



Kent Academic Repository

O'Hara, M. C., Chapple, S., Mahoney, P., McGraw, W. S., Schwartz, Gary T., Skinner, M. M. and Guatelli-Steinberg, D. (2026) *Dietary adaptation in Paranthropus robustus postcanine teeth*. *American Journal of Biological Anthropology*, 190 (4). ISSN 2692-7691. (In press)

Downloaded from

<https://kar.kent.ac.uk/115790/> The University of Kent's Academic Repository KAR

The version of record is available from

<https://doi.org/10.1002/ajpa.70332>

This document version

Publisher pdf

DOI for this version

Licence for this version

CC BY (Attribution)

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in **Title of Journal**, Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our [Take Down policy](https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies) (available from <https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies>).

RESEARCH ARTICLE OPEN ACCESS

Dietary Adaptation in *Paranthropus robustus* Postcanine Teeth

M. C. O'Hara¹  | S. Chapple² | P. Mahoney²  | W. S. McGraw³  | Gary T. Schwartz⁴  |
M. M. Skinner⁵ | D. Guatelli-Steinberg³ 

¹Department of Biology, Ball State University, Indiana, USA | ²School of Natural Sciences, Marlowe Building, University of Kent, Kent, UK | ³Department of Anthropology, The Ohio State University, Smith Laboratory, Columbus, Ohio, USA | ⁴School of Human Evolution and Social Change, Institute of Human Origins, Arizona State University, Tempe, Arizona, USA | ⁵Department of Archaeogenetics, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Correspondence: M. C. O'Hara (mackie.oharaali@bsu.edu)

Received: 10 March 2026 | **Revised:** 14 July 2026 | **Accepted:** 24 July 2026

Keywords: dental evolution | dietary adaptation | Durophagy | enamel thickness | hominin evolution | microevolution | *Paranthropus robustus*

ABSTRACT

Objectives: Recent studies of *Paranthropus robustus* crania identified temporal trends in features associated with increased bite force production, coinciding with environmental shifts toward more arid conditions. To test whether the evolution of postcanine teeth also reflects increasing mechanical demands associated with hard food consumption, we analyzed trends in the architecture of *P. robustus* postcanine teeth, including crown area, tooth shape, and average (AET) and relative (RET) enamel thickness.

Materials and Methods: 2D mesial sections were created from microCT scans of upper premolars ($n = 24$), upper molars ($n = 14$), and lower molars ($n = 16$) from multiple South African sites. Descriptive statistics, Mann–Whitney U tests, and Jonckheere–Terpstra tests were used to identify significant differences over time, with Holm–Bonferroni corrections applied for multiple comparisons.

Results: Significant temporal trends existed in premolar morphology with increased crown area (CA), absolute crown strength (ACS), overall enamel thickness (AET and RET), and increased enamel thickness over the occlusal half of the tooth. Upper molars increased in CA but no other measured variable. Lower molars showed no significant temporal trends in any measured variable.

Discussion: These results suggest rapid dental evolution in response to dietary pressures, with varying and independent rates of change between different tooth types. These findings support the hypothesis that selection resulted in shifts to *P. robustus* dental morphology to increase mechanical resistance, consistent with an expanding dietary niche that incorporated increasingly challenging foods.

1 | Introduction

Several dental features may relate to the consumption of mechanically resistant or hard-object foods (durophagy) in non-human primates, including hominins. Large tooth size (Constantino et al. 2012; Constantino et al. 2011; Janis and Fortelius 1988), low-crowned, “bunodont” teeth (Constantino et al. 2009; Kay and Hylander 1978; Kay 1981; Luke and Lucas 1983; Spears and Crompton 1996), thick enamel (L. Martin 1985; Janis and Fortelius 1988; Dumont 1995; Pampush et al. 2013), unevenly

distributed enamel (Gantt 1986; Molnar and Gantt 1977; Macho and Thackeray 1992, 1993; Schwartz 2000; Kono 2004; Lucas et al. 2008a; Thiery et al. 2017a, b, c), and high degrees of enamel decussation (Popowics et al. 2001, 2004; Lucas et al. 2008b) have all been suggested to protect teeth against cracks and/or crack propagation during hard-object feeding and thereby enhance the functional longevity of molars. These aspects of dental form are thought to represent adaptive responses to durophagous diets (Jolly 1970; Kay 1981; Janis and Fortelius 1988; Constantino et al. 2019).

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2026 The Author(s). *American Journal of Biological Anthropology* published by Wiley Periodicals LLC.

Summary

- Upper premolar enamel thickness in *Paranthropus robustus* increased significantly over time, consistent with selective pressure for hard-object feeding.
- Premolars showed more changes than upper or lower molars, suggesting mosaic rather than uniform dental evolution in the *P. robustus* lineage.

Paranthropus robustus is characterized by distinctive craniodental features, including molarized premolars and thick enamel, traditionally interpreted as adaptations for processing mechanically challenging foods (Bailey and Wood 2007; Williams 2015). A recent study (Martin et al. 2021) compared *P. robustus* crania from Drimolen (2.04–1.95mya) to those from Swartkrans Member 1 Hanging Remnant and Kromdraai B (~1.8mya). The authors identified a distinct temporal trend such that later (geologically younger) *P. robustus* were characterized by features including larger teeth and more anteriorly positioned sagittal crests and zygomatic roots, which are associated with production of greater bite forces (Martin et al. 2021). A drying period and expansion of shrubland-type vegetation in this region of South African is also documented between Drimolen and Swartkrans, leading Martin et al. (2021) to suggest that the lineage of *P. robustus* adapted to a diet that became increasingly more mechanically challenging over this time period:

...those morphological changes that are functionally related to the performance of the feeding apparatus [...] are dietary adaptations. Specifically, we infer (but cannot prove) that they resulted from ecologically driven directional or, perhaps, variability selection favouring increased efficiency at producing and withstanding higher bite forces. This probably expanded the *P. robustus* dietary niche to include more foods that are mechanically challenging to process, allowing increased ecological generalization. (Martin et al. 2021: 43)

Martin et al.'s (2021) analysis presents an excellent framework for evaluating whether dental form in *P. robustus* followed a similar trajectory. Given their claim that *P. robustus* was evolving in an environment becoming increasingly arid and was therefore capable of processing a more mechanically challenging foods with higher bite forces (Martin et al. 2021), we propose that, over time *P. robustus* teeth should evince morphological changes in tooth size, tooth shape, and/or enamel thickness that are consistent with an increased reliance on mechanically challenging foodstuffs.

1.1 | Dental Morphology and Durophagy

Many aspects of tooth size, tooth shape, and enamel thickness associated with durophagy may be related to body size or phylogenetic traits other than those necessary for durophagy:

to prevent teeth from cracking and be more fracture resistant than the food being consumed (Constantino et al. 2011; Lucas et al. 2008a, b; Luke and Lucas 1983). For example, thick enamel is more resistant to crack formation compared to thinner enamel, but thick enamel also lengthens the functional lifespan of enamel prior to dentin and pulp exposure with abrasive diets (Rabenold and Pearson 2011; Pampush et al. 2013). Likewise, larger teeth are generally more resistant to cracks under high masticatory loading (Janis and Fortelius 1988; Constantino et al. 2012; Constantino et al. 2011).

Teeth, and specifically enamel, are under strong selection pressure because enamel forms the occlusal surface and therefore makes direct contact with food objects, and any wear or damage accrued is permanent, as enamel does not remodel. During mastication, a food bolus is comminuted, that is, reduced to smaller, digestible sizes between the enamel surfaces of opposing teeth. If food is not properly processed due to inadequate or compromised teeth, nutrients may be inaccessible to an organism, leading to undernutrition (King et al. 2005). When hard foods are consumed, objects must be reduced without inducing mechanical failure of the teeth that process them. Primates with similar dietary needs for crushing and grinding, compared to shearing, share similar molar morphologies (Kay 1975; Gantt 1986; Guy et al. 2015; Thiery et al. 2017a, b, c). Selective pressures are therefore proposed to be based on the diet and masticatory needs of a species, as teeth are required to adequately process food throughout an individual's life (Janis and Fortelius 1988).

1.1.1 | Tooth Size

Given the same morphology, a larger tooth can protect against enamel cracks compared to a smaller tooth of similar morphology because wider occlusal surfaces sustain lower stresses per unit area compared to teeth with smaller occlusal surfaces (Janis and Fortelius 1988). In primates, absolutely larger teeth, particularly wider teeth, can withstand higher occlusal loads before enamel cracks appear (Constantino et al. 2012; Constantino et al. 2011; Constantino et al. 2009; Lawn and Lee 2009). When comparing the critical load required to generate margin fractures in sea otters, *Paranthropus boisei*, and *H. sapiens* molars, Constantino et al. (2011) concluded that because of their significantly larger and more thickly-enamelled teeth, *P. boisei* molars could withstand nearly three times the load of molars from *H. sapiens*. While large teeth may be selected for in certain lineages for a variety of reasons, tooth size also tends to increase with body size across species. Thus, in large-bodied species, large teeth will withstand high loads, potentially serving as an exaptation (Gould and Vrba 1982) to durophagy, as Schwartz et al. (2020) suggest may be the case for gorillas whose teeth are adapted to leaf-eating but in at least one population, can and do consume hard *Coula edulis* nuts (van Casteren et al. 2019).

1.1.2 | Tooth Shape

Tooth shape, specifically the geometric aspects of occlusal form such as cusp relief, may protect postcanine teeth during high loading. Molars are defined as “bunodont” when they possess low (low-relief or “short”), rounded cusps (Swindler 2002).

Limited shearing crests and relatively flat (low relief) crowns dissipate high occlusal forces generated when crushing hard/tough foods, preventing cracks and facilitating grinding (Jolly 1970; Kay 1981). Similarly, a relatively blunt cusp is suggested to be ideal for cracking a hard object and then reducing it via grinding (Jolly 1970; Luke and Lucas 1983; Constantino et al. 2009). Thus, low-relief molars with obtuse cusp angles are more effective at crushing objects and more resistant to high loads than those with highly angled and tall cusps (Kay and Hylander 1978; Spears and Crompton 1996). Species that crush hard objects are therefore expected to have low-relief (short) molars with more bunodont cusps and more obtuse cusp angles.

1.1.3 | Enamel Thickness

There have been at least three major claims about how enamel thickness varies between species and how it may relate to the ability to resist fracture: (1) Durophagy is often associated with thick enamel (usually measured with the index of relative enamel thickness, “RET”) (L. Martin 1985; Dumont 1995; Pampush et al. 2013), (2) durophagy will be associated with thickened enamel over cusp tips (Kono 2004; Lucas et al. 2008b; Chai 2018), and (3) the “functional” sides of teeth are bigger/thicker than the “non-functional” side (Kay 1975; Molnar and Gantt 1977; Khera et al. 1990; Schwartz 2000). This study examines these aspects of enamel thickness and its distribution in *P. robustus* and tests for evidence of directional change over time.

Enamel thickness has historically been measured using either summary measures (e.g., L. Martin (1985)’s indices of average enamel thickness, AET, and relative enamel thickness, RET) that model enamel as uniformly thick (or thin) across the crown, or by evaluating its complex distribution by using linear and regional measures of thickness at various locations on the crown (Grine and Martin 1988; Schwartz 2000). Thick enamel protects against wear in abrasive diets, and in diets that include hard foods (see Pampush et al. (2013)). Primates that specialize in consuming hard, resistant foods have been reported to have thicker indices of relative enamel thickness (RET) when compared to closely related soft-object feeding primates (Dumont 1995; McGraw et al. 2012).

According to Lucas et al. (2008b), an adaptation to durophagy involves an “uneven” distribution of enamel whereby cusp tips are reinforced with thickened enamel. This expectation is partially due to the fact that occlusal forces are maximized at cusp tips (Chai 2018). This thickening, or reinforcement, is suggested to protect the cusp tips from cracking. Thiery et al. (2017a, b, c) tested this hypothesis by measuring the unevenness of enamel in non-human primate upper second molars and found that more “uneven” enamel distribution is related to hard object feeding in cercopithecoid monkeys. That study, however, did not report the specific regions of the enamel cap that were thickened with respect to durophagy.

