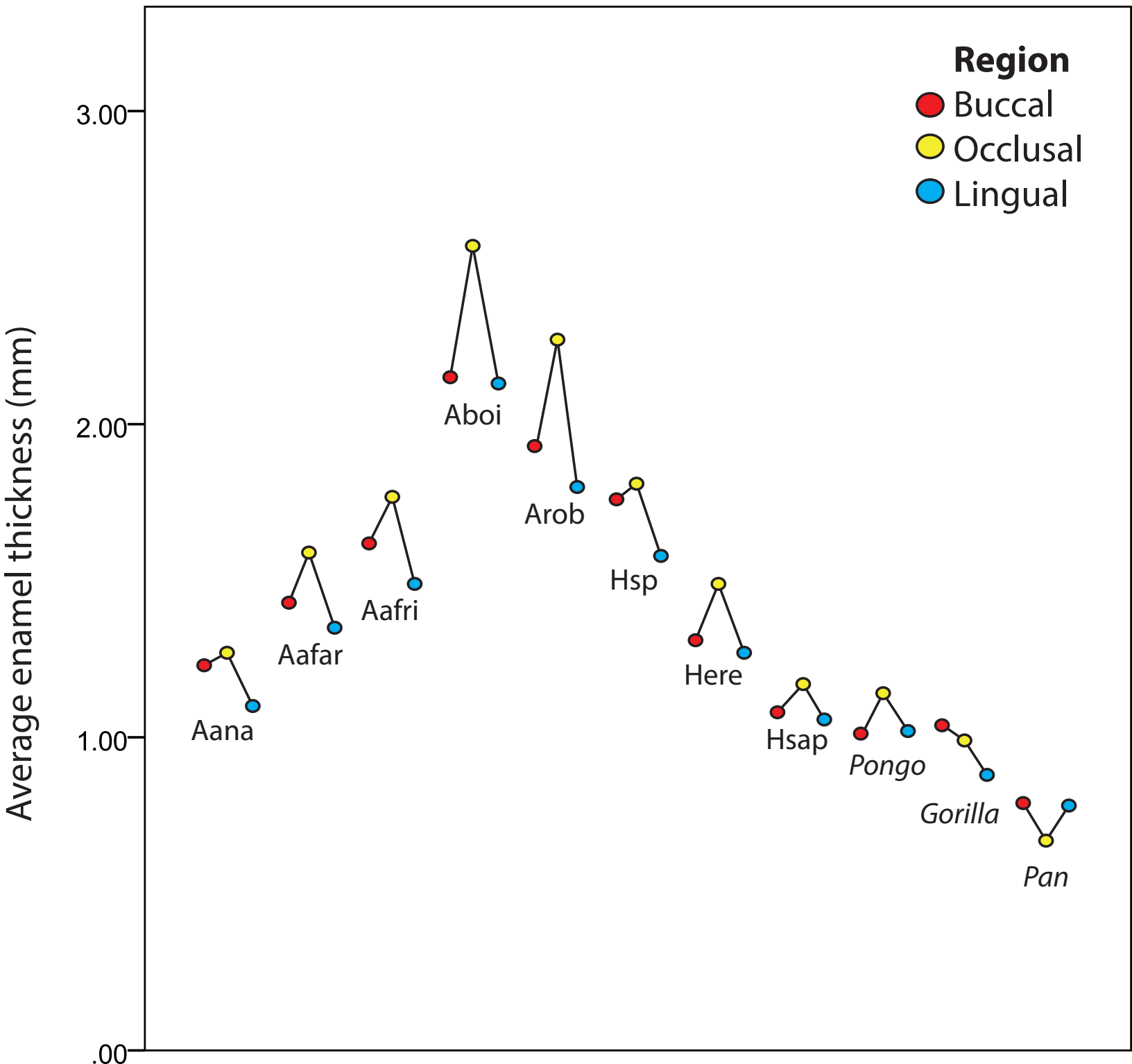

Region
Buccal
Occlusal
Lingual
Average enamel thickness (mm)
3.00
2.00
1.00
.00
Aana
Aafar
Aafri
Aboi
Arob
Hsp
Here
Hsap
Pongo
Gorilla
Pan

