Original Research Article

Folia Primatol
DOI: 10.1159/000502819

Received: March 25, 2019
Accepted after revision: August 20, 2019

A Novel Method for Assessing Enamel Thickness Distribution in the Anterior Dentition as a Signal for Gouging and Other Extractive Foraging Behaviors in Gummivorous Mammals

Keegan R. Selig[a] Sergi López-Torres[b] Adam Hartstone-Rose[c]
Leanne T. Nash[d] Anne M. Burrows[e, f] Mary T. Silcox[a]

[a]Department of Anthropology, University of Toronto Scarborough, Toronto, ON, Canada; [b]Department of Evolutionary Paleobiology, Roman Kozłowski Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland; [c]Department of Biological Sciences, North Carolina State University, Raleigh, NC, USA; [d]School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA; [e]Department of Physical Therapy, Duquesne University, Pittsburgh, PA, USA; [f]Department of Anthropology, University of Pittsburgh, Pittsburgh, PA, USA

Keywords
Gummivory · Computed microtomography · Strepsirrhines · Marsupials

Abstract

Gummivory poses unique challenges to the dentition as gum acquisition may often require that the anterior teeth be adapted to retain a sharp edge and to resist loading because they sometimes must penetrate a highly obdurate substrate during gum extraction by means of gouging or scraping. It has been observed previously that the enamel on the labial surface of the teeth used for extraction is thicker relative to that on the lingual surface in taxa that extract gums, while enamel is more evenly distributed in the anterior teeth of taxa that do not regularly engage in extractive behaviors. This study presents a quantitative methodology for measuring the distribution of labial versus lingual enamel thickness among primate and marsupial taxa in the context of gummivory. Computed microtomography scans of 15 specimens representing 14 taxa were analyzed. Ten measurements were taken at 20% intervals starting from the base of the crown of the extractive tooth to the tip of the cutting edge across the lingual and labial enamel. A method for including worn or broken teeth is also presented. Mann-Whitney U tests, canonical variates analysis, and between-group principal components analysis were used to examine variation in enamel thickness across taxa. Our results suggest that the differential distribution of enamel thickness in the anterior dentition can serve as a signal for gouging behavior; this methodology distinguishes between gougers, scrap-

KARGER

E-Mail karger@karger.com
www.karger.com/fpr

Keegan Rayne Selig
Department of Anthropology
University of Toronto Scarborough
Toronto, ON M1C 1A4 (Canada)
E-Mail keegan.selig@mail.utoronto.ca

ers, and nonextractive gummivores. Gouging taxa are characterized by significantly thicker labial enamel relative to the lingual enamel, particularly towards the crown tip. Examination of enamel thickness patterning in these taxa permits a better understanding of the adaptations for the extraction of gums in extant taxa and offers the potential to test hypotheses concerning the dietary adaptations of fossil taxa.

Introduction

Gummivory is a dietary niche in which gums are extracted from trees. Among mammals, only members of two orders are known to include significant portions of gums in their diets: primates and petaurid marsupials [Nash and Burrows, 2010; Smith, 2010; Mittermeier et al., 2013; Wilson and Mittermeier, 2015]. Within Primates, only a few taxa are known to consume large quantities of gums (marmosets, *Euoticus*, *Phaner*, *Nycticebus*, and *Otolemur*), while many others, particularly among strepsirrhines, supplement their diet with exudates [Burrows and Nash, 2010; Smith, 2010]. There are two means to access gums using the anterior dentition: gouging and scraping [Burrows and Nash, 2010]. In gouging taxa, the anterior teeth are used to chisel a hole through the tree bark to create a wound that encourages the flow of gums (as in *Callithrix* or *Nycticebus*); in scraping taxa, the anterior teeth are used to remove a hardened “plug” on an existing wound in the bark to encourage the flow of gums, which are then scraped with the toothcomb [as in *Euoticus* and *Otolemur*; Nash and Burrows, 2010]. Considering that dental enamel interacts directly with the substrate, it has been predicted that enamel may exhibit adaptations related to the extraction of this food source; for example, Hogg et al. [2011] noted that patterns of enamel decussation in the obligate gouger *Callithrix* differ from those observed in the closely related, nongouger *Saguinus* as an adaptation to resist maximum stress. It has also been hypothesized that the pattern of relative enamel thickness on the anterior dentition may reflect an adaptation to support extractive behaviors [Noble, 1969; Rosenberger, 1978]. Rosenberger [1978] and Burrows et al. [2019] observed that the lingual enamel is thinner relative to the labial enamel in samples of gouging and scraping taxa relative to taxa that do not use their anterior teeth in extractive foraging behaviors (Fig. 1). This differential distribution of enamel may be a means to resist tensile stress during extractive foraging, while also serving as an adaptation to preserve a sharp incisal edge on these teeth in a fashion similar to that observed among rodents and in *Daubentonia*, which completely lack enamel on the lingual aspect of the incisors [Noble, 1969; Rosenberger, 1978; Shellis and Hiiemae, 1986; Vinyard et al., 2009; Hogg et al., 2011; Kupczik and Chattah, 2014].

Although there has been a recent flourishing of new dental analysis methods for assessing diet, such as the suite of metrics referred to as dental topographic analysis [Ungar, 2002; Boyer et al., 2010; Bunn et al., 2011; Prufrock et al., 2016; López-Torres et al., 2018], none of these methods has been shown to provide a signal unique for the consumption of exudates. Such methods typically focus on the postcanine dentition but gummivory likely provides little selective pressure on molar topography. In fact, one of the only suggested dental signals for exudativory to date is the reduction of the M_3 [Burrows et al., 2015, 2019]. Therefore, examination of enamel thickness in the teeth used for gouging or scraping in a broad sample of strepsirrhines, haplorhines,

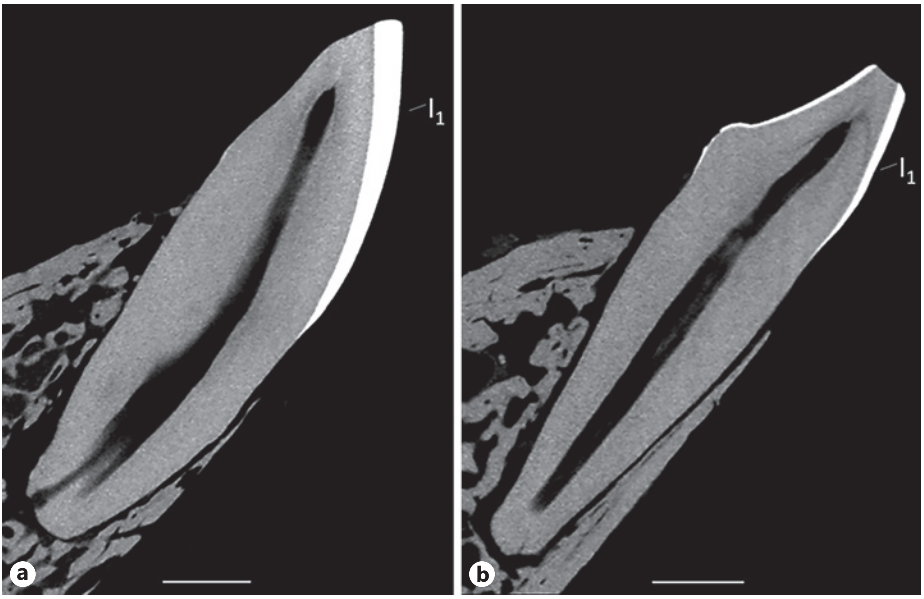

Fig. 1. Renderings of micro-CT scans of parasagittal sections through the right I_1 of *Callithrix jacchus* (AMNH 10927; **a**) and *Saguinus fuscicollis* (AMNH 73394; **b**) from Burrows et al. [2019, Fig. 8]. The labial side is on the right. Note that the labial enamel is thick, while the lingual enamel is absent in *C. jacchus*. Scale bars = 1 mm.

and other mammals may offer a signal for adaptation to extractive foraging not available from other methods. As exudates have been hypothesized to have made up a portion of the diet in stem primates [Beard, 1990, 1991; Boyer and Bloch, 2008; Andrews et al., 2016] and early strepsirrhines [Martin, 1979; Bearder and Martin, 1980], identification of these distributional patterns of enamel offers a potential evidentiary framework to test hypotheses concerning dietary adaptations of fossil taxa.