Schwartz (2000) found that upper lingual molar cusps have thicker enamel than their buccal

counterparts, especially in *H. sapiens* and *Pongo*. Maxillary lingual and mandibular buccal cusps have been referred to as “functional” or “loading” cusps and, in general, functional cusps tend to be more thickly enameled (Molnar and Gantt 1977; Schwartz 2000). During Phase I of the chewing cycle, food objects are crushed between the upper and lower functional/loading cusp tips (protocone and protoconid, respectively) and the opposing tooth’s occlusal basin (Kay 1975; Schwartz 2000). While the term “functional” is misleading given that both sides of the tooth are used during the breakdown of a food bolus, it is a useful shorthand for indicating the side of the tooth crown most engaged during crushing activities, which is particularly relevant for hard object feeding.

Because cusp tips approach the opposite occlusal basin when crushing a food bolus, hard object feeders should show evidence of enamel thickening in protocone and protoconid cusp tips and in their occlusal basins relative to their lateral walls (Macho and Berner 1994; Schwartz 2000; Kono 2004; Lucas et al. 2008a; Le Luyer et al. 2014). Alternatively, a recent study of enamel thickness and fracture potential suggests that cuspal enamel may be thickened simply as a developmental sequelae of selection for thicker enamel on lateral crown walls which would strengthen a crown against margin fractures (Schwartz et al. 2020).

1.2 | Goals

This study examines whether mechanically relevant aspects of the postcanine dentition in *P. robustus* follow a temporal trajectory that is equivalent to aspects of the cranium that are related to generating masticatory loads (Martin et al. 2021), and thereby reflect an additional anatomical signal of adaptations to changing dietary demand. Specifically, we propose that if *P. robustus* incorporated greater proportions of hard-object foods in its diet in response to an increasingly arid environment, we should see evidence that over that same time interval, the postcanine teeth became larger, with flatter or more bunodont cusps, more thickly enameled, and/or characterized by thicker enamel concentrated across the occlusal basin and cusp tips.

We test the following hypotheses:

- H1 (Tooth size and shape): If *P. robustus* postcanine teeth evolved toward greater resistance to mechanical loading, then the crown area and absolute crown strength (ACS) should increase, and cusp geometry should shift toward being flatter (i.e., more bunodont in the geologically younger samples).
- H2 (Whole-crown enamel thickness): If durophagy increased over time, average enamel thickness (AET) and relative enamel thickness (RET) should increase in geologically younger samples.
- H3 (Enamel distribution): If structural reinforcement was concentrated at sites of peak occlusal loading, linear and

regional enamel thickness should increase preferentially over the functional cusp tips and occlusal basin relative to the lateral and marginal walls, producing a more “uneven” distribution of enamel through time.

Given prior evidence that enamel thickness is more evolutionarily labile than crown size or shape (Hlusko 2016; Hlusko et al. 2004; Ungar and Sponheimer 2011), we further predict that H2 and H3 will show stronger and more consistent support than H1. We analyze temporal trends in cusp shape, crown size and strength, and enamel thickness distribution across different tooth types to test whether any observable changes align with expectations for adaptations to more mechanically resistant foods.

2 | Materials and Methods

2.1 | Sample

We examined digital 2D slices through the mesial cusps of *P. robustus* upper and lower postcanine teeth ($n = 54$), including lower first molars (LM1, $n = 8$), lower second molars (LM2, $n = 8$), upper first molars (UM1, $n = 8$), upper second molars (UM2, $n = 6$), upper third premolars (UP3, $n = 11$), and upper fourth premolars (UP4, $n = 13$). Specimens derive from the Drimolen Main Quarry (2.04–1.95 Ma), Swartkrans Members 1 Hanging Remnant (2.0–1.8 Ma), Member 2 (1.71–1.1 Ma), and Member 3 (1.3–0.6 Ma), and Kromdraai B (~1.8 Ma) (Table 1 and Table S5, (Herries and Adams 2013; Herries et al. 2020)). To facilitate the study of temporal trends, we organized the specimens into three time periods: (1) “Earlier” which includes the Drimolen specimens, (2) “Member 1 HR” which includes specimens from Swartkrans Member 1 HR, and (3) “Later,” which contains specimens from Kromdraai B and Swartkrans Members 2 and 3 (see Table 1).

2.2 | Sample Preparation

Micro-computed tomography (μ CT) scans were sourced from Ditsong National Museum of Natural History and the University

of the Witwatersrand. Two-dimensional slices across the mesial cusps were generated using the methods established by Skinner et al. (2013; 2015) using Dragonfly 22.0. A virtual plane of section that intersected the two dentin horns associated with the mesial cusps and that was oriented perpendicular to the cervical margin (see Figure 1) was saved as a TIFF file.

All 2D mesial planes of section TIFFs were mirrored (if necessary) so that the lingual side of the upper teeth was oriented to the left side of the image (Kono 2004). These are the “functional” sides of the upper premolars and molars. Following recommendations and methods established by O’Hara and Guatelli-Steinberg (2021), worn teeth were reconstructed using the Profile and Pen Tool methods (Saunders et al. 2007; Smith, Olejniczak, et al. 2012b). No linear or angle measurements were taken on reconstructed cusp tips; regional measurements were excluded from crowns reconstructed from “extensive” wear extending into the dentin horns (O’Hara and Guatelli-Steinberg 2021). The Supporting Information All Data.xlsx notes which teeth were reconstructed and exactly which measurements were taken for each tooth.

2.3 | Measurements

Features related to the categories of tooth size, tooth shape (e.g., cusp angles), enamel thickness distribution were measured, calculated, and analyzed (Figure 1, Table 2). To facilitate comparison of tooth size, tooth shape, and enamel thickness, we included multiple measurements from other studies (Figure S1, Tables S1–S4). This means that some features (e.g., tooth size) are evaluated using several measurements. However, statistical analyses described below will use Holm-Bonferroni corrections for multiple comparisons.

2.3.1 | Tooth Size

Tooth size was evaluated using three measurements, defined below: crown area (CA), bi-cervical diameter (BCD), and enamel dentin junction (EDJ) length (Figure 1, Table 1). In this study, CA is represented by the total area of the entire crown

TABLE 1 | *P. robustus* sample by tooth type and provenance.

	Lower molars		Upper molars		Upper premolars		Total
	LM1	LM2	UM1	UM2	UP3	UP4	
Older sites							46
Drimolen main quarry	1	1	2	0	1	2	7
Swartkrans member 1 HR	6	6	6	5	8	8	39
Younger sites							8
Kromdraai B	1	0	0	1	1	1	4
Swartkrans member 2	0	1	0	0	1	1	3
Swartkrans member 3	0	0	0	0	0	1	1
Total	8	8	8	6	11	13	54
	16		14		24		

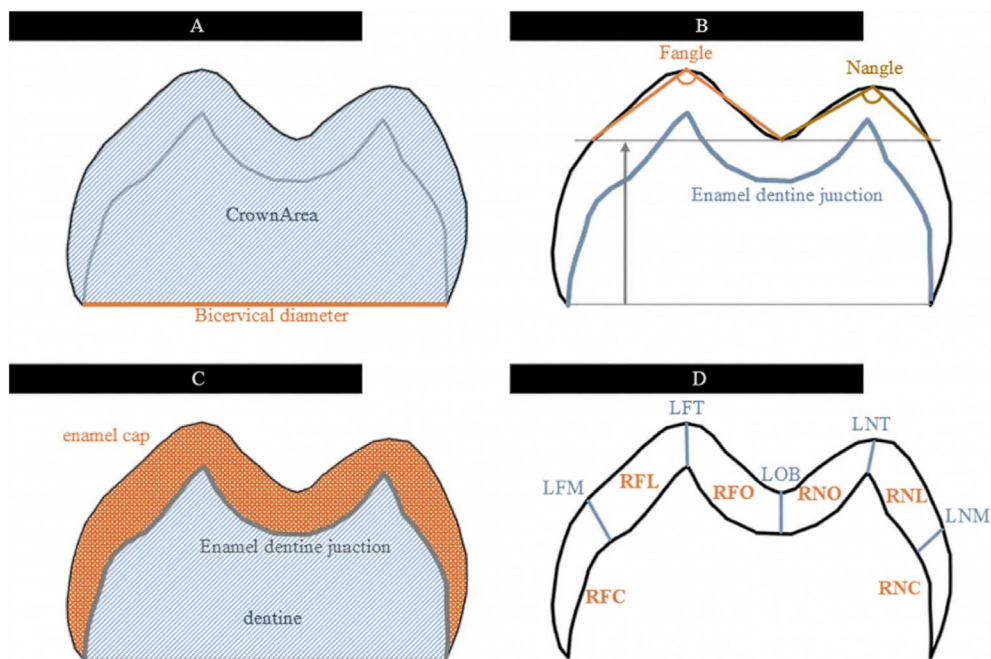


FIGURE 1 | Estimates of (A) tooth size, (B) tooth shape, (C) whole crown enamel thickness, and (D) linear (blue text) and regional (orange text) enamel thickness employed in this study.

(i.e., the enamel cap and dentin) that is exposed between the outer enamel surface and BCD of the 2D slice. BCD is defined as the length of a line that extends between the cemento-enamel junction on each side of the virtually sectioned tooth. EDJ length is the length a line running along that tissue interface from one cervical margin to the other (Table 1, Figure 1). A tendency to increase the amount of hard object, or mechanically resistant, foods should correspond to increasing CAs, EDJ lengths, and BCDs because larger tooth crowns are better able to dissipate high occlusal loads (Janis and Fortelius 1988; Constantino et al. 2012; Constantino et al. 2011; Lawn and Lee 2009).

2.3.2 | Tooth Shape

Tooth shape was evaluated using two direct measurements and two variables calculated from other measurements. Two measurements of cusp angle were taken on the functional (Fangle) and non-functional (Nangle) cusps. Cusp angles were measured as the included angle between the lowest point of the occlusal basin, the maximum extent of the cusp tip, and a point on the lateral wall where a line tangent to the occlusal basin and parallel to the BCD intersects with the outer enamel surface (see Figure 1B). Teeth that are more bunodont can better dissipate high loading forces, so increasing durophagy should be associated with cusp angles becoming more obtuse (Constantino et al. 2009).

To compare the degree of bunodonty between species while attempting to scale for overall differences in tooth size, a crown shape index (CSI) was calculated as the square root of CA divided by BCD (Table 3). Values greater than or equal to 1 represent teeth that are equally tall or taller than they are wide, while values less than 1 represent teeth that are wider than they are tall. Low-cusped, bunodont crowns will be wider than they are tall, so increasing levels of durophagy should be

associated with reductions in the CSI values and would typically be less than 1.

Finally, absolute crown strength ACS—developed by Schwartz et al. (2020) was included as it focuses on the combined role that both crown geometry and crown size play in determining the degree to which teeth resist fracture (i.e., failure) under loading. ACS is calculated as $\sqrt{(AET \cdot (BCD/2))}$ (Table 2). Given that durophagous species need to protect against cracking, increasing durophagy should be associated with increasing values of ACS.

2.3.3 | Whole Crown Enamel Thickness

Overall enamel thickness and its distribution across the crown are broken down into six categories: total enamel thickness across the virtual section through the crown, linear enamel thicknesses, regional enamel thicknesses, proportional linear enamel thicknesses scaled to AET, and proportional regional enamel thicknesses scaled to AET.

Average enamel thickness (AET) and relative enamel thickness (RET) were established by L. B. Martin (1983) as estimates of whole crown enamel thickness. AET is calculated by dividing the enamel cap area by the EDJ length (see Table 1, Figure 1C), while RET corrects AET for scaling effects by dividing the latter by the square root of dentin area and multiplying by 100. Thus, RET is a unitless index and is often used to compare overall enamel thickness between species of various body/tooth sizes, while AET is appropriate only when comparing teeth within a species because it is not scaled in any way (Smith, Kupczik, et al. 2012a). Durophagous groups are predicted to have greater AET and RET values compared to non-durophagous groups because thick enamel is expected to be protective against cracking

TABLE 2 | Tooth size, tooth shape, and enamel thickness variables.