Figure 6

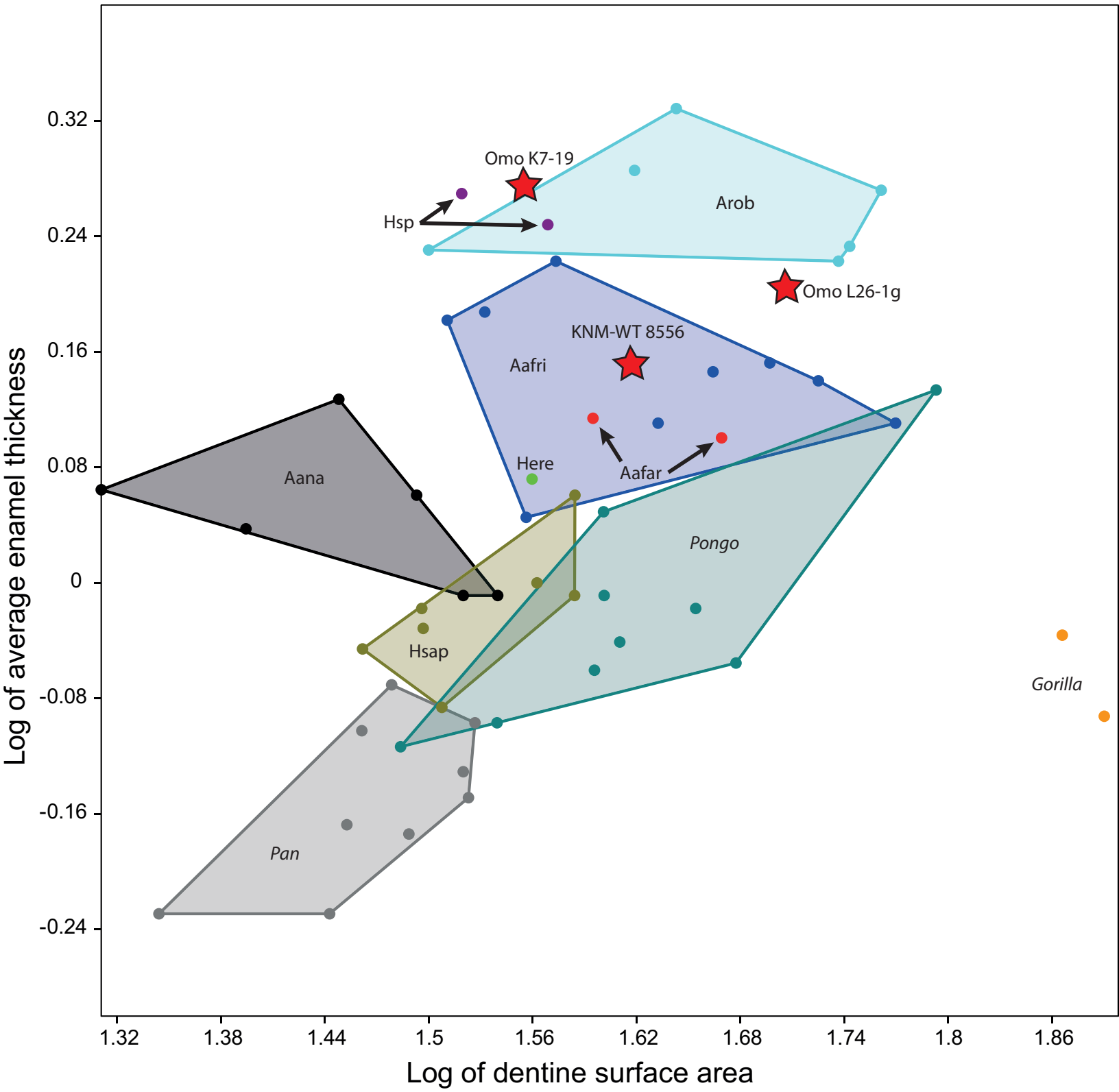

Omo K7-19
Hsp
Arob
Omo L26-1g
KNM-WT 8556
Aafri
Here
Aafar
Aana
Pongo
Hsap
Gorilla
Pan
0.32
0.24
0.16
0.08
0
-0.08
-0.16
-0.24
1.32
1.38
1.44
1.5
1.56
1.62
1.68
1.74
1.8
1.86
Log of average enamel thickness
Log of dentine surface area