There is a well-established literature on methods for measuring enamel thickness of primate molars [e.g., Kono, 2004; Olejniczak and Grine, 2006; Olejniczak et al., 2008; Smith et al., 2008; Benazzi et al., 2014]. However, there is less literature on methods for measuring enamel thickness of the anterior teeth, with previous work providing methods that allow for measuring relative or average enamel thickness across the entire crown [e.g., Olejniczak and Grine, 2006; Benazzi et al., 2014], for examining patterns of enamel thickness on the mesial and distal margins of the anterior teeth [e.g., Harris and Hicks, 1998], or for quantifying labial [e.g., Gillings and Buonocore, 1961] or lingual enamel thickness only [e.g., Gantt, 1977]. A method for examining the distribution of enamel across the crown of anterior teeth relevant to the behavioral patterns that have been suggested as tied to exudativory has yet to be established. This project seeks to fill that lacuna. Moreover, this project presents a modified methodology that allows inclusion of worn or damaged teeth, such that larger samples and potentially fragmentary fossils can also be assessed. Histological measurement of enamel thickness is becoming increasingly uncommon given the

Table 1. List of species included in the analysis as well as tooth position examined

Family	Species	Acquisition method	Tooth position	Museum code	DOI/ARK
Cebidae	*Saguinus fuscicollis*[a]	Opportunistic	Left I_1	AMNH 73394	ark:/87602/m4/M75830
	Callimico goeldii[a]	Opportunistic	Right I_1	AMNH 98367	ark:/87602/m4/M16160
	Callithrix jacchus[a]	Gouger	Left I_1	AMNH 19027	ark:/87602/m4/M75414
Galagidae	*Galago moholi*[a]	Scraper	Left C_1	USC 111003	n.a.
	Galago senegalensis	Scraper	Right C_1	MCZ 44132	doi:10.17602/M2/M2703
	Otolemur crassicaudatus[a]	Scraper	Right C_1	AMNH 88061	doi:10.17602/M2/M6365
	Euoticus elegantulus	Scraper	Right C_1	MCZ 18608	doi:10.17602/M2/M2829
Lorisidae	*Perodicticus potto*	Opportunistic	Left C_1	MCZ 42620	doi:10.17602/M2/M4715
	Perodicticus potto[a]	Opportunistic	Left C_1	USC 110001	ark:/87602/m4/M77484
	Loris tardigradus[a]	Opportunistic	Right C_1	USC 110002	n.a.
	Nycticebus coucang	Gouger	Right C_1	MCZ 36040	doi:10.17602/M2/M2720
	Nycticebus pygmaeus	Gouger	Left C_1	MCZ 36035	doi:10.17602/M2/M2719
Pitheciidae	*Cacajao calvus*[a]	Opportunistic	Right I_1	MCZ 1957	doi:10.17602/M2/M5156
Petauridae	*Dactylopsila trivirgata*[a]	Opportunistic[b]	Right I^1	AMNH 101984	ark:/87602/m4/M75882
	Petaurus breviceps[a]	Gouger	Right I^1	AMNH 159549	ark:/87602/m4/M75929

The “opportunistic” category is used for taxa that may occasionally eat gums but are not known to systematically use their anterior teeth to acquire them. n.a., not available. [a] These specimens were included in both the analysis of unworn teeth and that of worn teeth. [b] Although *Dactylopsila* is known to gouge with its lower incisor, the upper incisor (sampled here) is not involved in the gouging process [Kay and Hylander, 1978].

destructive nature of such methods; our novel approach makes use of nondestructive, high-resolution computed microtomography (micro-CT) data. However, the same methods could also be applied to histological sections if available.

Materials and Methods

The sample consists of 15 specimens representing 14 taxa, which were scanned on a Nikon XT H 225 ST high-resolution X-ray CT scanner at the Shared Materials Instrumentation Facility at Duke University or that were downloaded from MorphoSource [Boyer et al., 2016] (Table 1). Scan resolution ranges from 11.7 to 80.0 μm. The taxa in this analysis were chosen to represent closely related species characterized by different dietary niches. For example, *Callithrix jacchus* is a gouging gummivore, while the closely related *Saguinus fuscicollis* does not extract the exudates it consumes [Nash, 1986; Smith, 2010]. In our sample, *C. jacchus*, *Nycticebus coucang*, *N. pygmaeus*, and the petaurid marsupial *Petaurus breviceps* are considered gouging gummivores [Nash, 1986; Nash and Burrows, 2010; Nekaris et al., 2010; Smith, 2010]. Unlike most other gummivorous strepsirrhine taxa, which scrape rather than gouge, *Nycticebus* has been observed actively pushing the lower anterior teeth into bark to gouge into the tree to stimulate the flow of gums [Starr and Nekaris, 2013].

The taxa considered as scrapers are *Otolemur crassicaudatus, Galago moholi*, *G. senegalensis,* and *Euoticus elegantulus* as these taxa have been observed to use the buccal teeth to access gums [see Burrows and Nash, 2010; Nash and Burrows, 2010]. The closely related taxa included for comparison are *S. fuscicollis*, *Loris tardigradus*, *Cacajao calvus*, *Callimico goeldii,* and *Perodicticus potto.* While *P. potto* and *S. fuscicollis* do include exudates in their diets [Nash, 1986; Smith, 2010], field observations suggest that these taxa do not acquire exudates by gouging or scraping, rather they consume gums opportunistically as they flow freely from trees or, in the case of some tamarins, parasitize the holes gouged by sympatric marmosets [Oates, 1984; Sussman and Kinzey, 1984; Garber and Porter, 2010]. Similarly, the other taxa included for comparison have not been observed performing extractive behaviors but may be described as “opportunistic gummivores,” who may consume gums only when they are easily ingested.

The petaurid marsupial *Dactylopsila trivirgata* does gouge to extract insects and larvae, though it does not consume exudates [Rawlins and Handasyde, 2002]. Previous observations suggest that this taxon uses the lower teeth (only) to gouge into tree bark to access insects [Rawlins and Handasyde, 2002], while *Petaurus* likely uses both upper and lower teeth to gouge for exudates [Kay and Hylander, 1978]. Here we examine only the upper incisor for the marsupials in an attempt to discriminate between these different acquisition methods.

A goal of the current analysis was to use existing behavioral information about how the included taxa use their teeth for gouging and scraping. The tooth position used during the extractive behavior was selected for our analysis based on this information (Table 1), which means that we sampled different tooth positions as a reflection of different patterns of behavior. In the case of monkeys, these taxa are known to use the incisors to gouge [Rosenberger, 1978; Garber, 1984; Porter, 2001]; therefore, we herein study the lower central incisor in the haplorhine taxa. In contrast, we examined the lower canine in all strepsirrhine specimens as it forms the lateral part of the toothcomb. The toothcomb is used during gouging in the case of *Nycticebus* and in the scraping taxa, as it (the lower canine) forms part of the functional complex, along with the premolars, which are used by scrapers to remove the gum plug to encourage the gum to flow [Starr et al., 2011; Rosenberger, 2010; Burrows et al., 2019]. While the lower canine of nontoothcombed primates is more functionally distinct from the incisors, the lower canine in strepsirrhines is aligned with the lower incisors, meaning it likely incurs stresses and forces in much the same manner as the lower incisors of gouging monkeys. This is to say that the lingual and labial surfaces of the strepsirrhine lower canine are oriented in the same plane as the incisors, meaning these surfaces likely react to stress similarly to the incisors of monkeys.

We examined micro-CT scans, which were rendered in Avizo 9.0 using the “Isosurface” module [Visualization Sciences Group, 2009]. A “Slice” module was added and used to place a slice parasagittally through the tooth in the labiolingual plane with interpolation “on” and the user-defined texture map resolution set to 4,096 × 4,096 to ensure that resolution was high enough for accurate visualization of the enamel-dentine junction (EDJ) and the outer margin of the enamel. A total of 10 measurements were taken for each specimen, 5 from the lingual enamel and 5 from the labial enamel for each specimen (Fig. 2).

Method for Measuring Enamel Thickness in Unworn and Undamaged Teeth

The methodology described in this section requires teeth that are undamaged and largely unworn. In this case, a straight line (line A in Fig. 2) is drawn from the center of the cusp tip to the cervix on the labial aspect of the cross-section, as in Olejniczak and Grine [2006: Fig. 3]. Line B is then drawn from the cervix on the lingual side of the tooth to intersect line A at 90°; this intersection point may not correspond to the cervix on the labial side. The distance from line B to the tip of the cusp is measured (distance from line B to 100% in Fig. 2). Four lines are then drawn perpendicularly to line A at 20% increments to the cusp tip starting from line B. Measurements of enamel thickness are taken on both the labial and lingual aspects of the tooth at the level of each of these 20% lines perpendicular to the EDJ. Additional labial and lingual measurements are taken along a line drawn perpendicularly to line A at the top of the pulp cavity (pulpal measurement in Fig. 2) to provide an anatomically defined plane of measurement.

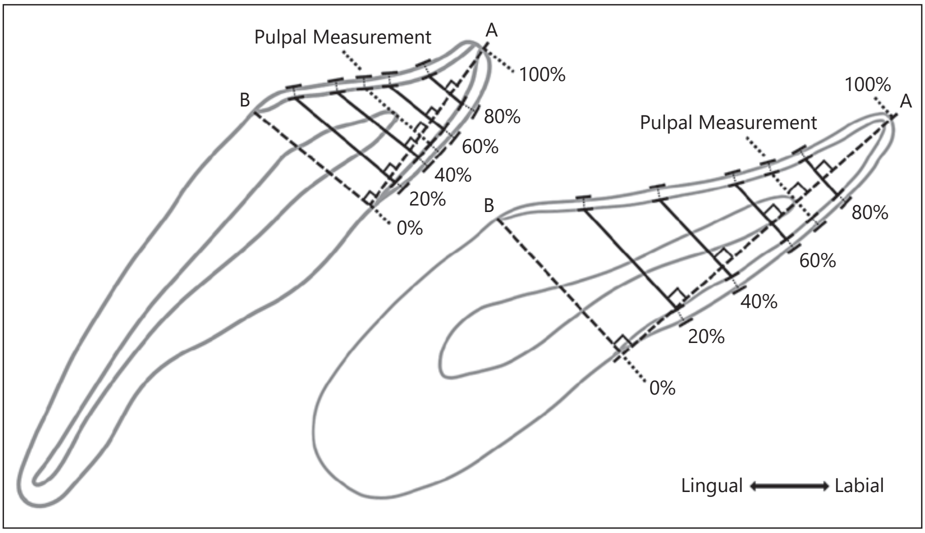

Fig. 2. Representation of the lower incisor of a monkey (image on left) and the lower canine of a strepsirrhine (image on right) showing where each of the 10 measurements are taken across the enamel on unworn or undamaged teeth.