Abbreviation	Variable name	Calculation	Figure 1
Tooth size			
CA	Crown area	Measured directly	A
BCD	Bi-cervical diameter	Measured directly	A
EDJ	Enamel-dentin junction length	Measured directly	B
Tooth shape			
Fangle	Functional cusp tip angle	Measured directly	B
Nangle	Non-functional cusp tip angle	Measured directly	B
CSI	Crown shape index	$\sqrt{(CA)/BCD}$	
ACS	Absolute crown strength	$\sqrt{(AET*(BCD/2))}$	
Whole crown enamel thickness			
AET	Average enamel thickness	Enamel cap area/dentin area	C
RET	Relative enamel thickness	$(AET/\sqrt{\text{dentin area}})*100$	C
Linear enamel thickness			
LFM	Linear functional margin	Measured directly	D
LFT	Linear functional cusp tip	Measured directly	D
LOB	Linear occlusal basin	Measured directly	D
LNT	Linear non-functional cusp tip	Measured directly	D
LNМ	Linear non-functional margin	Measured directly	D
Regional enamel thickness			
RFC	Regional functional cervical area	RFC enamel area/RFC EDJ length	D
RFL	Regional functional lateral wall area	RFL enamel area/RFL EDJ length	D
RFO	Regional functional occlusal area	RFO enamel area/RFO EDJ length	D
RNO	Regional non-functional occlusal area	RNO enamel area/RNO EDJ length	D
RNL	Regional non-functional lateral wall area	RNL enamel area/RNL EDJ length	D
RNC	Regional non-functional cervical area	RNC enamel area/RNC EDJ length	D
Proportional linear enamel thickness			
pLFM	LFM percent of AET	LFM/AET	
pLFT	LFT percent of AET	LFT/AET	
pLOB	LOB percent of AET	LOB/AET	
pLNT	LNT percent of AET	LNT/AET	
pLNМ	LNМ percent of AET	LNМ/AET	
Proportional regional enamel thickness			
pRFC	RFC percent of AET	RFC/AET	
pRFL	RFL percent of AET	RFL/AET	
pRFO	RFO percent of AET	RFO/AET	
pRNO	RNO percent of AET	RNO/AET	
pRNL	RNL percent of AET	RNL/AET	
pRNC	RNC percent of AET	RNC/AET	

TABLE 3 | Variables with significant directional trends over time identified with Holm-Bonferroni correction (Tables S6–S33).

Category	Variable	Tooth	Time Block	Direction
Tooth size	CA	UP4	By Site	Increases
		Upper Premolars	By Site	"
		Upper Molars	By Site	"
Tooth shape	ACS	UP4	By Site	"
		Upper Premolars	By Site	"
Whole crown ET	AET	UP4	By Site	"
		UP4	Older vs. Younger	"
		Upper Premolars	By Site	"
	RET	Upper Premolars	Older vs. Younger	"
		UP4	Older vs. Younger	"
		Upper Premolars	By Site	"
		Upper Premolars	Older vs. Younger	"
Linear ET	LFT	Upper Premolars	By Site	"
		Upper Premolars	Older vs. Younger	"
	LNT	Upper Premolars	By Site	"
		Upper Premolars	Older vs. Younger	"
Proportional linear ET	pLFM	Upper Premolars	By Site	Decreases
	pLFT	Upper Premolars	By Site	Increases
	pLNT	Upper Premolars	By Site	"
	pLNM	UP4	By Site	Decreases
		Upper Premolars	By Site	"
Regional ET	RFC	Upper Premolars	By Site	Increases
		UP4	By Site	"
		Upper Premolars	By Site	"
		Upper Premolars	Older vs. Younger	"
	RFO	Upper Premolars	By Site	"
	RNO	Upper Premolars	By Site	"
	RNL	Upper Premolars	By Site	"

during hard object feeding. Thus, if there is an increase in durophagy over time, then AET and RET values in *P. robustus* should increase from geologically older to younger points along the *P. robustus* lineage in South Africa.

2.3.4 | Linear Enamel Thickness

Unlike the indices described above, linear enamel thickness measurements provide information about the distribution of enamel over the crown by quantifying the exact thickness in specific areas. More than 30 linear measurements have been used in the literature to measure enamel thickness (see Figure S1). Depending on the tooth's morphology, some measurements are more comparable than others, but when

comparing among species, it is important to recognize that small differences in morphology can exaggerate differences in linear enamel thickness values between species (Smith et al. 2004; Smith et al. 2005; Suwa and Kono 2005). For example, if the cusp tip sits directly above the dentin horn in one species, the cusp tip enamel thickness will be smaller than one where the cusp tip sits lateral to the dentin horn. Skinner et al. (2015) note the substantial variation in measurements of enamel thickness depending on locations of measurement, and tooth types that have been used over the years and call into question the biological homology of the data that have been published (Figure S1).

In this study, we use both linear and regional enamel thicknesses (see below). Linear enamel thickness at the functional

and non-functional cusp tips, functional and non-functional lateral walls, and the deepest point of the occlusal basin is measured (Table 2, Figure 1D). Linear enamel thickness at the occlusal basin (LOB) was measured as the distance between the lowest point of the EDJ within the occlusal basin and the lowest point of the outer enamel surface (Macho and Berner 1994; Macho and Thackeray 1992, 1993; Schwartz 1997, 2000; Kono-Takeuchi et al. 1998; Olejniczak and Grine 2006). Linear enamel thickness at the functional and non-functional cusp tips (LFT and LNT, respectively) was measured as the distance between the apex of the dentin horn and the maximum extent of the outer enamel surface at that cusp (Beynon and Wood 1986; Grine and Martin 1988; Macho and Thackeray 1992, 1993; Macho and Berner 1994; Spoor et al. 1993; Schwartz 1997, 2000; Schwartz et al. 1998; Kono and Suwa 2005; Kono-Takeuchi et al. 1998; Ulhaas et al. 1999; Shimizu 2002; Dean and Schrenk 2003; Grine et al. 2005; Olejniczak and Grine 2006; Feeney 2009; Mahoney 2010; Le Luyer et al. 2014). Linear enamel thickness at the functional and non-functional lateral wall midpoints (LFM and LNM, respectively) was measured at the midpoint of the lateral wall's EDJ; a line perpendicular to the EDJ was measured from the EDJ midpoint to the outer enamel surface. Cusp tip measurements (LFT and LNT) were not taken on crowns that had been reconstructed due to wear (O'Hara and Guatelli-Steinberg 2021).

According to Lucas et al. (2008a), durophagous groups will have thick enamel over the cusp tips, so LFT and LNT are expected to be greater in durophagous species. However, it should be noted that interspecific body size and tooth size variation may make it difficult to identify durophagous signals in raw linear enamel thickness values. Given that hard objects are crushed between cusp tips and the opposing tooth's occlusal basin, the occlusal basin (LOB) is also expected to be thicker in durophagous species (Constantino et al. 2009). No specific expectations are predicted for the linear lateral wall margin measurements, but they may also trend thicker in durophagous species, as thicker marginal enamel may reduce margin fractures (Schwartz et al. 2020).

2.3.5 | Regional Enamel Thickness

Linear enamel thickness measurements are limited in their scope and can only provide information about a single point on an enamel crown. Thus, enamel thickness is also measured in zones or "regions" of the crown that roughly correspond to different stages of the chewing cycle to better represent the amount of enamel underlying masticatory forces.

We defined six regions in our study: functional and non-functional cervical (RFC and RNC), lateral (RFL and RNL), and occlusal zones (RFO and RNO) (Table 2, Figure 1D). The linear enamel thickness measures form the borders of the regions of enamel thickness to be measured. For example, the functional lateral region (RFL) is contained between the LFM and LFT measurement (Figure 1D). Each region's enamel thickness is calculated by dividing the area of enamel within the region by the EDJ length within the region (Table 2). Regional measurements were not taken on crowns that had been reconstructed to

"extensive" wear that extended into the dentin horns (O'Hara and Guatelli-Steinberg 2021).

The regional enamel thickness measures are based loosely on previous regions established by Kono (2004) and (Skinner et al. 2015) 2D regional buccal, occlusal, and lingual AET system. However, each of those three regions is divided into two, and cusps are referenced by functional status rather than side. This was done, in part, because Schwartz (2000) identified differences in linear enamel thickness on the buccal and lingual lateral walls, with the functional cusp side tending to have thicker enamel. Dividing the tooth into six parts (cervical, lateral, and occlusal thirds on both buccal and lateral sides) will also allow for increased power in identifying distribution trends across the crown. Keeping the measurements consistent across all tooth types and classes will make it possible to analyze inter- and intra-tooth trends. Crushing and grinding occur on both the functional and non-functional walls of the occlusal basin, so durophagous groups are expected to have thicker enamel in the RFO and RNO regions (Constantino et al. 2009). Thus, RFO and RNO are expected to be thicker in durophagous groups compared to non-durophagous, but no significant differences are expected for RFC, RFL, RNL, or RNC.

2.3.6 | Linear Enamel Thickness Scaled to AET

While linear and regional enamel thickness measurements are useful for identifying thickness and distribution of enamel within a group, variation in body and tooth size complicates raw values when comparing between groups. Thus, scaled variables were created to allow for the relative thickness and distribution of enamel to be compared between groups.

The five linear measures of enamel thickness were each divided by the tooth's AET to create 5 new variables: pLFM, pLFT, pLOB, pLNT, pLNM (Table 3). The calculated values represent the percent by which the region's enamel thickness differs from the whole crown enamel thickness (adapted from Kono (2004)). For example, a value of 0.75 would indicate the region was 75% as thick as the whole crown and a value of 1.50 would indicate the region was 50% thicker than the whole crown AET. These variables therefore provide a way to compare enamel distribution between crowns with differing crown sizes. Predictions for the linear enamel thickness values scaled to AET are the same as for the raw linear enamel thickness values: durophagous groups are expected to "stack" a greater proportion of their enamel along cusp tips and the occlusal basin, so the pLFT, pLOB, and pLNT values are expected to be significantly greater than non-durophagous groups.

2.3.7 | Regional Enamel Thickness Scaled to AET

The same method for scaling linear enamel thickness values was applied to the regional enamel zones to create 6 new variables: pRFC, pRFL, pRFO, pRNO, pRNT, pRNC (Table 2). As with the regional measures, pRFL, pRFO, and pRNO are expected to be thicker in durophagous groups compared to non-durophagous,

but no significant differences are expected for RNL, RFC, or RNC.

2.4 | Statistical Analysis

Mean and standard deviations were calculated for each of the measured variables (Table 2). Tooth types are grouped (upper premolar, upper molar, and lower molar) for each site and between older and younger sites with pooled periods (Older = Drimolen, SK Member 1 HR; Younger = Kromdraai B, SK Member 2, SK Member 3) (Tables S6–S33). Jonckheere-Terpstra tests were performed to identify whether significant trends in dental form could be identified between individual sites; Mann–Whitney U tests were used for two-group (Older vs. Younger) comparisons. The Jonckheere-Terpstra test was chosen because it can detect ordered differences among ordered groups, it is appropriate for temporal sequence data, it does not require that data follow a normal distribution, and it does not require equal sample sizes across groups. To control for family-wise error rate across multiple simultaneous comparisons within each variable category, Holm-Bonferroni correction was applied. The Holm-Bonferroni procedure ranks all *p*-values from smallest to largest and applies sequentially adjusted significance thresholds, providing greater statistical power than standard Bonferroni correction. Separate analyses were conducted for individual tooth types as well as pooled tooth types (upper premolars, upper molars, and lower molars). Tables S6–S33 document all analyses and comparisons.

3 | Results

All measured values are reported in the [Supporting Information](#) (file: ALL_DATA.xlsx). Descriptive statistics for (a) all teeth and (b) teeth sorted by individual tooth type and pooled tooth type are reported by site and by chronological period (older vs. younger) for tooth size (Tables S6–S9), tooth shape (Tables S10–S13), whole crown enamel thickness (Tables S14–S17), linear enamel thickness (Tables S18–S21), proportional linear enamel thickness (Tables S22–S25), regional enamel thickness (Tables S26–S29), and proportional regional enamel thickness (Tables S30–S33). Holm-Bonferroni significance is documented in each of the Tables S1–S33; Table 3 reports the measured variables with Holm-Bonferroni significant temporal trends.