Figure 7

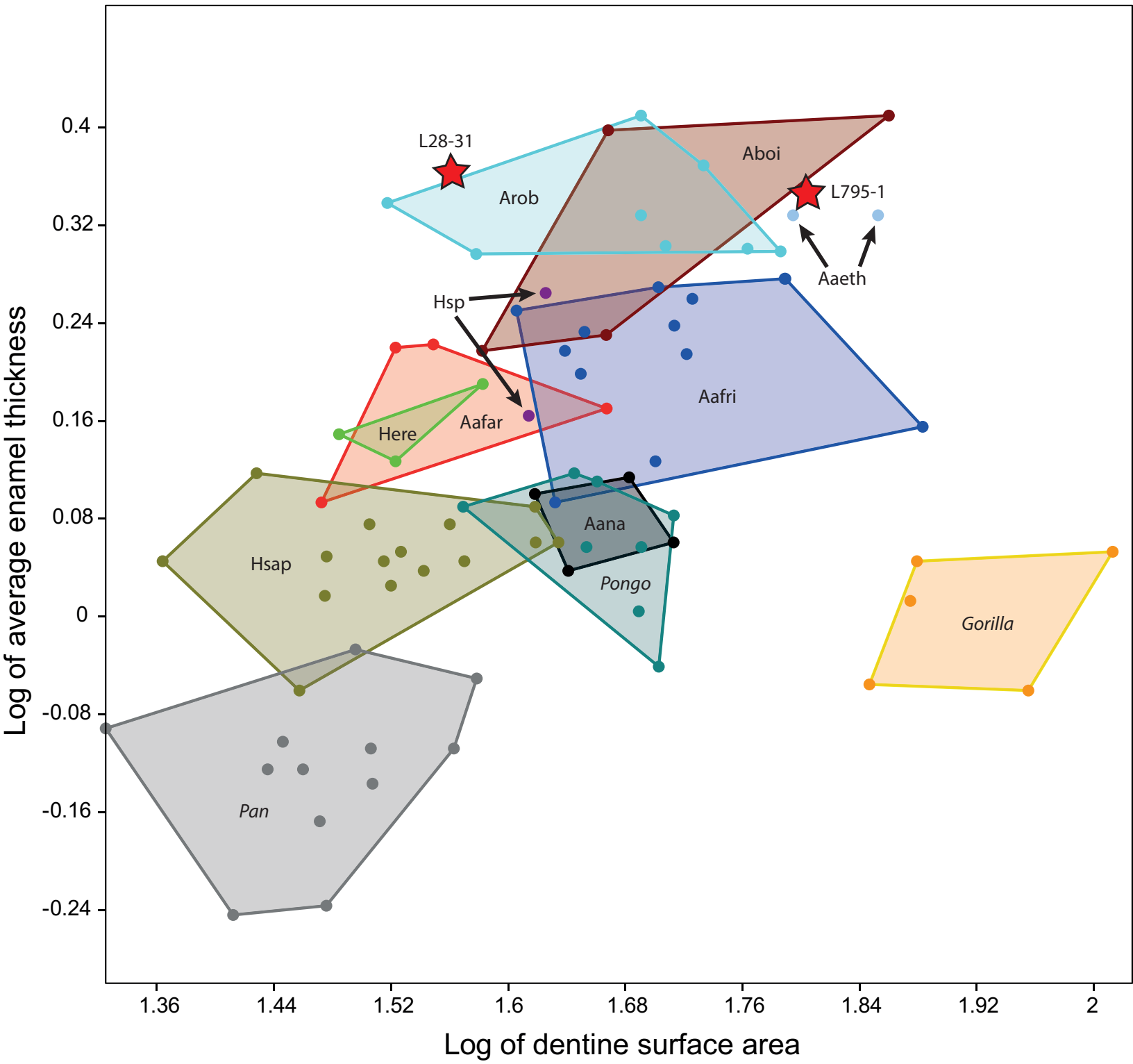
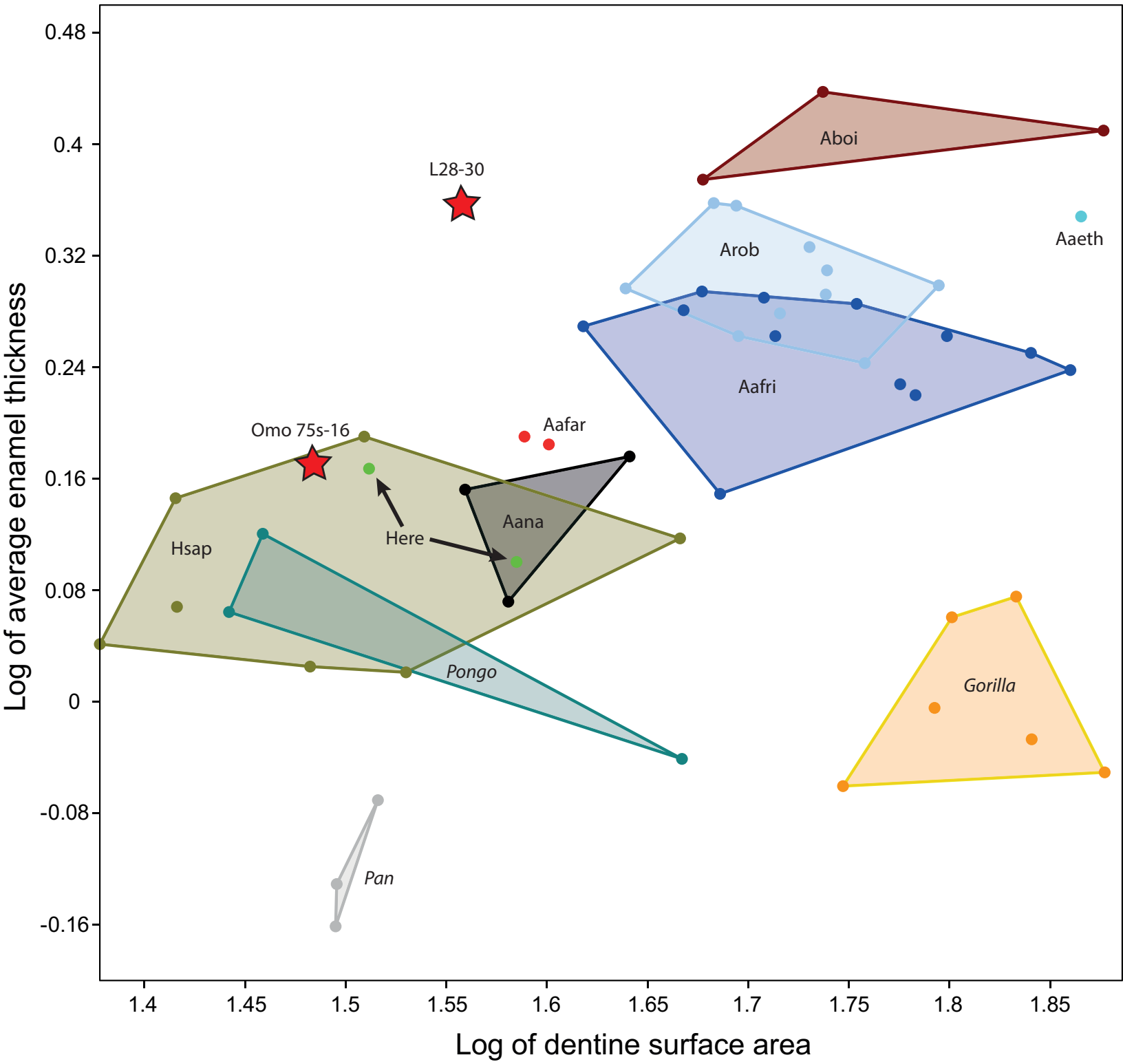