Method for Measuring Enamel Thickness in Worn or Damaged Teeth

This modified methodology does not require that the included teeth be unworn or undamaged. Although this method suffers from the disadvantage of sampling less of the cusp tip (where the difference in enamel thickness would be predicted to be most pronounced), it potentially allows for the inclusion of larger samples. In this modified version, a straight line (line A in Fig. 3) is drawn from the center of the cusp tip to the cervix on the labial aspect of the cross-section, as in Olejniczak and Grine [2006: Fig. 3]. Line B is then drawn from the cervix on the lingual side of the tooth to intersect line A at 90°; the intersection point may or may not be at the level of the cervix on the labial side. The distance from line B to the top of the pulp cavity is then measured (distance from line B to 100% in Fig. 3). Five lines are then drawn perpendicularly to line A at 20% increments of the distance between line B to the top of the pulp cavity, starting from line B and ending with the fifth line at the top of the pulp cavity. Measurements of enamel thickness are taken on both the labial and lingual aspects of the tooth where each of the 20% lines cross the enamel, perpendicularly to the EDJ. Measurements are taken from the EDJ to the outer margin of the enamel using the 2-dimensional measuring tool in Avizo.

This method ensures that even relatively worn or broken teeth can be included in an analysis so long as the top of the pulp cavity is present, and it is possible to define the plane of the midline at the tip of the tooth as preserved. Considering that teeth used to acquire gums are prone to wear, and because delicate fossil incisors and canines are susceptible to damage, the ability to include such specimens greatly increases the potential for large samples and for fossils to be analyzed. The top of the pulp cavity also serves as an anatomically defined point to guarantee the replicability of the measurements, and to ensure that these measurements are based on biologically relevant morphology rather than a landmark that changes dramatically throughout the life of an individual, such as a cusp tip.

Statistical Analyses

The software package PAST 3.19 [Hammer et al., 2001] was used for the statistical analyses. A Mann-Whitney U test was performed to analyze potential differences between labial and lin-

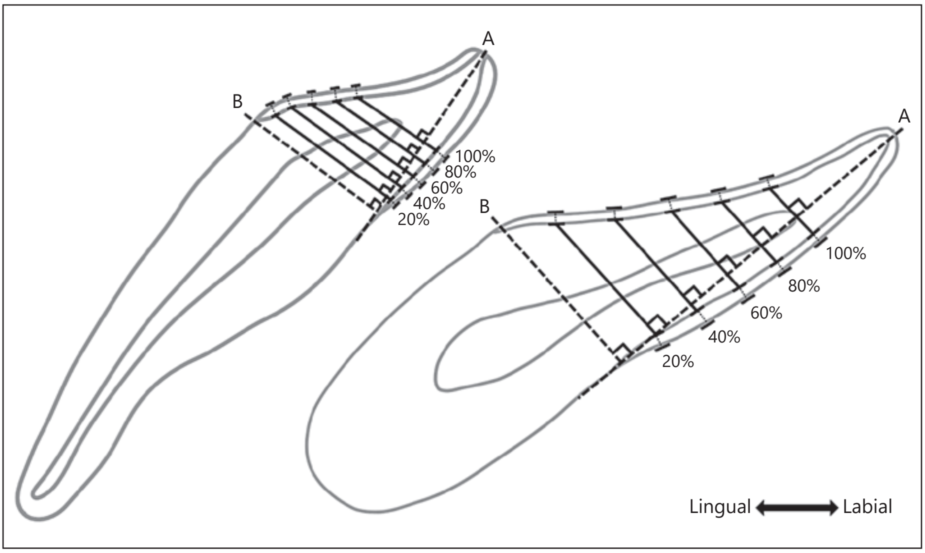

Fig. 3. Representation of the lower incisor of a monkey (image on left) and the lower canine of a strepsirrhine (image on right) showing where each of the 10 measurements are taken across the enamel on worn or damaged teeth.

gual enamel thickness. Canonical variate analysis (CVA) and between-group principal component analysis (bgPCA) of the correlation matrix were used to explore differences in patterns of enamel thickness in the included taxa. Although CVA is useful for distinguishing between groups and for classifying unknowns, a bgPCA does not require that the included groups have the same covariance matrix. Also, a CVA tends to separate groups even if the individuals come from the same population when the number of variables is close to the number of individuals, while the number of variables does not affect the separation of groups in a bgPCA [Mitteroecker and Bookstein, 2011]. Therefore, bgPCA serves as an alternative and perhaps better means for examining biological questions using small samples. In our analysis of worn or damaged teeth, we conducted two CVAs, one including all 10 measurements, like in the analysis of unworn teeth, and a second using only the measurements nearest the cutting edge of the tooth, at the 80 and 100% points (Fig. 3), as these measurements were best at discriminating between groups (see below).

We also performed an intraobserver error study to assess the repeatability of our method. One observer (K.R.S.) resliced and remeasured the lower right canine of *L. tardigradus* (University of South Carolina, Columbia, SC; USC 110002) 10 times over the course of 7 weeks with at least 48 h between observations. The measurements were taken following the protocol outlined above for complete teeth. We calculated the mean absolute percent difference (MAPD) following Grine et al. [2001] as:

$$\text{MAPD} = \frac{\text{observed value} - \text{sample mean}}{\text{sample mean}} \times 100.$$

We also calculated the coefficient of variation for each measurement over the course of the 10 trials. Finally, we used the repeated-measures analysis of variance (ANOVA) and Levene's test for homogeneity of variance to examine if mean and variance differed significantly between trials.

Table 2. Results of the intraobserver error study showing the mean absolute percent difference (MAPD) and the coefficient of variation (CV) for each measurement and the mean MAPD and CV across all 10 trials

	20% Lin	40% Lin	60% Lin	80% Lin	Pulpal Lin	20% Lab	40% Lab	60% Lab	80% Lab	Pulpal Lab	Mean
MAPD, %	5.16	7.69	7.27	5.16	0	5.16	7.27	2.53	6.48	6.48	5.32
CV	6.80	8.11	7.82	6.80	0	6.80	7.82	4.45	6.98	6.98	6.26

Lin, lingual measurements; Lab, labial measurements.

Results

Intraobserver Error Study

Results of the intraobserver error study are summarized in Table 2. We found a total MAPD of 5.32% over the course of 10 trials. A percent difference this low is consistent with other analyses of intraobserver error in the measurement of dental features such as microwear [e.g., Grine et al., 2002] and enamel thickness [e.g., Skinner et al., 2015], suggesting that this method is reliable. The measurement with the highest MAPD was the 40% lingual measurement with 7.69% difference throughout the trails, while the pulpal measurement on the lingual enamel was consistent throughout all 10 trials, with no variation in this measurement within a hundredth of a millimeter (i.e., 0% MAPD). Although 7.69% is slightly high relative to what is generally acceptable [see Skinner et al., 2015, for example], no measurement at the same location of the tooth varied by more than 0.01 mm over the course of the 10 trials. The coefficient of variation for each measurement is in line with previous measures of variation in the context of morphometrics [Sokal and Braumann, 1980; Grine et al., 2002]. The repeated-measures ANOVA reveals no significant differences between measurements for enamel thickness ($p = 0.080$, $F = 1.795$), and Levene's test for homogeneity of variance reveals that variance does not differ significantly ($p = 0.060$). This suggests that our measurements are precise and repeatable, even when the micro-CT scans are resliced, and measurements retaken.