3.1 | Tooth Size and Shape

Upper molar comparisons of CA, BCD, EDJ, Fangle, Nangle, CSI, and ACS revealed only one significant directional trend over time: CA (Table 3, Figure 2, Tables S6–S13). Given that there are so few molar specimens younger than Swartkrans Hanging Remnant, molar analyses should be considered exploratory. The two Drimolen UM1s and SK47 (Member 1HR) have the three smallest CAs in the upper molar sample, while the Kromdraai specimen (TM 1517) has the largest crown area. While BCD, EDJ, Fangle, Nangle, CSI, and ACS average means also increase across the time periods, none of those trends were significant, possibly due to low sample sizes (see Figure 2 for ACS increase). Lower molar comparisons revealed no significant directional trends over time (Table 3, Tables S6–S13).

Upper premolar CA and ACS both increased over time (Table 3, Figure 1, Tables S6–S9) perhaps because, all other things being equal, wider teeth will have higher ACS values. Like the upper molars, two early premolars from Drimolen (DNH 59 and DNH 22) had the smallest reported CA and ACS, while the Later SKX 26625 from Swartkrans Member 3 had the largest CA and highest ACS. Mean values for cusp geometry (i.e., Fangle and Nangle) decreased over time while CSI increased, but these trends were not significant (Tables S10–S13).

3.2 | Enamel Thickness

Upper and lower molar AET and RET means increased over time, but neither trend was significant (Figure 2, Tables S14–S17). Upper premolar AET and RET, on the other hand, both exhibited significant directional trends, increasing over time (Figure 2, Table 3, Tables S14–S17). UP4s increased in AET and RET by site and by chronology, but none of the UP3 trends were significant (Table 3, Tables S14–S17).

3.2.1 | Linear Enamel Thickness

No significant trends in upper or lower molar linear enamel thicknesses (LFM, LFT, LOB, LNT, LNM) or proportional to AET (pLFM, pLFT, pLOB, pLNT, pLNM) were identified (Tables S18–S25). An increase in upper molar LNT was identified between the Drimolen and Member 1HR samples ($p < 0.040$), but it was not significant after the Holm-Bonferroni correction (Table S20). A decrease in LFM and pLFM was found in two lower molar analyses, but did not reach Holm-Bonferroni significance (Tables S21 and S24).

Upper premolar linear enamel thicknesses increased at LFT and LNT (Figure 3, Table 3, Tables S18–S21). The trends were only significant with Holm-Bonferroni correction when upper premolars were combined, though UP4s achieved raw *p*-values less than 0.05 in several analyses. A proportional decrease in thickness was identified at the margin of the functional cusp wall (pLFM) and non-functional cusp wall (pLNM) when upper premolars were combined and compared across individual sites (Table S24).

3.2.2 | Regional Enamel Thickness

No significant trends in upper or lower molar regional enamel thickness measured directly (RFC, RFL, RFO, RNO, RNL, RNC) or proportional to AET (pRFC, pRFL, pRFO, pRNO, pRNL, pRNC) were identified (Figure 4, Tables S26–S33). An increase in pRFO was identified in UM1s between Drimolen and Swartkrans Member 1HR, but it was not significant after the Bonferroni correction (Table S30).

Upper premolar regional thickness increased significantly at RFC, RFL, RFO, RNO, RNL across individual sites (Figure 4, Table 3 and Tables S26–S29). UP4s followed the same trend, but only reached Holm-Bonferroni significance for RFL (Table 3 and Table S26). Proportional means tended to increase, but none of the trends were significant (Tables S30–S33).

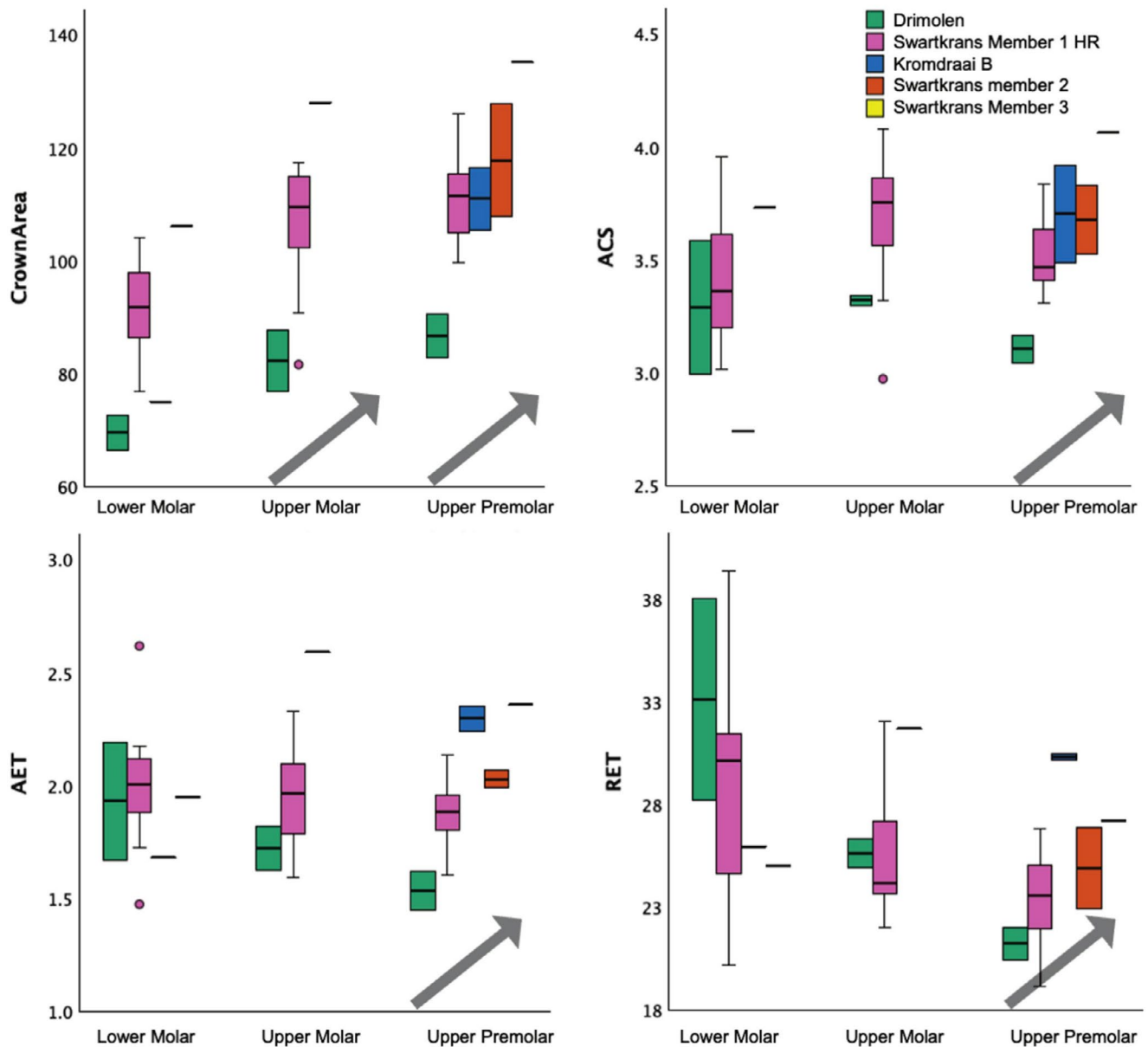


FIGURE 2 | Box plots of lower molar, upper molar, and upper premolar crown area (CA) (top left), ACS (top right), AET (bottom left), and RET (bottom right) values across the five sites. Gray arrows indicate significant directional trends over time identified after Holm-Bonferroni corrections.

4 | Discussion

P. robustus postcanine teeth underwent significant changes across the lineage's chronology, particularly in occlusal enamel features. Our results provide some support for the three hypotheses. H1, predicting increases in crown size and a shift toward flatter, more bunodont cusp geometry, received partial support: CA increased significantly in both upper premolars and upper molars, while ACS increased significantly only in upper premolars. However, no cusp shape variables showed significant directional trends in any tooth type. H2, predicting increases in whole-crown enamel thickness, was supported in upper premolars, where both AET and RET increased significantly over time, but not in upper or lower molars. H3, predicting a shift toward thicker enamel concentrated over the functional cusp tips and occlusal basin relative to the lateral and marginal walls, received the strongest support, but only in upper premolars (Figure 5). Linear and regional enamel thicknesses

increased over the occlusal basin and cusp tips in premolars (LFT, LNT, RFC, RFO, RNO, RNL, Figure 5), with a proportional decrease along the marginal walls (pLFM, pLNM, Figure 5). Within upper premolars, enamel thickness and its distribution (H2, H3) showed more consistent evidence of directional change than did tooth size and shape (H1).

Based on these findings, we suggest that dental features of different tooth types (molars and premolars) may show different rates of detectable morphological change. However, we note that the molar results are exploratory given the limited number of later samples. In just a few hundred thousand years, *P. robustus* premolars underwent a significant directional transformation in both tooth size and enamel thickness, while *P. robustus* molars increased slightly only in size (CA). This difference suggests that selective pressures may act more strongly on certain tooth types, possibly due to their specific roles in food processing. Indeed,

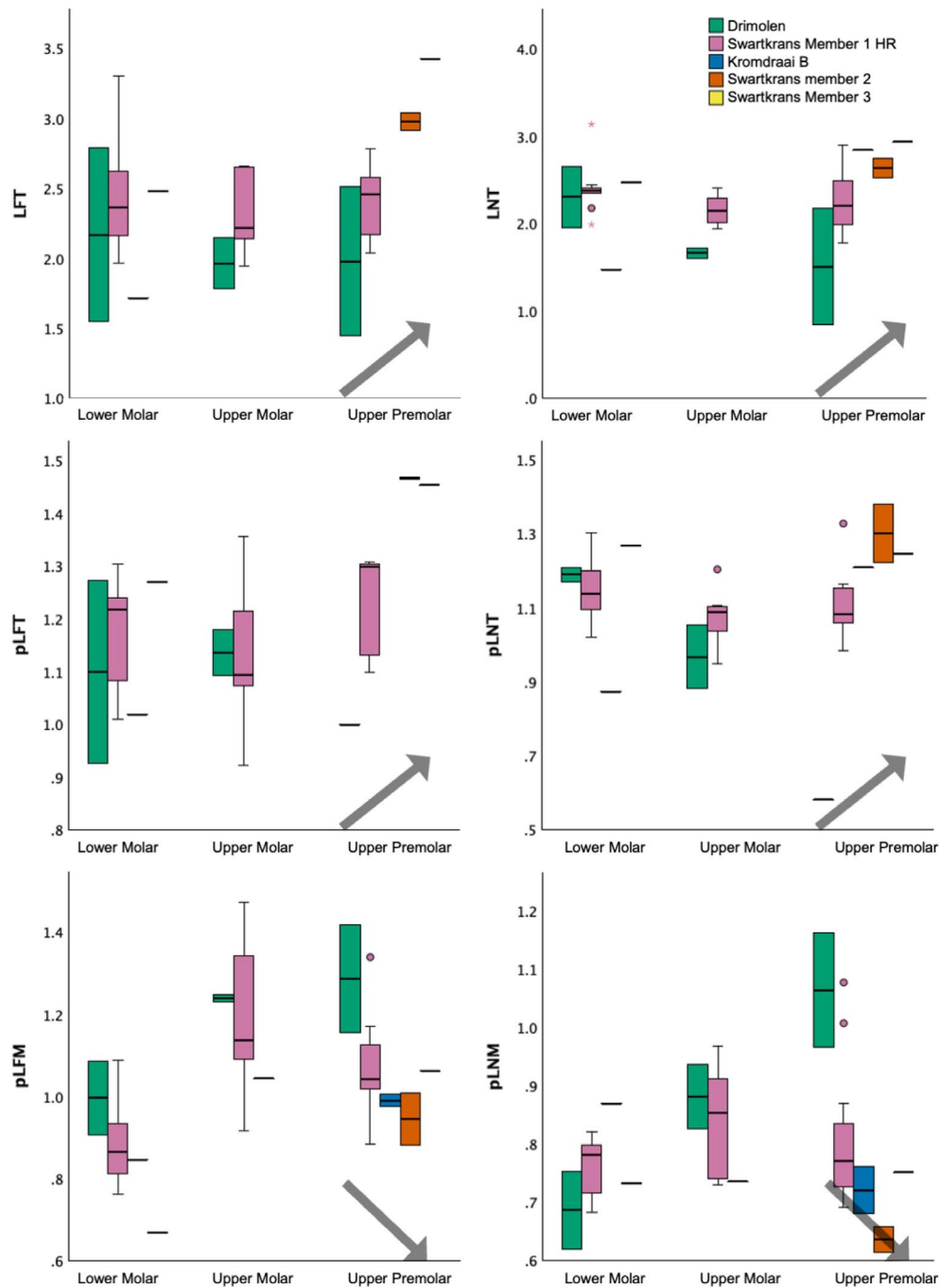


FIGURE 3 | Box plots of lower molar, upper molar, and upper premolar linear cusp tip thickness (top, LFT and LNT), proportional cusp tip thicknesses (middle, pLFT, pLNT), and proportional lateral margins (bottom, pLFM, pLNM) across the five sites. Gray arrows indicate significant directional trends over time identified after Holm-Bonferroni corrections.