L28-31
Arob
Aboi
L795-1
Aaeth
Hsp
Aafri
Aafar
Here
Aana
Pongo
Hsap
Gorilla
Pan
0.4
0.32
0.24
0.16
0.08
0
-0.08
-0.16
-0.24
1.36
1.44
1.52
1.6
1.68
1.76
1.84
1.92
2
Log of average enamel thickness
Log of dentine surface area

Figure 8


0.48
0.4
0.32
0.24
0.16
0.08
0
-0.08
-0.16
Log of average enamel thickness
1.4
1.45
1.5
1.55
1.6
1.65
1.7
1.75
1.8
1.85
Log of dentine surface area
L28-30
Aboi
Aeth
Arob
Aafri
Aafar
Omo 75s-16
Here
Aana
Hsap
Pongo
Gorilla
Pan

Supplementary Material 1

Click here to download Supplementary Material: Supplementary Figure 1_Reconstructed_enamel.pdf

Supplementary Material 2

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Supplementary Material 3

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Supplementary Material 4

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Supplementary Material 5

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Supplementary Material 6

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Supplementary Material 7

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Supplementary Material 8

Click here to download Supplementary Material: Supplementary Figure 8_A_boisei_M1_M2_M3.pdf

Supplementary Material 9

Click here to download Supplementary Material: Supplementary Figure 9_A_robustus_M1.pdf

Supplementary Material 10

Click here to download Supplementary Material: Supplementary Figure 10_A_robustus_M2.pdf

Supplementary Material 11

Click here to download Supplementary Material: Supplementary Figure 11_A_robustus_M3.pdf

Supplementary Material 12

Click here to download Supplementary Material: Supplementary Figure 12_Homo_erectus_all.pdf

Supplementary Material 13

Click here to download Supplementary Material: Supplementary Figure 13_Homo_sp_all.pdf

Supplementary Material 14

Click here to download Supplementary Material: Supplementary Figure 14_Homo_sap_modern_M1_M2_M3.pdf

Supplementary Material 15

Click here to download Supplementary Material: Supplementary Figure 15_Pan troglodytes MPI_M1_M2_M3.pdf

Supplementary Material 16

Click here to download Supplementary Material: Supplementary Figure 16_Pan troglodytes ZMB_M1_M2_M3.pdf

Supplementary Material 17

Click here to download Supplementary Material: Supplementary Figure 17_Pan paniscus_M1_M2.pdf

Supplementary Material 18

Click here to download Supplementary Material: Supplementary Figure 18_Gorilla_M1_M2_M3.pdf

Supplementary Material 19

Click here to download Supplementary Material: Supplementary Figure 19_Pongo_M1_M2_M3.pdf