Measurement of Enamel Thickness in Unworn and Undamaged Teeth

Measurements of enamel thickness using this method are summarized in Table 3 and Figure 4. The overall pattern of enamel thickness suggests that the gouging taxa do have thicker labial enamel relative to the lingual enamel (Fig. 4). It is noteworthy, however, that taxa such as *E. elegantulus* and *P. potto* also seem to show a greater disparity between the thickness of the lingual and labial enamel relative to other taxa. A Mann-Whitney U test could not be performed to test for differences between lingual and labial enamel thickness among gougers due to the small sample size ($n = 2$) for these taxa *(C. jacchus, P. breviceps)*. However, a Mann-Whitney U test suggests that there are no significant differences between lingual or labial enamel thickness in either the opportunistic or scraping taxa (Table 4). A CVA including all 10 measurements was conducted to determine whether these measurements can discriminate between the gouging, scraping, and opportunistic taxa (Fig. 5). Loadings for axis 1 (93.01% of the variation explained) are negative for the lingual measurements and

Table 3. Results of the measurement (mm) of enamel thickness for specimens represented by complete and unworn teeth

Specimen No.	Species	20% Lin	40% Lin	60% Lin	80% Lin	Pulpal Lin	20% Lab	40% Lab	60% Lab	80% Lab	Pulpal Lab
AMNH 19027	*C. jacchus*	0.03	0.03	0.03	0.02	0.03	0.17	0.26	0.30	0.27	0.27
AMNH 73394	*S. fuscicollis*	0.05	0.05	0.05	0.06	0.05	0.06	0.09	0.09	0.11	0.11
AMNH 101984	*D. trivirgata*	0.12	0.16	0.19	0.20	0.22	0.15	0.18	0.19	0.20	0.18
AMNH 159549	*P. breviceps*	0.04	0.05	0.05	0.10	0.05	0.08	0.13	0.15	0.18	0.16
USC 110001	*P. potto*	0.06	0.06	0.06	0.04	0.05	0.07	0.08	0.09	0.08	0.08
AMNH 88061	*O. crassicaudatus*	0.08	0.07	0.06	0.07	0.06	0.07	0.07	0.09	0.10	0.10
USC 111003	*G. moholi*	0.03	0.04	0.04	0.04	0.05	0.06	0.06	0.05	0.06	0.05
USC 110002	*L. tardigradus*	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.07	0.08	0.07
AMNH 18608	*E. elegantulus*	0.06	0.04	0.05	0.06	0.06	0.10	0.10	0.10	0.10	0.09
AMNH 98367	*C. goeldii*	0.06	0.07	0.09	0.07	0.09	0.08	0.08	0.10	0.10	0.11
MCZ 1957	*C. calvus*	0.18	0.20	0.22	0.21	0.19	0.19	0.24	0.24	0.25	0.22

Lin, lingual measurements; Lab, labial measurements. Measurements are in millimeters. AMNH, American Museum of Natural History, New York, NY; USC, University of Southern California, Los Angeles, CA; MCZ, Harvard Museum of Comparative Zoology, Cambridge, MA; DPC, Duke Primate Center, Durham, NC. Our specimens of *N. pygmaeus*, *N. coucang*, and *G. senegalensis* were not included in this part of the analysis as this methodology requires relatively unworn teeth.

Table 4. Results of the Mann-Whitney U tests including *p* values ($\alpha = 0.05$) and U statistics of unworn and undamaged teeth testing for differences between labial and lingual enamel thickness for each measurement in the gougers, scrapers, and opportunists

Lingual vs. labial enamel thickness measurement	20%	40%	60%	80%	Pulpal
Gougers	–	–	–	–	–
Scrapers	$U = 2.5$ $p = 0.507$	$U = 1.5$ $p = 0.261$	$U = 1.5$ $p = 0.268$	$U = 1.5$ $p = 0.261$	$U = 2.5$ $p = 0.500$
Opportunistic	$U = 13$ $p = 0.465$	$U = 12$ $p = 0.374$	$U = 11.5$ $p = 0.322$	$U = 9.5$ $p = 0.199$	$U = 12.5$ $p = 0.418$

positive for the labial measurements, which suggest that variation along this axis is the product of differential enamel thickness (Table 5). The gouging taxa plot in distinct space from the scraping and opportunistic taxa, which overlap along axis 1. On axis 2 (6.99% of the variance explained) all loadings are negative; in a conventional PCA this would be interpreted as implying that the values along that axis are a proxy for size. However, it is worth noting that in a CVA the emphasis on between-group discrimination means that this axis is not just a simple proxy for size. The scraping taxa happen to be among the smallest included in the sample (with the exception of *Otolemur*), therefore, this may partially explain why they plot in distinct space from the other groups along this axis, though this could also be a result of phylogeny, as these taxa are more closely related to each other than the taxa within the other groups.

A between-group PCA based upon all 10 variables was also conducted on the sample of unworn teeth (Fig. 5). In this case, the loadings for bgPC 1 (65.04% of the variance explained) are negative for the lingual measurements and positive for the labial measurements (Table 5). Separation of groups is less clear as several scraping

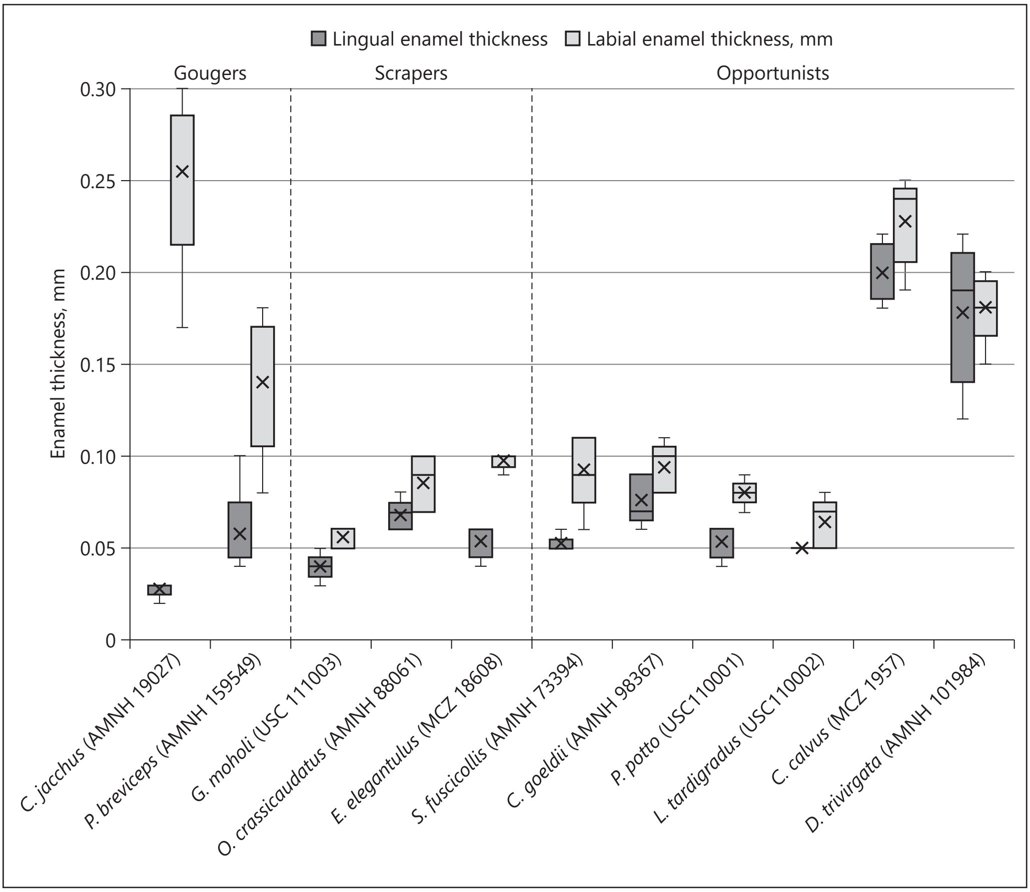

Fig. 4. Box plots of the unworn teeth included in the analysis. For each specimen, we plotted each of the 5 lingual measurements and each of the 5 labial measurements. Therefore, each box plot represents the range of measurements along an aspect of the enamel and comprises multiple variables. The X denotes the means, the horizontal lines denote the medians, the boxes represent the upper and lower quartiles, and whiskers denote the highest and lowest values for each individual.

and opportunistic taxa overlap. However, gouging taxa plot in distinctive morphospace along this axis. The loadings suggest that variation along bgPC 2 (34.96% of the variance explained) may be the result of dental size as each variable is positively loaded and therefore positively correlated (Table 5). As grouping variables are included in a bgPCA, this interpretation may not be as clear as in a conventional PCA.

Measurement of Enamel Thickness in Worn or Damaged Teeth

Measurements of enamel thickness using this method are summarized in Table 6 and Figure 6. As in the case with the above analysis, the overall pattern of enamel thickness among taxa analyzed suggests that the gougers have thicker labial enamel

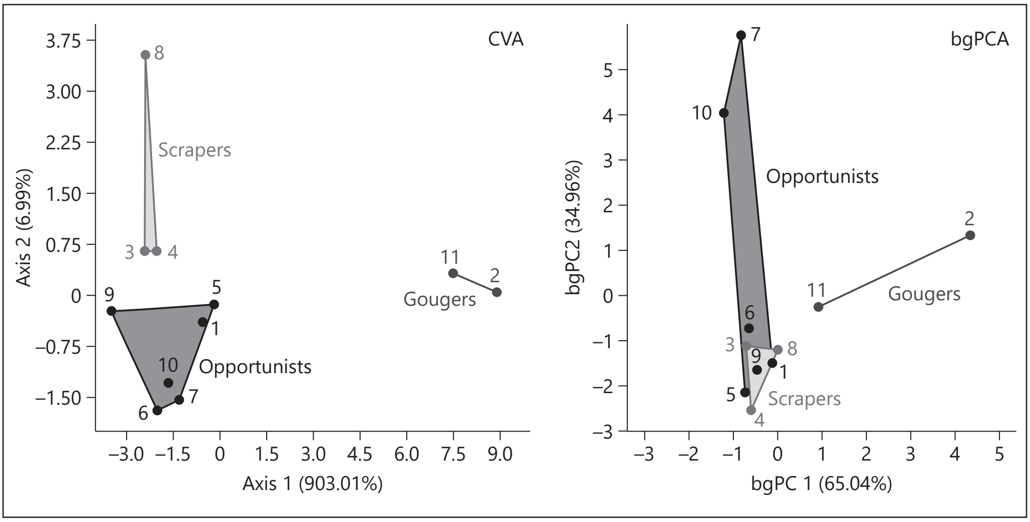

Fig. 5. Plots of the canonical variate analyses (CVA; left) and between-group principal component analyses (bgPCA; right) of the unworn and undamaged teeth of all 10 measurements (i.e., as pictured in Fig. 2): 1, *Saguinus fuscicollis*; 2, *Callithrix jacchus;* 3, *Otolemur crassicaudatus*; 4, *Galago moholi*; 5, *Loris tardigradus*; 6, *Callimico goeldii;* 7, *Cacajao calvus*; 8, *Euoticus elegantulus*; 9, *Perodicticus potto*; 10, *Dactylopsila trivirgata*; 11, *Petaurus breviceps.*

