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Dental sculpting and compensatory shearing crests demonstrated in a Wear series of *Presbytis rubicunda* (Cercopithecoidea, Colobidae) with dental topography analysis

James D. Pampush[1,2] | Paul E. Morse[3,4] | Richard F. Kay[5,6]

[1]Department of Health and Human Performance, High Point University, High Point, North Carolina, USA

[2]Department of Physician Assistant Studies, High Point University, High Point, North Carolina, USA

[3]Department of Cell & Developmental Biology, University of Colorado Anschutz Medical Campus, Aurora, Colorado, USA

[4]Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

[5]Department of Evolutionary Anthropology, Duke University, Durham, North Carolina, USA

[6]Division of Earth and Climate Sciences, Nicholas School, Duke University, Durham, North Carolina, USA

Correspondence

James D. Pampush, Department of Health and Human Performance, High Point University, High Point, North Carolina 27260 USA.
Email: jpampush@highpoint.edu

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Abstract

Objectives: Maintaining effective and efficient occlusal morphology presents adaptive challenges for mammals, particularly because mastication produces interactions with foods and other materials that alters the geometry of occlusal surfaces through macrowear and/or catastrophic failure (i.e. "chipping"). Altered occlusal morphologies are often less effective for masticating materials of given diet—but not always—some species exhibit dental sculpting, meaning their dentitions are set up to harness macrowear to hone their occlusal surfaces into more effective morphologies (i.e. secondary morphologies). Here we show that dental sculpting is present in the folivorous *Presbytis rubicunda* of Borneo.

Methods: Thirty-one undamaged lower second molars of *P. rubicunda* exhibiting various stages of macroscopic wear were micro-CT scanned and processed into digital surfaces. The surfaces were measured for convex Dirichlet normal energy (vDNE, a measure of surface sharpness), and degree of surface wear. Regression analyses compared surface sharpness with several measures of wear to test for the presence and magnitude of dental sculpting.

Results: Positive correlations between the wear proxies and vDNE reveal that *P. rubicunda* wear in such a way as to become sharper, and therefore more effective chewing surfaces by exposing enamel-dentine junctions on their occlusal surfaces and then honing these junctions into sharpened edges. Compared to another primate folivore in which increasing surface sharpness with macrowear has been demonstrated (i.e., *Alouatta palliata*), the worn surfaces are similarly sharp, but the dental sculpting process appears to be different.

Discussion: The results presented here suggest that not only do some primates exhibit dental sculpting and the attendant secondary morphology, but that there appear to be multiple different morphological configurations that can achieve this result. *P. rubicunda* has thicker enamel and a more stereotyped wear pattern than *A. palliata*, although both show positive correlations of occlusal surface sharpness (vDNE) with various wear proxies. These findings shed light on the varied approaches for the maintenance of effective and efficient occlusal surfaces in primates.