Fannin et al. (2025a) demonstrated that in non-human primates, premolar size is more strongly associated with chewing performance than first molar size.

Our findings complement recent research by Martin et al. (2021), who identified distinct temporal trends in *P. robustus* craniofacial form from Drimolen (2.04–1.95 mya) compared to those from both Swartkrans Member 1 Hanging Remnant and Kromdraai (~1.8 mya). The morphological changes they identified, including larger teeth and more anteriorly positioned sagittal crests and zygomatic roots, are

consistent with a masticatory configuration that could produce and resist greater magnitude bite forces. Our dental evidence supports their assertion that these changes represented adaptations to a more durophagous diet. Thus, the changes in premolars, particularly the increased CA and ACS, along with thicker and redistributed enamel, may relate to increasing molarization of premolars, a characteristic feature of *P. robustus* (Bailey and Wood 2007; Leece et al. 2022; Robinson 1954). This molarization process appears to have occurred during periods of environmental aridification, possibly reflecting adaptation to a diet with more resistant or mechanically challenging foods.

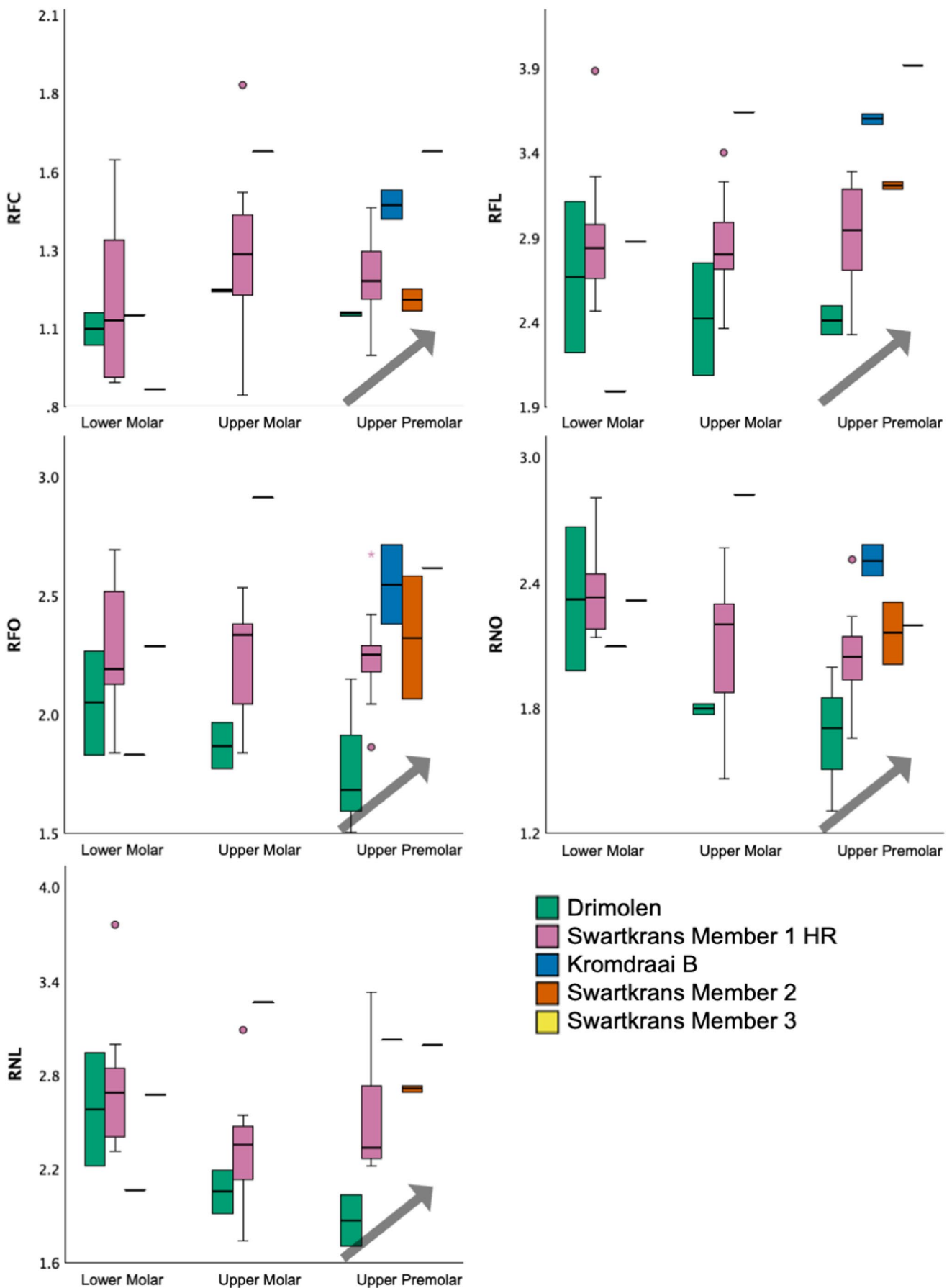


FIGURE 4 | Box plots of lower molar, upper molar, and upper premolar regional thickness measurements across five sites: Top, RFC and RFL; middle, RFO and RNO; bottom, RNL. Gray arrows indicate significant directional trends over time identified after Holm-Bonferroni corrections.

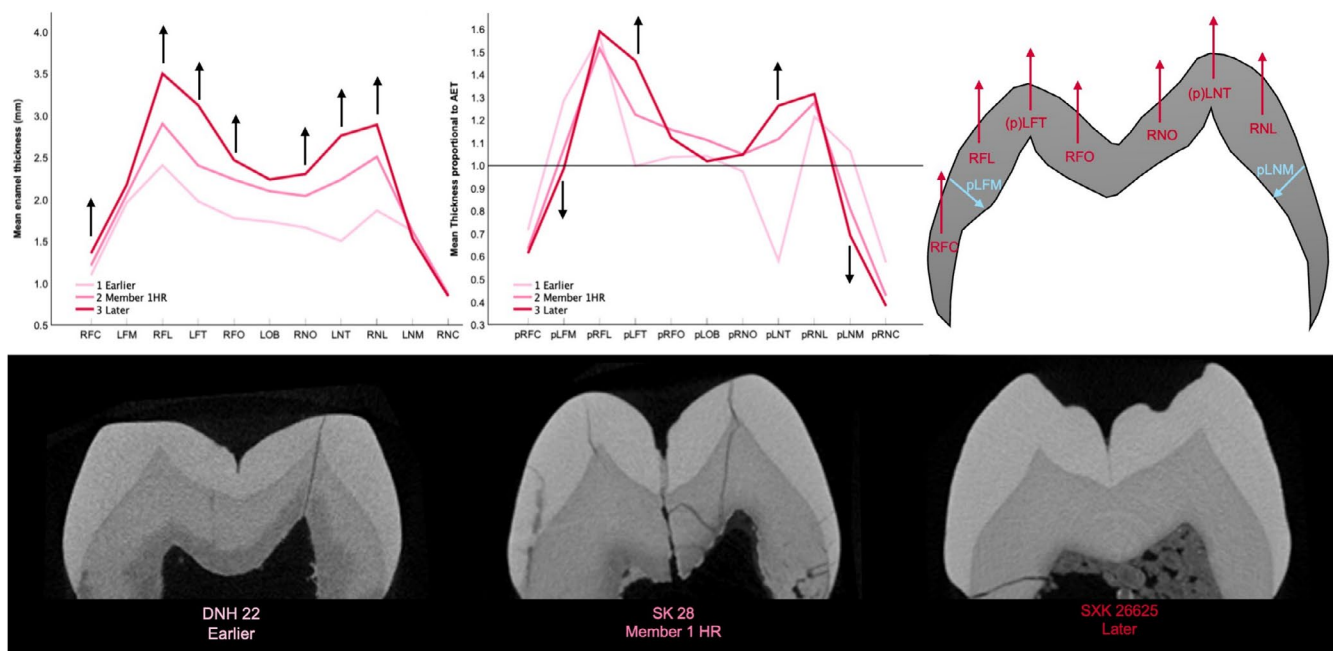


FIGURE 5 | Upper premolar trends. Top: (left) Line graph of linear and regional measured values from three time periods. Black arrows indicate significant trends. (middle) Line graph of linear and regional proportional values from the three time periods. Horizontal black line at $y = 1$ represents the AET. Black arrows indicate significant trends. (right) Cartoon of a tooth showing the locations where significant positive (red) and negative (trends) were observed. Bottom: Representative premolars from three sites.

We note that behavior changes such as selecting for more mechanically challenging foods likely predated the morphological change in premolars (Fannin, Seyoum, et al. 2025b).

The results of this investigation are important for several reasons. First, they suggest rapid evolution over short time periods in response to environmental shifts. While enamel thickness was the aspect of dental crowns that was most frequently identified as shifting, CA also increased in both molars and premolars, potentially indicating that multiple dental features can respond to selective pressures, though perhaps at different rates. It seems that the distribution of enamel thickness is fairly evolvable and that some aspects of it are linked to shifts in the internal architecture of crowns that are likely linked to durophagy. Based on the present study, it seems that the distribution of enamel thickness may be the aspect of crown anatomy most responsive to dietary changes on short evolutionary timescales within hominins. If true, our results align nicely with previous research on the evolvability of dental design (Hlusko 2016; Hlusko et al. 2004).

Multiple studies have connected hard object feeding with thick enamel in primates (Lucas et al. 2008a, b; Kay 1975; Dumont 1995; Pampush et al. 2013; McGraw et al. 2014; Guatelli-Steinberg et al. 2022). Beyond whole-crown estimates of enamel thickness (i.e., AET and RET), the amount of enamel covering the cusp tips and occlusal basins has received considerable attention in relation to hard object feeding. Thicker enamel over the cusps has sometimes been construed as “uneven” enamel and linked to hard object feeding (Lucas et al. 2008b; Constantino et al. 2009; Thiery et al. 2017a, b, c). Generally, thicker cusp tips and/or thicker enamel in the occlusal basin have been expected in species with hard diets as a structural adaptation to

resist fracture by limiting crack formation and propagation (Constantino et al. 2009; Chai 2018; Schwartz et al. 2020). Kono and Suwa (2008) emphasize the importance of occlusal enamel thickness as a potential adaptation for high masticatory loads when chewing hard/large food objects. Additionally, thick lateral walls help dissipate the high stresses that occur during food processing (Benazzi et al. 2013; Benazzi et al. 2016). In our upper premolar sample, this pattern is reflected in significant increases in RFC, RFO, RNO, and RNL across sites, along with increases in RFL at both the UPR and pooled premolar levels (Table 3). Here, we highlight changes in occlusal and cervical enamel during a period when diet was likely becoming harder for *P. robustus*.