Table 5. Loadings for the CVA and bgPCA for the unworn and undamaged specimens

	CVA – axis 1	CVA – axis 2	bgPCA – PC 1	bgPCA – PC 2
20% lingual	–0.00290	–0.01294	–0.35941	0.21383
40% lingual	–0.00379	–0.02221	–0.30463	0.33674
60% lingual	–0.00490	–0.02376	–0.29747	0.34846
80% lingual	–0.00353	–0.02024	–0.24256	0.42022
Pulpal lingual	–0.00357	–0.02239	–0.32230	0.30462
20% labial	0.003793	–0.01034	0.29766	0.34815
40% labial	0.009457	–0.01400	0.32896	0.29106
60% labial	0.010140	–0.01539	0.33399	0.28021
80% labial	0.011772	–0.01682	0.33010	0.28866
Pulpal labial	0.010652	–0.01684	0.33091	0.28692

relative to the lingual enamel. However, this difference is not as pronounced in *Petaurus,* likely because a different aspect of the crown was analyzed. Again, *P. potto* (both specimens) shows a greater disparity between the distribution of lingual and labial enamel thickness than might be expected (see below). As worn or damaged teeth can be included using this modified method, a Mann-Whitney U test was possible for all three groups as they encompass a larger number of specimens. The test

Table 6. Results of the measurement (mm) of enamel thickness for the specimens represented by worn or damaged teeth

Specimen No.	Species	20% Lin	40% Lin	60% Lin	80% Lin	100% Lin	20% Lab	40% Lab	60% Lab	80% Lab	100% Lab
AMNH 73394	*S. fuscicollis*	0.04	0.05	0.04	0.05	0.05	0.05	0.06	0.10	0.11	0.12
AMNH 98367	*C. goeldii*	0.07	0.07	0.13	0.09	0.11	0.08	0.09	0.10	0.11	0.11
AMNH 19027	*C. jacchus*	0.03	0.03	0.04	0.03	0.03	0.13	0.16	0.22	0.26	0.27
USC 111003	*G. moholi*	0.06	0.06	0.04	0.04	0.03	0.05	0.05	0.04	0.04	0.04
MCZ 44132	*G. senegalensis*	0.06	0.06	0.06	0.06	0.05	0.08	0.09	0.10	0.08	0.08
AMNH 88061	*O. crassicaudatus*	0.05	0.08	0.06	0.06	0.06	0.07	0.09	0.10	0.10	0.11
USC 110001	*P. potto*	0.04	0.06	0.06	0.06	0.06	0.08	0.09	0.09	0.08	0.08
MCZ 42620	*P. potto*	0.10	0.10	0.10	0.10	0.08	0.14	0.14	0.13	0.13	0.15
USC 110002	*L. tardigradus*	0.05	0.05	0.08	0.09	0.07	0.06	0.07	0.06	0.07	0.06
MCZ 36040	*N. coucang*	0.09	0.11	0.12	0.12	0.11	0.14	0.15	0.17	0.18	0.17
MCZ 36035	*N. pygmaeus*	0.10	0.11	0.08	0.09	0.08	0.16	0.15	0.15	0.15	0.15
AMNH 101984	*D. trivirgata*	0.11	0.14	0.16	0.18	0.18	0.16	0.18	0.18	0.19	0.19
AMNH 159549	*P. breviceps*	0.03	0.03	0.03	0.04	0.06	0.04	0.05	0.06	0.10	0.17
MCZ 1957	*C. calvus*	0.20	0.26	0.23	0.25	0.23	0.24	0.24	0.24	0.26	0.24

Lin, lingual measurements; Lab, labial measurements; AMNH, American Museum of Natural History, New York, NY; USC, University of South Carolina, Columbia, SC; MCZ, Harvard Museum of Comparative Zoology, Cambridge, MA. Our specimen of *Euoticus elegantulus* (MCZ 180608) was not included in this part of the analysis as the labial enamel was chipped such that one of our measurements would have passed through an area lacking enamel.

suggests there is a significant difference between the lingual and labial enamel thickness in the gouging taxa, whereas there are no significant differences in enamel thickness for the scraping or opportunistic gum feeders (Table 7). There is a significant difference in the distribution of enamel thickness in the case of the gougers for the measurements at 100% ($U = 0$, $p = 0.029$), while there is a near-significant difference for the measurement at 80% ($U = 1$, $p = 0.0601$). A CVA was used to determine whether the groups can be discriminated (Fig. 7). When all 10 measurements are included, the loadings for axis 1 (99.20% of the variation explained) are all negative, which suggest that differences in dental size are represented here to some degree (Table 8), although as discussed above it is important to keep in mind that in a CVA analysis this is not a simple proxy only for size because of its emphasis on between-group discrimination. The loadings for axis 2 (0.80% of the variation explained) are negative for the lingual measurements and positive for the labial measurements at 60, 80, and 100% (Table 8). This suggests that separation along this axis is a product of differential patterns of enamel thickness, particularly those patterns closer to the tip of the cusp. There is some overlap between the gougers and scrapers, specifically with *N. coucang* plotting within the distribution of the opportunistic gummivores along axis 2; however, there is good separation between the rest of the groups.

As the Mann-Whitney U test indicates that measurements which best characterize the differences between lingual and labial enamel thickness occur towards the incisal margin of the tooth, a second CVA was conducted using only the 80 and 100% measurements (i.e., 4 measurements; Fig. 7). In this case, loadings along axis 1 (76.10% of the variation explained) are negative for the lingual measurements and positive for the labial measurements (Table 9). Thus, differences in enamel distribution are characterizing variation along this axis. While the gougers and scrapers do not overlap along axis 1, two opportunistic gummivores overlap with the range of values of goug-

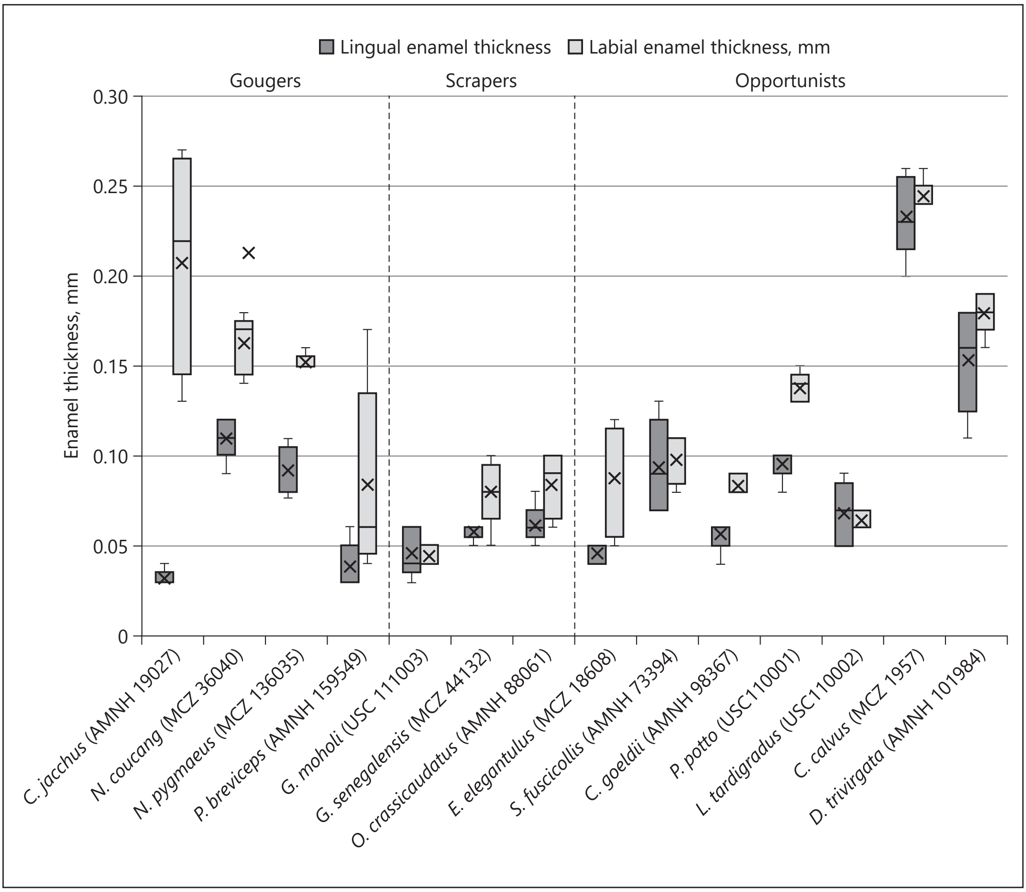

Fig. 6. Box plots of the worn or damaged teeth included in the analysis. For each specimen, we plotted each of the 5 lingual measurements and each of the 5 labial measurements. Therefore, each box plot represents the range of measurements along an aspect of the enamel and comprises multiple variables. The X denotes the means, the horizontal lines denote the medians, the boxes represent the upper and lower quartiles, and whiskers denote the highest and lowest values for each individual.