KEYWORDS

convex DNE, enamel thickness, folivory, maroon leaf monkey

1 | INTRODUCTION

Chewing—and the teeth for it—are central to what it means to be a mammal because this behavior and attendant morphologies dramatically improve the efficiency of energy/nutrient extraction from food, enabling the evolution of other high-energy-demanding features traditionally considered quintessentially mammalian (Crompton & Parker, 1978; Janis & Fortelius, 1988; Kemp, 2005; Lucas, 2006; Morris et al., 1977; Ungar, 2010; Würsch et al., 1986). As such, chewing adaptations (such as cheek teeth) have been evaluated in an astonishing number of ways (e.g., Berthaume & Kupczik, 2021; Biggerstaff, 1977; Bucinell et al., 2010; Crompton & Parker, 1978; Daegling et al., 2011; Fortelius, 1985; Hiiemae, 1978; Hylander & Johnson, 1997; Janis, 1990; Karme et al., 2016; Lucas & Luke, 1984; Maas & Dumont, 1999; Mills, 1973; Perry et al., 2010; Taylor, 2002; Ungar, 2015; Vinyard & Ravosa, 1998). Yet, one area (among others) worth further exploration is the *change* in chewing-related morphologies throughout the lifespan; thereby exploring presumed morphological adaptations in dynamic context. This work focuses on the maintenance of effective comminution through the lifespan as inferred from molar form. We assume that this will involve a tension between an optimal occlusal geometry needed for efficient and effective break down of food materials versus the inevitable and accumulating alterations to that same occlusal geometry from various sources of wear resulting from normal use (Galbany et al., 2011; Galbany et al., 2014; Galbany et al., 2016; Galbany et al., 2020; Janis & Fortelius, 1988; Teaford, 1981; Ungar & M'Kirera, 2003; Ungar & Williamson, 2000). Below we justify this framework, and then reexamine prior findings of the relationship between wear and tooth sharpness in *Alouatta*, a folivorous platyrrhine, in contrast to a new sample of *Presbytis rubicunda*, a folivorous colobine monkey from South Asia. Using dental topography methods, we ask whether the lower second molars of *P. rubicunda* exhibit dental sculpting: defined below as a means of *maintaining* effective occlusal surfaces for their particular masticatory demands as their surfaces are altered with wear. Contrasting the *P. rubicunda* molars with the previously published wear series from *Alouatta* (i.e., Pampush et al., 2016a; Pampush et al., 2018) alongside data on enamel thickness helps to contextualize these new findings, and generate new hypothesis about the patterns observed when comparing dynamic dental morphologies of primate folivores.

1.1 | Background

Often studied only as morphological "snapshots," dental morphologists have developed models characterizing the relationship between food material properties and the cheek tooth occlusal geometries needed to efficiently and effectively break them down (e.g., Berthaume, 2016; Berthaume et al., 2013; Kay, 1975; Lucas, 2006; Ungar, 2010; Zuccotti et al., 1998). Summarizing these findings when considering the overall shape of the molar occlusal surface, there appear to be two primary competing demands presented by the material properties of food that largely define the functional poles of the mammalian "postcanine morphospace." Stiff, hard, and brittle materials are most efficiently crushed or mashed and require a rounded, pulverizing occlusal arrangement. Flexible but tough materials need to be cut, pierced, or sliced, and teeth must be sharp to optimally achieve this function (Berthaume, 2014; Constantino et al., 2011; Fortelius, 1985; Gregory, 1916; Kay, 1975, 1977, 1978, 1981; Lucas, 2006; Osborn, 1888). These two morphological demands are clearly at cross-purposes and therefore plotting or measuring dental features along this morphological continuum should prove insightful in adaptive contexts. As such, many studies in primates have borne out these model predictions, with leaf-eating species possessing sharp cutting teeth, and hard-object feeding frugivores possessing rounded pulverizing teeth (e.g., Allen et al., 2015; Bunn et al., 2011; Kay, 1975; Kinzey, 1992). Meanwhile some taxa occupy a morphological zone between these distinct form-functional relationships, exhibiting what Lucas has termed "wedge-shaped" teeth (Lucas, 2006). Within primates, most of these characterizations between molar form and food properties are based entirely on observations of teeth in an unworn state. Less studied is how primate dental morphologies cope with macrowear based surface alterations, which must effect chewing efficiency if the form is changed.