The environmental context of the changes in crown architecture that we have identified is particularly significant. The shift toward more arid conditions and the expansion of shrubland vegetation likely created new dietary resources, and thus challenges, that required rapid evolutionary responses. The ability of *P. robustus* to adapt its dental morphology, particularly in premolars, demonstrates the species' evolvability in the face of environmental change. This likely played a crucial role in the species' survival across approximately 1 million years of environmental fluctuation, during which it successfully exploited an increasingly challenging diet.

Isotopic signals from the enamel of hominins and penecontemporary mammals have revealed that *P. robustus* consumed a significant proportion of C_4 plants, such as tropical grasses, sedges, and underground storage organs (USOs), which were abundant in its environment during periods of climatic variability (Yeakel et al. 2007; Grine et al. 2012; Sponheimer et al. 2006). Stable carbon isotopes of *P. robustus* dental enamel indicates a

mixed C_3/C_4 diet, with approximately 25%–35% C_4 resource consumption (Lee-Thorp et al. 2007). Laser ablation profiles reveal a highly flexible diet with substantial intra-tooth $\delta^{13}C$ variation of up to 5‰, indicating seasonal to interannual dietary shifts between C_3 -dominated and C_4 -enriched foods (Sponheimer et al. 2006). The temporal trends identified here coincide with significant environmental changes in South Africa during the early Pleistocene. Strontium analysis of *P. robustus* teeth from Swartkrans and Kromdraai indicates exploitation of both savanna and riparian woodland habitats, with approximately 30% of strontium derived from woodland environments (Sillen et al. 2025), speaking to both variation in habitat and flexibility of diet. Recent research has documented a pronounced drying period and expansion of shrubland-type vegetation during this time (Caley et al. 2018). *P. robustus* likely inhabited a combination of ever-changing and ever-drying environments, including both open grasslands and wooded areas, requiring a flexible dietary repertoire that could shift to accommodate changing environmental conditions. One benefit of having thick enamel covering the entire occlusal surface of a tooth is that it is protective against both hard and abrasive foods (Constantino et al. 2011; Constantino et al. 2009; Lawn and Lee 2009; Lee et al. 2009), so while we emphasize the evolution of upper premolar enamel thickness distribution in relation to hard object feeding, it could have been useful when faced with abrasive foods.

Dental microwear texture analysis corroborates the flexible dietary strategy inferred from isotopic data. *P. robustus* teeth exhibit significantly higher complexity (Asfc) and lower anisotropy (epLsar) measures than does *Australopithecus africanus*, consistent with more frequent consumption of hard, brittle foods (Scott et al. 2005). In fact, *P. robustus* scores significantly higher than *A. africanus* for 11 of 16 texture variables related to feature complexity, size, and depth (Peterson et al. 2018). High variance in complexity values have been suggested to reflect diets in which hard objects may have been consumed periodically as fallback foods during resource scarcity (Ungar and Sponheimer 2011). On the other hand, *P. robustus* and the sooty mangabey (*Cercocebus atys*), an habitual hard-object feeder (McGraw et al. 2014), share multiple similarities in dental form (Guatelli-Steinberg et al. 2023; Scheinblum et al. 2025). Their similarities may suggest similar feeding regimes (Scheinblum et al. 2025; Guatelli-Steinberg et al. 2023). When comparing *P. robustus* microwear by site, however, Peterson et al. (2018) found no significant mean differences in molar microwear, a signal that would have suggested increases in hard-object feeding. They did note that the variance in microwear features differed among sites, but it was not possible to track trends in dental microwear over time. Although we cannot specifically connect the temporal trends found in our sample to significant temporal trends in microwear, we are confident that the pattern of tooth size and enamel thickness changes observed in *Paranthropus robustus* would have served it well in a changeable habitat.

The consistent signal in this study is that differences were found in upper premolar crown form, not upper or lower molars, with the exception of CA increasing in upper molars (Table 3, Figure 2). The lack of significant trends in lower molars, despite more lower molars ($n = 16$) than upper molars ($n = 14$) may reflect weaker selective pressures on lower molars, or may reflect limited statistical power given the small representation from Drimolen and the

younger sites (Table S5). The asymmetry in results found in upper premolars versus either set of molars, though, gives some support to the idea that selection may have been active preferentially on premolars. Our goal was to include the molar data as a set of preliminary observations that should provide the basis for future analyses that include larger samples, especially given the many new samples that have been recovered and described from continued excavations at Drimolen (e.g., see Leece et al. 2022; Leece et al. 2023). Depending on those new findings and their morphology, it may be worth considering that the temporal trends identified here may reflect population level or intraspecific diversity within *P. robustus*.

5 | Conclusions

The rapid dental evolution observed in *P. robustus* between 2.04 and 0.6 Ma, evident primarily in upper premolars rather than molars, provides insight into the pace and pattern of hominin adaptation to environmental change. Upper premolar CA, ACS, AET, and RET all increased over this interval, accompanied by a redistribution of enamel toward occlusal and cuspal regions. Upper molars showed a more limited response, with only CA increasing significantly, while lower molars showed no significant temporal trends in any measured variable. The varying degrees of change between different dental features and tooth types suggest a complex pattern of dental evolution, where some features were more responsive to selective pressures than others. These results have implications for understanding the mechanisms of dental adaptation in other hominin lineages. Future studies may benefit from examining whether similar patterns of dental evolution occur in other hominin species during periods of environmental change.

Author Contributions

M. C. O'Hara: conceptualization, investigation, writing – original draft, methodology, visualization, formal analysis. **M. M. Skinner:** resources, writing – review and editing, visualization. **D. Guatelli-Steinberg:** supervision, conceptualization, writing – review and editing. **W. S. McGraw:** supervision, writing – review and editing. **Gary T. Schwartz:** writing – review and editing, supervision. **P. Mahoney:** supervision, writing – review and editing. **S. Chapple:** visualization, data curation, writing – review and editing.

Acknowledgments

For access to tomographic scans and associated digital data, the authors thank Ditsong National Museum of Natural History, South Africa and the Evolutionary Studies Institute, University of the Witwatersrand. For production of the CT scans of material from Swartkrans and Kromdraai, the authors thank Matthew Skinner and Jean-Jacques Hublin, Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology. This study was supported by the Max Planck Society, The Ohio State University, National Science Foundation Graduate Research Fellowship Program Grant No. DGE-1343012 to Mackie O'Hara. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the National Science Foundation. This project has received funding from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement number 101026776. The authors acknowledge the use of Claude to convert digitally transcribed voice recordings about

the interpretation of results by the first author into full sentences. All AI-generated suggestions were reviewed, revised, and approved by the authors, who take full responsibility for the accuracy and integrity of the work.

Funding

This work was supported by the Max Planck Society. National Science Foundation, DGE-1343012. HORIZON EUROPE Marie Skłodowska-Curie Actions, 101026776.

Data Availability Statement

All data are included in the [Supporting Information](#) ALL_DATA.xlsx and have been uploaded to Zenodo Repository DOI: [10.5281/zenodo.21537150](https://doi.org/10.5281/zenodo.21537150).

References

- Bailey, S., and B. Wood. 2007. "Trends in Postcanine Occlusal Morphology Within the Hominin Clade: The Case of Paranthropus." In *Dental Perspectives on Human Evolution*, edited by S. Bailey and J. J. Hublin, 33–52. Springer Netherlands.
- Benazzi, S., H. N. Nguyen, O. Kullmer, and J. J. Hublin. 2013. "Unravelling the Functional Biomechanics of Dental Features and Tooth Wear." *PLoS One* 8, no. 7: e69990. <https://doi.org/10.1371/journal.pone.0069990>.
- Benazzi, S., H. N. Nguyen, O. Kullmer, and K. Kupczik. 2016. "Dynamic Modelling of Tooth Deformation Using Occlusal Kinematics and Finite Element Analysis." *PLoS One* 11, no. 3: e0152663. <https://doi.org/10.1371/journal.pone.0152663>.
- Beynon, A. D., and B. A. Wood. 1986. "Variations in Enamel Thickness and Structure in East African Hominids." *American Journal of Physical Anthropology* 70: 177–193. <https://doi.org/10.1002/ajpa.1330700205>.
- Caley, T., T. Extier, J. A. Collins, et al. 2018. "A Two-Million-Year-Long Hydroclimatic Context for Hominin Evolution in Southeastern Africa." *Nature* 560, no. 7716: 76–79. <https://doi.org/10.1038/s41586-018-0309-6>.
- Chai, H. 2018. "Dentin Horn Angle and Enamel Thickness Interactively Control Tooth Resilience and Bite Force." *Acta Biomaterialia* 75: 279–286. <https://doi.org/10.1016/j.actbio.2018.06.001>.
- Constantino, P. J., B. R. Lawn, P. J. Constantino, et al. 2019. "Dental Fracture Mechanics: What Broken Teeth Can Reveal About Diet and Feeding Behavior. The Role of Tooth Enamel Mechanical Properties in Primate Dietary Adaptation." *American Journal of Physical Anthropology* 148, no. 2: 171–177. <https://doi.org/10.1002/ajpa.21576>.
- Constantino, P. J., J. J. Lee, D. Morris, et al. 2011. "Adaptation to Hard-Object Feeding in Sea Otters and Hominins." *Journal of Human Evolution* 61, no. 1: 89–96. <https://doi.org/10.1016/j.jhevol.2011.02.009>.
- Constantino, P. J., J. J. W. Lee, Y. Gerbig, et al. 2012. "The Role of Tooth Enamel Mechanical Properties in Primate Dietary Adaptation." *American Journal of Physical Anthropology* 148, no. 2: 171–177.
- Constantino, P. J., P. W. Lucas, J. J. Lee, and B. R. Lawn. 2009. "The Influence of Fallback Foods on Great Ape Tooth Enamel." *American Journal of Physical Anthropology* 140, no. 4: 653–660. <https://doi.org/10.1002/ajpa.21096>.
- Dean, M. C., and F. Schrenk. 2003. "Enamel Thickness and Development in a Third Permanent Molar of Gigantopithecus Blacki." *Journal of Human Evolution* 45, no. 5: 381–387. <https://doi.org/10.1016/j.jhevol.2003.08.009>.
- Dumont, E. R. 1995. "Enamel Thickness and Dietary Adaptation Among Extant Primates and Chiropterans." *Journal of Mammalogy* 76: 1127–1136. <https://doi.org/10.2307/1382663>.
- Fannin, L. D., D. Guatelli-Steinberg, J. Arft-Guatelli, M. Clauss, N. J. Dominy, and W. S. McGraw. 2025a. "Chewing Performance and the Structure of Primate Communities." *Proceedings of the Royal Society B: Biological Sciences* 292, no. 2061: 1–10. <https://doi.org/10.1098/rspb.2025.2158>.
- Fannin, L. D., C. M. Seyoum, V. V. Venkataraman, et al. 2025b. "Behavior Drives Morphological Change During Human Evolution." *Science* 389, no. 6759: 488–493. <https://doi.org/10.1126/science.ado2359>.
- Feeney, R. N. 2009. "Microtomographic Analysis of Sexual Dimorphism and Dental Tissue Distribution in Hominin Molars."
- Gantt, D. G. 1986. "Enamel Thickness and Ultrastructure in Hominoids: With Reference to Form, Function, and Phylogeny." *Comparat Pri Bio* 1: 453–475.
- Gould, S. J., and E. S. Vrba. 1982. "Exaptation- a Missing Term in the Science of Form." *Paleobiology* 8: 4–15. <https://doi.org/10.1017/S0094837300004310>.
- Grine, F. E., and L. L. Martin. 1988. "Enamel Thickness and Development in Australopithecus and Paranthropus."
- Grine, F. E., M. A. Spencer, B. Demes, H. F. Smith, D. S. Strait, and D. A. Constant. 2005. "Molar Enamel Thickness in the Chacma Baboon, *Papio ursinus* (Kerr 1792)." *American Journal of Physical Anthropology* 128, no. 4: 812–822. <https://doi.org/10.1002/ajpa.20076>.
- Grine, F. E., M. Sponheimer, P. S. Ungar, J. Lee-Thorp, and M. F. Teaford. 2012. "Dental Microwear and Stable Isotopes Inform the Paleocology of Extinct Hominins." *American Journal of Physical Anthropology* 148, no. 2: 285–317. <https://doi.org/10.1002/ajpa.22086>.
- Guatelli-Steinberg, D., G. T. Schwartz, M. C. O'Hara, K. Gurian, J. Rychel, and W. S. McGraw. 2022. "Molar Form, Enamel Growth, and Durophagy in *Cercocebus* and *Lophocebus*." *American Journal of Biological Anthropology* 179: 386–404. <https://doi.org/10.1002/ajpa.24592>.
- Guatelli-Steinberg, D., G. T. Schwartz, M. C. O'Hara, et al. 2023. "Aspects of Molar Form and Dietary Proclivities of African Colobines." *Journal of Human Evolution* 180: 103384. <https://doi.org/10.1016/j.jhevol.2023.103384>.
- Guy, F., V. Lazzari, E. Gilissen, and G. Thiery. 2015. "To What Extent Is Primate Second Molar Enamel Occlusal Morphology Shaped by the Enamel-Dentine Junction?" *PlosOne* 10: e0138802. <https://doi.org/10.1371/journal.pone.0138802>.
- Herries, A. I., and J. W. Adams. 2013. "Clarifying the Context, Dating and Age Range of the Gondolin Hominins and Paranthropus in South Africa." *Journal of Human Evolution* 65, no. 5: 676–681. <https://doi.org/10.1016/j.jhevol.2013.06.007>.
- Herries, A. I. R., J. M. Martin, A. B. Leece, et al. 2020. "Contemporaneity of Australopithecus, Paranthropus, and Early Homo Erectus in South Africa." *Science* 368, no. 6486: eaaw7293. <https://doi.org/10.1126/science.aaw7293>.
- Hlusko, L. J. 2016. "Elucidating the Evolution of Hominid Dentition in the Age of Phenomics, Modularity, and Quantitative Genetics." *Annals of Anatomy* 203: 3–11. <https://doi.org/10.1016/j.aanat.2015.05.001>.
- Hlusko, L. J., G. Suwa, R. T. Kono, and M. C. Mahaney. 2004. "Genetics and the Evolution of Primate Enamel Thickness: A Baboon Model." *American Journal of Physical Anthropology* 124, no. 3: 223–233. <https://doi.org/10.1002/ajpa.10353>.
- Janis, C. M., and M. Fortelius. 1988. "On the Means Whereby Mammals Achieve Increased Functional Durability of Their Dentitions, With Special Reference to Limiting Factors." *Biological Reviews of the Cambridge Philosophical Society* 63: 197–230. <https://doi.org/10.1111/j.1469-185X.1988.tb00630.x>.
- Jolly, C. J. 1970. "The Seed-Eaters: A New Model of Hominid Differentiation Based on a Baboon Analogy." *Man* 5: 5–26. <https://doi.org/10.2307/2799566>.