ers along axis 1, in this case, a specimen of *Perodicticus potto* and *Saguinus fuscicollis.* The loadings for axis 2 (23.90% of the variation explained) are all positive (Table 9), and, thus, differences in dental size are characterizing much of the variation along this axis (but see discussion about CVA above). Although separation of group polygons is not as clear as in the CVA based on all 10 measurements, much more of the variation in the second analysis including only the 80 and 100% measurements is a product of differences in enamel distribution (23.80 vs. 0.80%) rather than differences in overall size (76.10 vs. 99.20%).

A bgPCA for all 10 measurements identified two bgPCs, the first of which characterizes 72.62% of the total variation (Fig. 5). The loadings for bgPC 1 are all positive

Table 7. Results of the Mann-Whitney U test including *p* values ($\alpha = 0.05$) and U statistics of worn or damaged teeth testing for differences between labial and lingual enamel thickness for each measurement in the gougers, scrapers, and opportunists

Lingual vs. labial enamel thickness measurement	20%	40%	60%	80%	100%
Gougers	$U = 2$ $p = 0.1102$	$U = 2$ $p = 0.1059$	$U = 2$ $p = 0.1124$	$U = 1$ $p = 0.0606$	$\mathbf{U = 0}$ $\mathbf{p = 0.0294}$
Scrapers	$U = 2.5$ $p = 0.5002$	$U = 3$ $p = 0.6531$	$U = 2.5$ $p = 0.4936$	$U = 2.5$ $p = 0.5002$	$U = 2$ $p = 0.3827$
Opportunistic	$U = 16.5$ $p = 0.3363$	$U = 17.5$ $p = 0.4036$	$U = 20$ $p = 0.6096$	$U = 17$ $p = 0.3700$	$U = 16.5$ $p = 0.3363$

Bold lettering indicates significant results.

(Table 8), and, thus, variation along this axis may be driven by dental size. Again, due to the nature of an analysis that accounts for grouping, size alone does not determine the location on the plot of a given specimen, which explains why not all of the largest taxa plot with one another. Along bgPC 2 (27.38% of the variation explained), loadings are negative for all lingual measurements and positive for all labial measurements (Table 8), and, thus, separation of groups along this axis is the result of differential enamel thickness. Although there is much overlap between dietary functional groups along bgPC 2, particularly among opportunists and scrapers, there is a separation of groups in this analysis in a plot of both axes (Fig. 7), with the gougers plotting separately from the opportunists.

A bgPCA including only the 80 and 100% measurements identified two bgPCs as well (Fig. 5). The loadings for the first bgPC (69.12% of variation explained) are all positive (Table 9), which again indicates that size may be characterizing the variation along this axis. The loadings of bgPC 2 (30.88% of the variation explained) are negative for the lingual measurements and positive for the labial measurements, which indicates that differences in the distribution of enamel across the teeth are characterizing the separation of groups along this axis. Here, groups plot much in the same manner as in the bgPCA with all 10 measurements (Fig. 7), with overlap between some gouging taxa (*N. pygmaeus* and *N. coucang*) and the opportunistic feeders along the second axis.

Discussion and Conclusion

Our results suggest that the differential distribution of enamel thickness in the anterior dentition can serve as a signal for gouging behavior. Our results also suggest that a complete crown is not needed to discriminate between gouging and nongouging taxa. Labial enamel is relatively thicker compared to the lingual enamel in taxa that gouge to extract exudates. A similar pattern is seen in taxa that scrape to access gums but is not as strongly expressed as in the gouging taxa. In our sample, this contrast with scraping taxa did not meet statistical significance, although potential dif-

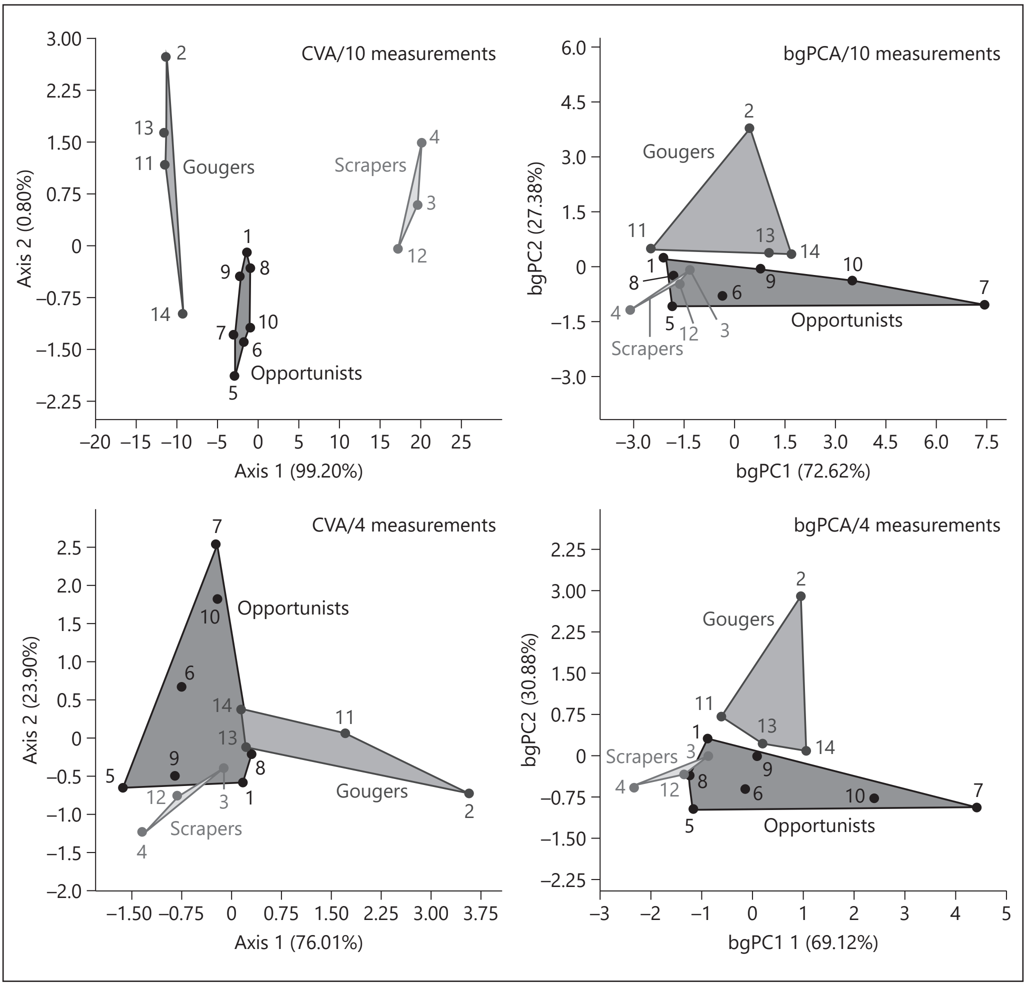

Fig. 7. Plots of the canonical variate analyses (CVA; left) and between-group principal component analyses (bgPCA; right) for the sample including worn teeth, with analyses including 10 measurements (top; see Fig. 3) and 4 measurements (bottom; taken at the 80 and 100% lines in Fig. 3): 1, *Saguinus fuscicollis*; 2, *Callithrix jacchus*; 3, *Otolemur crassicaudatus*; 4, *Galago moholi*; 5, *Loris tardigradus*; 6, *Callimico goeldii*; 7, *Cacajao calvus*; 8 and 9, *Perodicticus potto*; 10, *Dactylopsila trivirgata*; 11, *Petaurus breviceps*; 12, *Galago senegalensis*; 13, *Nycticebus pygmaeus*; 14, *Nycticebus coucang*.

ferences may have been masked by the low power of the test due to small sample sizes. In particular, it is notable that scraping taxa plotted amongst the gouging taxa along axis 2 in our CVA including 10 measurements on worn teeth, reflecting similarities in the way that their enamel thickness is patterned. It seems that in either case, thicker labial enamel provides a means to resist stress [Kupczik and Chattah, 2014] and keep a sharp incisal edge for both gougers and scrapers.