One aspect of mammalian oral biology that exacerbates the tension between functionally optimal occlusal geometries and the gradual wearing down of teeth is that most mammals possess a singular set of adult teeth. The vast majority of mammals are diphyodont, which may be a prerequisite for the evolution of precise occlusion, enabling efficient chewing in the first place (Crompton & Jenkins, 1968). But diphyodonty limits the availability of replacing a tooth, as reptiles do, should a tooth become too worn, damaged, or lost all together. One constant among the sprawling interacting combinations of dental morphology and food materials found among mammalian taxa is that nearly all masticatory actions incur some level of dental tissue loss or damage (Agrawal et al., 1997; Constantino et al., 2009; Constantino et al., 2011; Fortelius & Solounias, 2000; Janis, 1984, 1990; Lucas, 2006; Lucas et al., 2013; Lucas & Omar, 2012). While this loss or damage of dental tissue (i.e., enamel, dentine, or cementum) may occur at highly variable rates depending on a wide range of ecological, morphological, and/or behavioral factors (Fortelius & Solounias, 2000; Galbany et al., 2011; Galbany et al., 2020; Spradley et al., 2016; Teaford & Glander, 1996; Ungar et al., 1995), in sufficient quantity it will ultimately transform the shape of the occlusal surface (Cuozzo et al., 2014; M'Kirera & Ungar, 2003; Ungar, 2005; Ungar et al., 2018; Ungar & M'Kirera, 2003; Yamashita et al., 2016; Zuccotti et al., 1998). Changes on the visible macro-scale during adulthood will result in alterations to the occlusal geometry that will almost certainly modify the breakdown efficiency of secondary (permanent) teeth that cannot be replaced. Thus, mammals must address an adaptive challenge: how to *maintain* an occlusal shape capable of efficient and effective comminution while overcoming the lifelong effects of macrowear-induced geometric changes to occlusal morphologies?

Across mammals, there appear to be two broad strategies for the maintenance or optimization of adult dental function in the face of macrowear. In the first case (1), some species appear to have teeth that are set up to resist geometric changes from macrowear, with morphologies aimed at preserving the original occlusal geometry throughout the individual's lifespan. This approach presumably aligns with particular diets, but can be achieved through multiple non-exclusionary morphological, histological, and behavioral adaptations (Kay, 1975; Pampush et al., 2013; Schwartz, 2000). Eventually however, it seems even most of these morphologies will be compromised when the integrity of the teeth fails after a lifetime of repeated loading (Constantino et al., 2010; Lucas et al., 2008; Morse et al., 2023). Conversely (2), other taxa seemingly benefit from macrowear and its attendant occlusal alterations, relying on selective loss of dental tissue(s) to sharpen teeth into more efficient and effective masticatory surfaces, the clear sign of which is the inferred *improvement* of the tooth's ability to reduce the size of chewed food particles with changes from macrowear (Crompton et al., 1994; Fortelius, 1985; Janis & Fortelius, 1988; Lanyon & Sanson, 1986). Many primates clearly fall into the former category, possessing brachydont teeth with rounded, thickly-enameled cusps, whereby the observable lifetime alterations to the occlusal surface do not appear to confer any mechanical advantage, or may even be disadvantageous in the effective breakdown of their dietary materials (Constantino et al., 2010; Lucas et al., 2008; Morse et al., 2023; Sauther et al., 2002). The second strategy (wherein macrowear is harnessed to functionally improve the geometry of the occlusal surface), has seen mixed reporting in *Alouatta* (more below) (cf Anthony, 1994; Dennis et al., 2004; Pampush, Spradley, et al., 2016), but has not been conclusively demonstrated in any other primates.

Recognizing the improved ability of worn ungulate postcanine teeth to process flexible but tough foods like grasses and leaves, Fortelius (1985) coined the term "secondary morphology" to describe the worn, but potentially more efficient state of the cheek teeth. With wear, the occlusal surfaces of hypsodont teeth—with their interposed layers of enamel, dentine, and cementum, each with differing material properties—exhibit sharper features after some macrowear-based "breaking in" period (Damuth & Janis, 2011; Evans et al., 2005; Fortelius, 1985; Fortelius & Solounias, 2000; Janis & Fortelius, 1988; Osborn & Lumsden, 1978; Popowics & Fortelius, 1997). A very similar phenomenon has been observed in the molars of highly folivorous koalas (Lanyon & Sanson, 1986). Describing a process—as opposed to a state—Ungar (2008, 2015) termed the transformation from unworn dental morphology into secondary morphology "enamel sculpting," but at the prompting of a reviewer during a prior publication (i.e., Pampush et al., 2016a) the authors here have settled on the term "dental sculpting," to account for the varied and interacting dental tissues. Regardless of the preferred terminology, while this phenomenon has been clearly observed in ungulates and other mammals (e.g., Fortelius, 1985; Osborn & Lumsden, 1978), no primates possess hypsodont teeth with similar interposed layering of variable dental tissues (with perhaps the exception of *Theropithecus* [Jolly, 1972]), suggesting that primates may generally lack the morphological prerequisites for dental sculpting and secondary morphology (Swindler, 2002; Ungar, 2010).