- Kay, R. F. 1975. "The Functional Adaptations of Primate Molar Teeth." *American Journal of Physical Anthropology* 43: 195–216. <https://doi.org/10.1002/ajpa.1330430211>.
- Kay, R. F. 1981. "The Nut-Crackers - a New Theory of the Adaptations of the Ramapithecinae." *American Journal of Physical Anthropology* 55: 141–151. <https://doi.org/10.1002/ajpa.1330550203>.
- Kay, R., and W. Hylander. 1978. "The Dental Structure of Mammalian Folivores With Special Reference to Primates and Phalangerioidea (Marsupialia)." *Proceedings of the National Academy of Sciences of the United States of America* 102, no. 46: 16579–16583. <https://doi.org/10.1073/pnas.0508377102>.
- Khera, S. C., C. W. Carpenter, J. D. Vetter, and R. N. Staley. 1990. "Anatomy of Cusps of Posterior Teeth and Their Fracture Potential." *Journal of Prosthetic Dentistry* 64: 139–147. [https://doi.org/10.1016/0022-3913\(90\)90170-h](https://doi.org/10.1016/0022-3913(90)90170-h).
- King, S. J., S. J. Arrigo-Nelson, S. T. Pochron, et al. 2005. "Dental Senescence in a Long-Lived Primate Links Infant Survival to Rainfall." *Proceedings of the National Academy of Sciences of the United States of America* 102, no. 46: 16579–16583. <https://doi.org/10.1073/pnas.0508377102>.
- Kono, R. T. 2004. "Molar Enamel Thickness and Distribution Patterns in Extant Great Apes and Humans: New Insights Based on a 3-Dimensional Whole Crown Perspective." *Anthropological Science* 112, no. 2: 121–146. <https://doi.org/10.1537/ase.03106>.
- Kono, R. T., and G. Suwa. 2005. "Effects of Molar Crown Orientation to Measures of Lateral Enamel Thickness in the Mesial Cusp Section." *Bulletin of the National Science Museum, Tokyo. Series B, Botany* 31: 11–22.
- Kono, R., and G. Suwa. 2008. "Enamel Distribution Patterns of Extant Human and Hominoid Molars: Occlusal Versus Lateral Enamel Thickness." *Anthropological Science* 116: 217–229.
- Kono-Takeuchi, R., G. Suwa, E. Kanazawa, and T. Tanijiri. 1998. "A New Method of Evaluating Enamel Thickness Based on a Three-Dimensional Measuring System." *Anthropological Science* 105: 217–229.
- Lawn, B. R., and J. J. Lee. 2009. "Analysis of Fracture and Deformation Modes in Teeth Subjected to Occlusal Loading." *Acta Biomaterialia* 5, no. 6: 2213–2221. <https://doi.org/10.1016/j.actbio.2009.02.001>.
- Le Luyer, M., S. Rottier, and P. Bayle. 2014. "Brief Communication: Comparative Patterns of Enamel Thickness Topography and Oblique Molar Wear in Two Early Neolithic and Medieval Population Samples." *American Journal of Physical Anthropology* 155, no. 1: 162–172. <https://doi.org/10.1002/ajpa.22562>.
- Lee, J. J., J. Y. Kwon, H. Chai, P. W. Lucas, V. P. Thompson, and B. R. Lawn. 2009. "Fracture Modes in Human Teeth." *Journal of Dental Research* 88, no. 3: 224–228. <https://doi.org/10.1177/0022034508330055>.
- Leece, A. B., J. M. Martin, S. Baker, et al. 2023. "New Hominin Dental Remains From the ~ 2.04–1.95 Ma Drimolen Main Quarry, South Africa." *Annals of Human Biology* 50, no. 1: 407–427.
- Leece, A. B., J. M. Martin, A. I. R. Herries, A. Riga, C. G. Menter, and J. Moggi-Cecchi. 2022. "New Hominin Dental Remains From the Drimolen Main Quarry, South Africa (1999–2008)." *American Journal of Biological Anthropology* 179, no. 2: 240–260. <https://doi.org/10.1002/ajpa.24570>.
- Lee-Thorp, J. A., M. Sponheimer, and J. Luyt. 2007. "Tracking Changing Environments Using Stable Carbon Isotopes in Fossil Tooth Enamel: An Example From the South African Hominin Sites." *Journal of Human Evolution* 53, no. 5: 595–601. <https://doi.org/10.1016/j.jhevol.2006.11.020>.
- Lucas, P., P. Constantino, B. Wood, and B. Lawn. 2008a. "Dental Enamel as a Dietary Indicator in Mammals." *BioEssays* 30, no. 4: 374–385. <https://doi.org/10.1002/bies.20729>.
- Lucas, P. W., P. J. Constantino, and B. A. Wood. 2008b. "Inferences Regarding the Diet of Extinct Hominins: Structural and Functional Trends in Dental and Mandibular Morphology Within the Hominin Clade." *Journal of Anatomy* 212, no. 4: 486–500. <https://doi.org/10.1111/j.1469-7580.2008.00877.x>.
- Luke, D. A., and P. W. Lucas. 1983. "The Significance of Cusps." *Journal of Oral Rehabilitation* 10: 197–206. <https://doi.org/10.1111/j.1365-2842.1983.tb01413.x>.
- Macho, G. A., and M. E. Berner. 1994. "Enamel Thickness and the Helicoidal Occlusal Plane." *American Journal of Physical Anthropology* 94, no. 3: 327–337. <https://doi.org/10.1002/ajpa.1330940304>.
- Macho, G. A., and J. F. Thackeray. 1992. "Computed Tomography and Enamel Thickness of Maxillary Molars of Plio-Pleistocene Hominids From Sterkfontein, Swartkrans, and Kromdraai (South Africa): An Exploratory Study." *American Journal of Physical Anthropology* 89, no. 2: 133–143. <https://doi.org/10.1002/ajpa.1330890202>.
- Macho, G. A., and J. F. Thackeray. 1993. "Computed Tomography and Intercuspal Angulation of Maxillary Molars of Plio-Pleistocene Hominids From Sterkfontein, Swartkrans and Kromdraai (South Africa): An Exploratory Study." *Zeitschrift für Morphologie und Anthropologie* 79: 261–269.
- Mahoney, P. 2010. "Two-Dimensional Patterns of Human Enamel Thickness on Deciduous (dm1, dm2) and Permanent First (M1) Mandibular Molars." *Archives of Oral Biology* 55, no. 2: 115–126. <https://doi.org/10.1016/j.archoralbio.2009.11.014>.
- Martin, J. M., A. B. Leece, S. Neubauer, et al. 2021. "Drimolen Cranium DNH 155 Documents Microevolution in an Early Hominin Species." *Nature Ecology & Evolution* 5, no. 1: 38–45. <https://doi.org/10.1038/s41559-020-01319-6>.
- Martin, L. B. 1983. "The Relationships of the Latter Miocene Hominoidea." *Journal of Human Evolution* 12: 261–269.
- Martin, L. 1985. "Significance of Enamel Thickness in Hominoid Evolution." *Nature* 314: 260–263. <https://doi.org/10.1038/314260a0>.
- McGraw, W. S., J. D. Pampush, and D. J. Daegling. 2012. "Brief Communication: Enamel Thickness and Durophagy in Mangabeys Revisited." *American Journal of Physical Anthropology* 147, no. 2: 326–333. <https://doi.org/10.1002/ajpa.21634>.
- McGraw, W. S., A. E. Vick, and D. J. Daegling. 2014. "Dietary Variation and Food Hardness in Sooty Mangabeys (*Cercocebus atys*): Implications for Fallback Foods and Dental Adaptation." *American Journal of Physical Anthropology* 154, no. 3: 413–423. <https://doi.org/10.1002/ajpa.22525>.
- Molnar, S., and D. G. Gantt. 1977. "Functional Implications of Primate Enamel Thickness." *American Journal of Physical Anthropology* 46: 447–454. <https://doi.org/10.1002/ajpa.1330460304>.
- O'Hara, M. C., and D. Guatelli-Steinberg. 2021. *Reconstructing Tooth Crown Heights and Enamel Caps: A Comparative Test of Three Existing Methods With Recommendations for Their Use*. <https://doi.org/10.1002/ar.24637>.
- Olejniczak, A. J., and F. E. Grine. 2006. "Assessment of the Accuracy of Dental Enamel Thickness Measurements Using Microfocal X-Ray Computed Tomography." *Anatomical Record. Part A, Discoveries in Molecular, Cellular, and Evolutionary Biology* 288, no. 3: 263–275. <https://doi.org/10.1002/ar.a.20307>.
- Pampush, J. D., A. C. Duque, B. R. Burrows, D. J. Daegling, W. F. Kenney, and W. S. McGraw. 2013. "Homoplasy and Thick Enamel in Primates." *Journal of Human Evolution* 64, no. 3: 216–224. <https://doi.org/10.1016/j.jhevol.2013.01.009>.
- Peterson, A., E. F. Abella, F. E. Grine, M. F. Teaford, and P. S. Ungar. 2018. "Microwear Textures of Australopithecus Africanus and Paranthropus Robustus Molars in Relation to Paleoenvironment and Diet." *Journal of Human Evolution* 119: 42–63. <https://doi.org/10.1016/j.jhevol.2018.02.004>.