Table 8. Loadings for the CVA and bgPCA of worn or damaged teeth including all 10 measurements

	CVA – axis 1	CVA – axis 2	bgPCA – PC 1	bgPCA – PC 2
20% lingual	–0.00042	–0.013709	0.31523	–0.31887
40% lingual	–0.00041	–0.018324	0.29384	–0.36909
60% lingual	–0.000909	–0.02651	0.32329	–0.29669
80% lingual	–0.00100	–0.027087	0.32871	–0.28044
100% lingual	–0.001196	–0.025163	0.3455	–0.22047
20% labial	–0.0018272	–0.0070296	0.3497	0.20217
40% labial	–0.0018151	–0.0062879	0.34642	0.21665
60% labial	–0.0023556	0.0001695	0.30341	0.34796
80% labial	–0.0032826	0.0035781	0.28718	0.38275
100% labial	–0.0036479	0.010447	0.256	0.43753

Table 9. Loadings for the CVA and bgPCA of worn or damaged teeth including 4 measurements

	CVA – axis 1	CVA – axis 2	bgPCA – PC 1	bgPCA – PC 2
80% lingual	–0.01031	0.052508	0.48191	–0.53829
100% lingual	–0.00723	0.052503	0.51823	–0.45658
80% labial	0.031579	0.041148	0.51982	0.45251
100% labial	0.039675	0.036557	0.47854	0.54499

In the CVA based upon 4 measurements of worn teeth, a specimen of *P. potto* and *S. fuscicollis* (Fig. 7) plot at the edge of the polygon, overlapping the distribution of the gouging taxa. However, field observations suggest that these taxa do not acquire exudates by gouging or scraping [Garber, 1984; Oates, 1984]. Our result could be influenced by the close phylogenetic relationship between *P. potto* and the other lorisids, and between *S. fuscicollis* and the confamilial *C. jacchus*, which may indicate that relatively thicker labial enamel may be a primitive character and the nonextractive behaviors of *P. potto* and *S. fuscicollis* are derived [Burrows et al., 2015]. Our results could also indicate that further research and field observation are needed on taxa such as *P. potto* (as well as on other African, non-Malagasy, strepsirrhines) to determine exactly how gums are recovered and how the anterior dentition is used during that process. Even if it is a rare behavior, the mechanical requirements of gouging could necessitate adaptations to the anterior teeth. As both specimens of *P. potto* show a rather pronounced difference between lingual and labial enamel thickness (Fig. 6), our results could suggest that this taxon may show morphological affinities for gouging, even if it does not make regular use of this behavior in the wild.

Considering that there was a significant difference in the worn sample between lingual and labial enamel thickness in the gougers in only the measurement closest to the cusp tip, and separation of groups (behaviors) was greater in the sample of unworn teeth, our results suggest the differences characterizing gouging and nongouging taxa are most prominent towards the incisal margin or tip of the tooth; this pattern can be

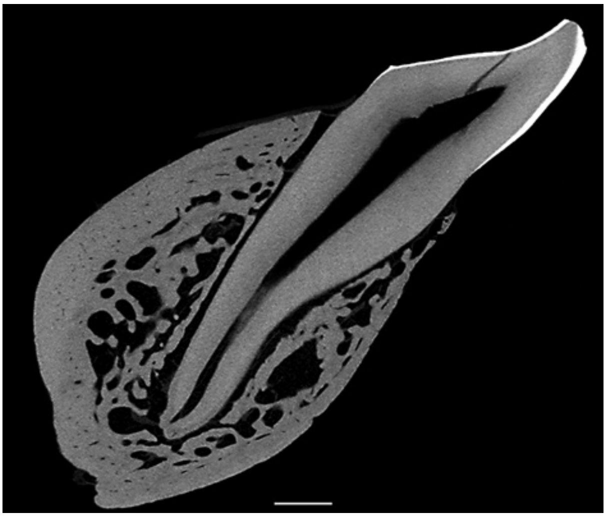

Fig. 8. Rendering of a micro-CT scan of a parasagittal section through the right C_1 of *Nycticebus coucang* (USC 110003) from Burrows et al. [2019, Fig. 9a]. Labial side is on the right. Note that the difference between lingual and labial enamel thickness is greatest near the tip of the tooth. Scale bar = 1 mm.

observed in virtual sections for some taxa (e.g., *N. coucang*, Fig. 8). The marked contrast in enamel thickness near the tip of the tooth is not surprising as it is the part of the tooth that will likely incur most of the stress during gouging behavior and is also the part of the tooth that needs to be the most chisel-like to penetrate a substrate.

One potential source of variation has to do with the mixing of maxillary and mandibular elements, as well as mixing incisors and canines in our sample. While it is likely that these teeth differ in terms of overall patterns of enamel distribution, our method is picking up on the biomechanical patterns exhibited by these teeth, as variation in all of our data reduction analyses is characterized either by the ratio of lingual to labial enamel or by overall size. This suggests that all the included dental elements collected from gouging taxa are characterized by a pattern of enamel reflecting a means for reducing stress on the tooth and for keeping a sharp incisal edge, regardless of the homology of those elements. Another potential source of variation is in that the top of the pulp canal is used as a landmark for several of the measurements. While this does provide an anatomically defined landmark, the deposition of secondary dentine under the influence of wear could cause the position of this landmark to move. Although it is unlikely that this causes substantial amounts of variation, more research is needed in order to address how the deposition of secondary dentine at the top of the pulp canal plays a role in the position of this landmark in nonhuman primates and other mammals.

This method offers a quantitative means to distinguish between gouging and scraping taxa, and those that are best described as "opportunistic gummivores." It also provides potential insight into the dietary adaptations of extinct taxa, which could be included in a discriminant analysis like that above [see López-Torres et al., in press]. This method provides a means to examine enamel thickness on nondestructive micro-CT scans, but could also be used to measure enamel thickness on histological sections if CT data are not available. High-resolution micro-CT data are needed to accurately visualize the EDJ, but data of sufficient quality are starting to become more commonly available, and neutron-based computed microtomography might allow for the visualization of relative enamel thickness in fossils that are difficult to image using traditional micro-CT [Urciuoli et al., 2018]. In the case of worn or broken teeth, so long as the top of the pulp cavity is preserved, the method proposed here ensures that both worn and broken teeth can be measured with informative accuracy. Future studies will use this approach to illuminate the evolution of gummivory in primates and other mammals.

Acknowledgments

We thank Doug Boyer for kindly providing access to his lab space and Justin Gladman for help with micro-CT scanning at Duke University and the Shared Materials Instrumentation Facility. We are grateful to Neil Duncan for facilitating a loan from the American Museum of Natural History. We also thank MorphoSource as well as curators and collections staff at the American Museum of Natural History (AMNH, New York, NY; AMNH 88061 and AMNH 98367), and the Harvard Museum of Comparative Zoology (MCZ, Cambridge, MA; MCZ 1957; MCZ 44132; MCZ 42620; MCZ 36040; MCZ 36035) for allowing upload of micro-CT scans. We thank two anonymous reviewers and Christophe Soligo for the substantial improvements their comments made to this paper.

Statement of Ethics

The authors have no ethical conflicts to disclose.

Disclosure Statement

The authors have no conflicts of interest to declare.

Funding Sources

Costs associated with travel and micro-CT scanning were supported by a Pilot Research Grant to K.R.S. from the Department of Anthropology, University of Toronto, travel funding from Duquesne University to A.M.B., and an NSERC Discovery Grant to M.T.S.

Author Contributions

K.R.S. collected and analyzed data and wrote the first draft. All authors contributed to conceptualizing the study, interpreting the data, and editing the text.

References

Andrews CA, Rambeloarivony H, Génin F, Masters JC (2016). Why cheirogaleids are bad models for primate ancestors: a phylogenetic reconstruction. In *The Dwarf and Mouse Lemurs of Madagascar: Biology, Behavior and Conservation Biogeography of Cheirogaleidae* (Lehman SM, Radespiel U, Zimmermann E, eds.), pp 94–112. Cambridge, Cambridge University Press.

Beard KC (1990). Gliding behaviour and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). *Nature* 345: 340–341.

Beard KC (1991). Vertical posture and climbing in the morphotype of Primatomorpha: implications for locomotor evolution in primate history. In *Origine(s) de la bipédie chez les hominidés* (Coppens Y, Senut B, eds.), pp 79–87. Paris, CNRS.

Bearder SK, Martin RD (1980). Acacia gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). *International Journal of Primatology* 1: 103–128.

Benazzi S, Panetta D, Fornai C, Toussaint M, Gruppioni G, Hublin J-J (2014). Technical note: guidelines for the digital computation of 2D and 3D enamel thickness in hominoid teeth. *American Journal of Physical Anthropology* 153: 305–313.

Boyer DM, Bloch JI (2008). Evaluating the mitten-gliding hypothesis for Paromomyidae and Micromomyidae (Mammalia, "Plesiadapiformes") using comparative functional morphology of new Paleogene skeletons. In *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay* (Sargis EJ, Dagosto M, eds.), pp 233–284. New York, Kluwer.

Boyer DM, Evans AR, Jernvall J (2010). Evidence of dietary differentiation among late Paleocene-early Eocene plesiadapids (Mammalia, Primates). *American Journal of Physical Anthropology* 142: 194–210.

Boyer DM, Gunnell GF, Kaufman S, McGeary T (2016). MorphoSource – archiving and sharing 3D digital specimen data. *Journal of Paleontology* 22: 157–181.