Despite lacking obvious morphological correlates in their cheek teeth (like hypsodonty and the complex layering of dental tissues), many primate species would seemingly benefit from dental sculpting since they often possess other longevity- or dietary-related characteristics that functionally and logically pair with the phenomenon. For instance, like nearly all mammals, primates are diphyodont—therefore lacking replacement teeth—and this problem is seemingly exacerbated by the unusually long lifespans of primates (Charnov & Berrigan, 1993; Harvey et al., 1987; Hill, 1993; Kappeler, 1996). Furthermore, like ungulates, there are many primate taxa whose diets are composed of large quantities of folivorous materials requiring slicing, piercing, and cutting for efficient processing (Fleagle, 1999; Kay, 1975; Yamashita, 1996, 1998, 2008). These are the very same materials that cause substantial amounts of dietary wear (Janis & Fortelius, 1988), which ungulates seem to harness to produce more effective secondary morphologies, rather than possessing morphologies set up to resist macrowear's surface alterations.

Given the arguments and observations advanced above, naturally there have been several prior attempts to identify dental sculpting in primate taxa, and even to link it to reproductive outcomes. In one interesting but rarely cited work, Anthony (1994) compared molar wear patterns and diets across several primate genera including the platyrrhines *Ateles* and *Alouatta*, the cercopithecoid *Trachypithecus*, and the lemuroids *Lepilemur* and *Hapalemur*. Working from the hypothesis that the exposed enamel-dentine junctions on the occlusal surface function as cutting edges or "compensatory shearing crests," Anthony (1994) documented that relative crest length exhibited a curvilinear relationship to occlusal surface dentine exposure, rising in the early stages of wear before peaking with moderate amounts of wear and declining again with higher wear levels. While the overall pattern was consistent across taxa, Anthony noted that (1994, p. 52), "for any given state of wear, the more folivorous primate always shows a greater degree of relative crest development than the more frugivorous primate." This might indicate that there is some selective pressure for folivores to have longer "compensatory shearing crests" if it can be shown that such crests are in fact sharp enough to be effective in shearing masticatory actions—consistent with our current understanding of chewing dynamics. But such accurate measures and demonstrations have remained mostly speculative in primate dental morphology studies to date, though there have been some developments in methodology necessary to testing the compensatory shearing crest hypothesis.