- Popowics, T. E., J. M. Rensberger, and S. W. Herring. 2001. "The Fracture Behaviour of Human and Pig Molar Cusps." *Archives of Oral Biology* 46, no. 1: 1–12. [https://doi.org/10.1016/S0003-9969\(00\)00102-3](https://doi.org/10.1016/S0003-9969(00)00102-3).
- Popowics, T. E., J. M. Rensberger, and S. W. Herring. 2004. "Enamel Microstructure and Microstrain in the Fracture of Human and Pig Molar Cusps." *Archives of Oral Biology* 49, no. 8: 595–605. <https://doi.org/10.1016/j.archoralbio.2004.01.016>.
- Rabenold, D., and O. M. Pearson. 2011. "Abrasive, Silica Phytoliths and the Evolution of Thick Molar Enamel in primates, With Implications for the Diet of *Paranthropus Boisei*." *PLoS One* 6, no. 12: e28379. <https://doi.org/10.1371/journal.pone.0028379>.
- Robinson, J. T. 1954. "The Genera and Species of the Australopithecinae." *American Journal of Physical Anthropology* 12, no. 2: 181–200.
- Saunders, S. R., A. H. Chan, B. Kahlon, H. F. Kluge, and C. M. FitzGerald. 2007. "Sexual Dimorphism of the Dental Tissues in Human Permanent Mandibular Canines and Third Premolars." *American Journal of Physical Anthropology* 133, no. 1: 735–740. <https://doi.org/10.1002/ajpa.20553>.
- Scheinblum, J., W. S. McGraw, K. Gurian, and D. Guatelli-Steinberg. 2025. "Enamel Prism Angle Variation and Hard-Object Feeding in Cercopithecoids With Known Diets." *American Journal of Biological Anthropology* 188, no. 3: e70167. <https://doi.org/10.1002/ajpa.70167>.
- Schwartz, G. T. 1997. Taxonomic & Functional Aspects of Enamel Cap Structure in South African Plio-Pleistocene Hominids: A High-Resolution Computed Tomographic Study."
- Schwartz, G. T. 2000. "Taxonomic and Functional Aspects of the Patterning of Enamel Thickness Distribution in Extant Large-Bodied Hominoids." *American Journal of Physical Anthropology* 111: 221–244.
- Schwartz, G. T., A. McGrosky, and D. S. Strait. 2020. "Fracture Mechanics, Enamel Thickness and the Evolution of Molar Form in Hominins." *Biology Letters* 16, no. 1: 20190671. <https://doi.org/10.1098/rsbl.2019.0671>.
- Schwartz, G. T., J. F. Thackeray, C. Reid, and J. F. van Reenan. 1998. "Enamel Thickness and the Topography of the Enamel-Dentine Junction in South African Plio-Pleistocene Hominids With Special Reference to the Carabelli Trait." *Journal of Human Evolution* 35: 523–542. <https://doi.org/10.1006/jhev.1998.0237>.
- Scott, R. S., P. S. Ungar, T. S. Bergstrom, et al. 2005. "Dental Microwear Texture Analysis Shows Within-Species Diet Variability in Fossil Hominins." *Nature* 436, no. 7051: 693–695. <https://doi.org/10.1038/nature03822>.
- Shimizu, D. 2002. "Functional Implications of Enamel Thickness in the Lower Molars of Red Colobus (*Procolobus Badius*) and Japanese Macaque (*Macaca Fuscata*)." *Journal of Human Evolution* 43: 605–620. [https://doi.org/10.1016/S0047-2484\(02\)00016-3](https://doi.org/10.1016/S0047-2484(02)00016-3).
- Sillen, A., C. Dean, and V. Balter. 2025. "Geochemical Chronologies in *Paranthropus Robustus* Teeth Inform Habitat and Life Histories." *Nature Ecology & Evolution* 9, no. 9: 1731–1738. <https://doi.org/10.1038/s41559-025-02798-1>.
- Skinner, M. M., Z. Alemseged, C. Gaunitz, and J. J. Hublin. 2015. "Enamel Thickness Trends in Plio-Pleistocene Hominin Mandibular Molars." *Journal of Human Evolution* 85: 35–45. <https://doi.org/10.1016/j.jhevol.2015.03.012>.
- Skinner, M. M., T. L. Kivell, S. Potze, and J. J. Hublin. 2013. "Microtomographic Archive of Fossil Hominin Specimens From Kromdraai B, South Africa." *Journal of Human Evolution* 64, no. 5: 434–447. <https://doi.org/10.1016/j.jhevol.2013.01.007>.
- Smith, T. M., K. Kupczik, Z. Machanda, M. M. Skinner, and J. P. Zermeno. 2012a. "Enamel Thickness in Bornean and Sumatran Orangutan Dentitions." *American Journal of Physical Anthropology* 147, no. 3: 417–426. <https://doi.org/10.1002/ajpa.22009>.
- Smith, T. M., L. B. Martin, D. J. Reid, L. de Bonis, and G. D. Koufos. 2004. "An Examination of Dental Development in *Graecopithecus Freybergi* (= *Ouranopithecus Macedoniensis*)." *Journal of Human Evolution* 46, no. 5: 551–577. <https://doi.org/10.1016/j.jhevol.2004.01.006>.
- Smith, T. M., A. J. Olejniczak, L. B. Martin, and D. J. Reid. 2005. "Variation in Hominoid Molar Enamel Thickness." *Journal of Human Evolution* 48, no. 6: 575–592. <https://doi.org/10.1016/j.jhevol.2005.02.004>.
- Smith, T. M., A. J. Olejniczak, J. P. Zermeno, et al. 2012b. "Variation in Enamel Thickness Within the Genus *Homo*." *Journal of Human Evolution* 62, no. 3: 395–411. <https://doi.org/10.1016/j.jhevol.2011.12.004>.
- Spears, I. R., and R. H. Crompton. 1996. "The Mechanical Significance of the Occlusal Geometry of Great Ape Molars in Food Breakdown." *Journal of Human Evolution* 31: 517–535. <https://doi.org/10.1006/jhev.1996.0072>.
- Sponheimer, M., B. H. Passey, D. J. de Ruiter, D. Guatelli-Steinberg, T. E. Cerling, and J. A. Lee-Thorp. 2006. "Isotopic Evidence for Dietary Variability in the Early Hominin *Paranthropus Robustus*." *Science* 314, no. 5801: 980–982. <https://doi.org/10.1126/science.1133827>.
- Spoor, C. F., F. W. Zonneveld, and G. A. Macho. 1993. "Linear Measurements of Cortical Bone and Dental Enamel by Computed Tomography: Applications and Problems." *American Journal of Physical Anthropology* 91: 469–484. <https://doi.org/10.1002/ajpa.1330910405>.
- Suwa, G. E. N., and R. T. Kono. 2005. "A Micro-CT Based Study of Linear Enamel Thickness in the Mesial Cusp Section of Human Molars: Reevaluation of Methodology and Assessment of Within-Tooth, Serial, and Individual Variation." *Anthropological Science* 113, no. 3: 273–289. <https://doi.org/10.1537/ase.050118>.
- Swindler, D. R. 2002. "Primate Dentition: An Introduction to the Teeth of Non Human Primates."
- Thiery, G., G. Gillet, V. Lazzari, G. Merceron, and F. Guy. 2017a. "Was *Mesopithecus* a Seed Eating Colobine? Assessment of Cracking, Grinding and Shearing Ability Using Dental Topography." *Journal of Human Evolution* 112: 79–92. <https://doi.org/10.1016/j.jhevol.2017.09.002>.
- Thiery, G., F. Guy, and V. Lazzari. 2017b. "Investigating the Dental Toolkit of Primates Based on Food Mechanical Properties: Feeding Action Does Matter." *American Journal of Primatology* 79, no. 6: 1–15. <https://doi.org/10.1002/ajp.22640>.
- Thiery, G., V. Lazzari, A. Ramdarshan, and F. Guy. 2017c. "Beyond the Map: Enamel Distribution Characterized From 3D Dental Topography." *Frontiers in Physiology* 8: 524. <https://doi.org/10.3389/fphys.2017.00524>.
- Ulhaas, L., W. Henke, and H. Rothe. 1999. "Variation in Molar Enamel Thickness of the Genera *Cercopithecus* and *Colobus*." *L'Anthropologie* 37: 265–271.
- Ungar, P. S., and M. Sponheimer. 2011. "The Diets of Early Hominins." *Science* 334: 190–193. <https://doi.org/10.1126/science.1207701>.
- van Casteren, A., E. Wright, K. Kupczik, and M. M. Robbins. 2019. "Unexpected Hard-Object Feeding in Western Lowland Gorillas." *American Journal of Physical Anthropology* 170, no. 3: 433–438. <https://doi.org/10.1002/ajpa.23911>.
- Williams, F. L. 2015. "Dietary Proclivities of *Paranthropus robustus* From Swartkrans, South Africa." *Anthropological Review* 78: 1–19. <https://doi.org/10.1515/anre-2015-0001>.
- Yeakel, J. D., N. C. Bennett, P. L. Koch, and N. J. Dominy. 2007. "The Isotopic Ecology of African Mole Rats Informs Hypotheses on the Evolution of Human Diet." *Proceedings of the Biological Sciences* 274, no. 1619: 1723–1730. <https://doi.org/10.1098/rspb.2007.0330>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Most common linear measurements of enamel thickness. See tables below for explanation of measurements. (image: *Homo naledi* U.W. 101–1006 UM2 mesial section, for illustrative purposes only). B=buccal; L=lingual. **Table S1:** Explanation of linear enamel thickness measurements depicted on Figure S1 associated with the lateral walls. **Table S2:** Explanation of linear enamel thickness measurements depicted on Figure 1.1 associated with the base of the occlusal basin. **Table S3:** Explanation of linear enamel thickness measurements depicted on Figure 1.1 associated with the walls of the occlusal basin. **Table S4:** Explanation of linear enamel thickness measurements depicted on Figure 1.1 associated with cusp tips. **Table S5:** *P. robustus* individuals listed by provenance and age. **Table S6:** Tooth Size—Individual Tooth Type by Site. **Table S7:** Tooth Size—Individual Tooth Type by Chronological Period. **Table S8:** Tooth Size—Tooth Type by Site. **Table S9:** Tooth Size—Jaw Type (Pooled) by Chronological Period. **Table S10:** Tooth Shape—Individual Tooth Type by Site. **Table S11:** Tooth Shape—Individual Tooth Type by Chronological Period. **Table S12:** Tooth Shape—Jaw Type (Pooled) by Site. **Table S13:** Tooth Shape—Jaw Type (Pooled) by Chronological Period. **Table S14:** Whole Crown Enamel Thickness—Individual Tooth Type by Site. **Table S15:** Whole Crown Enamel Thickness—Individual Tooth Type by Chronological Period. **Table S16:** Whole Crown Enamel Thickness—Jaw Type (Pooled) by Site. **Table S17:** Whole Crown Enamel Thickness—Jaw Type (Pooled) by Chronological Period. **Table S18:** Linear Enamel Thickness—Individual Tooth Type by Site. **Table S19:** Linear Enamel Thickness—Individual Tooth Type by Chronological Period. **Table S20:** Linear Enamel Thickness—Jaw Type (Pooled) by Site. **Table S21:** Linear Enamel Thickness—Jaw Type (Pooled) by Chronological Period. **Table S22:** Proportional Linear Enamel Thickness—Individual Tooth Type by Site. **Table S23:** Proportional Linear Enamel Thickness—Individual Tooth Type by Chronological Period. **Table S24:** Proportional Linear Enamel Thickness—Jaw Type (Pooled) by Site. **Table S25:** Proportional Linear Enamel Thickness—Jaw Type (Pooled) by Chronological Period. **Table S26:** Regional Enamel Thickness—Individual Tooth Type by Site. **Table S27:** Regional Enamel Thickness—Individual Tooth Type by Chronological Period. **Table S28:** Regional Enamel Thickness—Jaw Type (Pooled) by Site. **Table S29:** Regional Enamel Thickness—Jaw Type (Pooled) by Chronological Period. **Table S30:** Proportional Regional Enamel Thickness—Individual Tooth Type by Site. **Table S31:** Proportional Regional Enamel Thickness—Individual Tooth Type by Chronological Period. **Table S32:** Proportional Regional Enamel Thickness—Jaw Type (Pooled) by Site. **Table S33:** Proportional Regional Enamel Thickness—Jaw Type (Pooled) by Chronological Period.