Bunn JM, Boyer DM, Lipman Y, St. Clair EM, Jernvall J, Daubechies I (2011). Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. *American Journal of Physical Anthropology* 145: 247–261.

Burrows AM, Nash LT (2010). Search for dental signals of exudativory in galagos. In *The Evolution of Exudativory in Primates* (Burrows AM, Nash LT, eds.), pp 211–233. New York, Springer.

Burrows AM, Hartstone-Rose A, Nash LT (2015). Exudativory in the Asian loris, *Nycticebus*: evolutionary divergence in the toothcomb and M_3. *American Journal of Physical Anthropology* 158: 663–672.

Burrows AM, Nash LT, Hartstone-Rose A, Silcox MT, López-Torres S, Selig KR (2019). Dental signatures for exudativory in living primates, with comparisons to other gouging mammals. *The Anatomical Record* DOI: 10.1002/ar.24048.

Gantt DG (1977). *Enamel of Primate Teeth: Its Thickness and Structure with Reference to Functional and Phyletic Implications*. PhD dissertation, Washington University.

Garber PA (1984). Proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus oedipus geoffroyi*. *International Journal of Primatology* 5: 1–15.

Garber PA, Porter LM (2010). The ecology of exudate production and exudate feeding in *Saguinus* and *Callimico*. In *The Evolution of Exudativory in Primates* (Burrows AM, Nash LT, eds.), pp 89–108. New York, Springer.

Gillings B, Buonocore M (1961). An investigation of enamel thickness in human lower incisor teeth. *Journal of Dental Research* 40: 105–118.

Grine FE, Stevens NJ, Jungers WL (2001). An evaluation of dental radiograph accuracy in the measurement of enamel thickness. *Archives of Oral Biology* 46: 1117–1125.

Grine FE, Ungar PS, Teaford MF (2002). Error rates in dental microwear quantification using scanning electron microscopy. *Scanning: The Journal of Scanning Microscopies* 24: 144–153.

Hammer Ø, Harper DAT, Ryan PD (2001). PAST: Paleontological Statistics Software Package for education and data analysis. *Palaeontologia Electronica* 4: 1–9.

Harris EF, Hicks JD (1998). A radiographic assessment of enamel thickness in human maxillary incisors. *Archives of Oral Biology* 43: 825–831.

Hogg RT, Ravosa MJ, Ryan TM, Vinyard CJ (2011). The functional morphology of the anterior masticatory apparatus in tree-gouging marmosets (Cebidae, Primates). *Journal of Morphology* 272: 833–849.

Kay RF, Hylander WL (1978). The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia). In *The Ecology of Arboreal Folivores* (Montgomery GG, ed.), pp 173–191. Washington, Smithsonian Institution Press.

Kono RT (2004). Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. *Journal of Anthropological Sciences* 112: 121–146.

Kupczik K, Chattah NL-T (2014). The adaptive significance of enamel loss in the mandibular incisors of cercopithecine primates (Mammalia: Cercopithecidae): a finite element modelling study. *PLoS One* 9: e97677.

López-Torres S, Selig KR, Burrows AM, Silcox MT (in press). The toothcomb of *Karanisia clarki* – was this species an exudate-feeder? In *Behaviour, Ecology and Evolutionary Biology of Lorises and Pottos* (Nekaris KAI, Burrows AM, eds.). Cambridge, Cambridge University Press.

López-Torres S, Selig KR, Prufrock KA, Lin D, Silcox MT (2018). Dental topographic analysis of paromomyid (Plesiadapiformes, Primates) cheek teeth: more than 15 million years of changing surfaces and shifting ecologies. *Historical Biology* 30: 76–88.

Martin RD (1979). *Phylogenetic Aspects of Prosimian Behavior*. New York, Academic Press.

Mittermeier RA, Wilson DE, Rylands AB (2013). *Handbook of the Mammals of the World,* vol III: Primates. Barcelona, Lynx Edicions.

Mitteroecker P, Bookstein F. (2011). Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. *Evolutionary Biology* 38: 100–114.

Nash LT (1986). Dietary, behavioral, and morphological aspects of gummivory in primates. *Yearbook of Physical Anthropology* 29: 113–137.

Nash LT, Burrows AM (2010). Introduction: advances and remaining sticky issues in the understanding of exudativory in primates. In *The Evolution of Exudativory in Primates* (Burrows AM, Nash LT, eds.), pp 1–23. New York, Springer.

Nekaris KAI, Starr CR, Collins RL, Wilson A (2010). Comparative ecology of exudate feeding by lorises (*Nycticebus, Loris*) and pottos (*Perodicticus, Arctocebus*). In *The Evolution of Exudativory in Primates* (Burrows AM, Nash LT, eds.), pp 156–168. New York, Springer.

Noble HW (1969). Comparative aspects of amelogenesis imperfecta. *Proceedings of the Royal Society of Medicine* 62: 1295–1297.

Oates JF (1984). The niche of the potto, *Perodicticus potto*. *International Journal of Primatology* 5: 51–61.

Olejniczak A, Grine F (2006). Assessment of the accuracy of dental enamel thickness measurements using microfocal X-ray computed tomography. *Anatomical Record* 288A: 263–275.

Olejniczak AJ, Tafforeau P, Feeney RNM, Martin LB (2008). Three-dimensional primate molar enamel thickness. *Journal of Human Evolution* 54: 187–195.

Porter LM (2001). Dietary differences among sympatric Callitrichinae in northern Bolivia: *Callimico goeldii, Saguinus fuscicollis* and *S. labiatus*. *International Journal of Primatology* 22: 961–992.

Prufrock KA, Boyer DM, Silcox MT (2016). The first major primate extinction: an evaluation of paleoecological dynamics of North American stem primates using a homology free measure of tooth shape. *American Journal of Physical Anthropology* 159: 683–697.

Rawlins DR, Handasyde KA (2002). The feeding ecology of the striped possum *Dactylopsila trivirgata* (Marsupialia: Petauridae) in far north Queensland, Australia. *Journal of Zoology* 257: 195–206.

Rosenberger AL (1978). Loss of incisor enamel in marmosets. *Journal of Mammalogy* 59: 207–208.

Rosenberger AL (2010). Adaptive profile versus adaptive specialization: fossils and gummivory in early primate evolution. In *The Evolution of Exudativory in Primates* (Burrows AM, Nash LT, eds.), pp 273–296. New York, Springer.

Shellis RP, Hiiemae KM (1986). Distribution of enamel on the incisors of Old World monkeys. *American Journal of Physical Anthropology* 71: 103–113.

Skinner MM, Alemseged Z, Gaunitz C, Hublin J-J (2015). Enamel thickness trends in Plio-Pleistocene hominin mandibular molars. *Journal of Human Evolution* 85: 35–45.

Smith AC (2010). Exudativory in primates: interspecific patterns. In *The Evolution of Exudativory in Primates* (Burrows AM, Nash LT, eds.), pp 45–87. New York, Springer.

Smith TM, Olejniczak AJ, Reh S, Reid DJ, Hublin J-J (2008). Brief communication: enamel thickness trends in the dental arcade of humans and chimpanzees. *American Journal of Physical Anthropology* 136: 237–241.

Sokal RR, Braumann CA (1980). Significance tests for coefficients of variation and variability profiles. *Systematic Biology* 29: 50–66.

Starr CR, Nekaris KAI (2013). Obligate exudativory characterizes the diet of the pygmy slow loris *Nycticebus pygmaeus*. *American Journal of Primatology* 75: 1054–1061.

Starr C, Nekaris KAI, Streicher U, Leung, LKP (2011). Field surveys of the Vulnerable pygmy slow loris *Nycticebus pygmaeus* using local knowledge in Mondulkiri Province, Cambodia. *Oryx* 45: 135–142.

Sussman RW, Kinzey WG (1984). The ecological role of Callitrichidae: a review. *American Journal of Physical Anthropology* 64: 419–449.

Ungar P (2002). Reconstructing the diets of fossil primates. In *Reconstructing Behavior in the Primate Fossil Record* (Plavcan JM, Kay RF, Jungers WL, van Schaik CP, eds.), pp 261–296. New York, Kluwer Academic/Plenum Publishers.

Urciuoli A, Zanolli C, Fortuny J, Almécija S, Schillinger B, Moyà-Solà S, Alba DM (2018). Neutron-based computed microtomography: *Pliobates cataloniae* and *Barberapithecus huerzeleri* as a test-case study. *American Journal of Physical Anthropology* 166: 987–993.

Vinyard CJ, Wall CE, Williams SH, Mork AL, Armfield BA, de Oliveira Melo LC, Valença-Montenegro MM, Valle YBM, de Oliveira MAB, Lucas PW (2009). The evolutionary morphology of tree gouging in marmosets. In *The Smallest Anthropoids: The Marmoset/*Callimico *Radiation* (Ford SM, Porter LM, Davis LC, eds.), pp 395–409. New York, Springer.

Visualization Sciences Group (2009). *Avizo*. Burlington, Mercury Computer Systems.

Wilson DE, Mittermeier RA (2015). *Handbook of the Mammals of the World*, vol V: Monotremes and marsupials. Barcelona, Lynx Edicions.