In a series of seminal papers focused on documenting the changing functional abilities of primate molars through wear series and attempting to show dental sculpting among some primate folivores, Ungar, and colleagues founded the research area of dental topography (Dennis et al., 2004; M'Kirera & Ungar, 2003; Ungar & Williamson, 2000; Zuccotti et al., 1998). They recognized a key challenge: find an informative measurement(s) and protocol(s), which could be universally applied across homology-free surfaces, thereby opening up wear series to functional morphology studies (Ungar & M'Kirera, 2003). Using the tools and software at their disposal, Ungar et al. proposed three ArcGIS[i]-based measures that could be plausibly linked to the cutting ability of an occlusal surface: *slope*, calculated as the surface-wide average angle of deviation from a pre-assigned occlusal plane; *angularity*, measured as the surface-wide average change in localized slope (or the first derivative of *slope*); and occlusal relief (OR), which is a ratio of total surface area of the occlusal portion of the tooth over the occlusal plane footprint. In some way or another, Ungar et al. proposed that these measures would capture the relative cutting ability of the surfaces they analyzed. These proposed measures could be taken from digital estimations of the tooth surfaces produced through scanning and digitally processing teeth (or dental casts), as many researchers have done since (e.g., Berthaume, Lazzari & Guy, 2018b; Ungar et al., 2018; Ungar & M'Kirera, 2003; Ungar & Williamson, 2000; Zuccotti et al., 1998). Using these measures in a dental topography study of howling monkey molars, Ungar et al. showed that while their presumed measures of cutting ability did not increase with wear—nor did they attempt to link their topography measures directly to the lengths of compensatory shearing crests—their *slope* and *angularity* measures did exhibit higher than expected values on the heavily worn *Alouatta* molars (Dennis et al., 2004). In a similar series of studies, using the above measurements, Ungar and colleges explored dental sculpting in a number of other primates including *Pan*, *Gorilla*, several cercopithecoids, and platyrrhines (Bunn & Ungar, 2009; Klukkert et al., 2012; M'Kirera & Ungar, 2003; Ungar et al., 2018). Their findings in *Alouatta* are consistent with their broader body of work such that, while they have not shown any increases in inferred molar cutting ability correlated with dental wear, they have consistently shown that more folivorous taxa tend to maintain higher values of *slope* and *angularity* through wear series than do non-folivorous primates, suggestive of dental sculpting if more accurate measurements can be developed (Bunn & Ungar, 2009; Ungar & M'Kirera, 2003; Ungar & Williamson, 2000; Zuccotti et al., 1998). In another important early dental topography paper using techniques developed by Ungar (2005); King et al. (2005) documented changes in the molar surface structure of the indriid strepsirrhine *Propithecus edwardsi* and noted that they also develop "compensatory shearing crests" as their teeth wear down. The ribbons of exposed enamel-dentine junctions were argued by these authors to be at least as sharp as the initial cusps, presumably prolonging the functional lifespan of the teeth. They then linked this wear pattern to offspring survival, however, recent scholars have had difficulty replicating the offspring-survival results (cf. Heffernan et al., 2022; King et al., 2005).

Building upon Ungar's initial dental topography work by refining digitization protocols and exploring new measurements not restricted to what can be calculated using ArcGIS (Ungar et al., 2018), researchers have added many new dental topography metrics aimed at characterizing the functional properties of teeth (e.g., Berthaume et al., 2019; Berthaume & Schroer, 2017; Boyer, 2008; Evans et al., 2005; Evans et al., 2007; Guy et al., 2013). Dirichlet normal energy (DNE), is one worthy of further examination given its performance in a number of studies. First proposed as an estimate of overall crown curvature (Bunn et al., 2011) this measurement has shown a promising ability to characterize tooth surfaces along expected dietary guidelines in a functionally intuitive way; wherein species expected to need more cutting ability for their diet (e.g., folivores, insectivores) show higher DNE values than those whose diets (e.g., frugivores, hard-object feeders) do not seem to place those same demands on cutting efficiency (Winchester et al., 2014). Taking these results to mean that DNE tracks the cutting ability of teeth, functional morphologists have since deployed it to assess the sharpness of teeth in studies of dietary adaptation (e.g., Berthaume, Delezene & Kupczik, 2018a; Berthaume & Schroer, 2017; Ledogar et al., 2013); and they have been right to do so since its underlying mathematics are built on measuring both the length and relative sharpness of the most aggressively curved features on the surface (Pampush et al., 2022). As a measure of overall sharpness, DNE would seem to be an ideal tool to measure how well a tooth could function in cutting actions, and since it is homology free in its application (i.e., does not rely on identifying specific landmarks on the occlusal surface), this measure could be used to test for dental sculpting and the compensatory shearing crest hypothesis within primates.

Applying DNE to a wear series of *Alouatta palliata* molars, Pampush et al. showed that as these monkeys' teeth wear down, their DNE values climb, indicating an increase in sharpness through the wear series, a result consistent with the dental sculpting hypothesis (Pampush et al., 2016a). In a follow-up, Pampush et al. confirmed some further dental sculpting expectations when showing that the taxonomically similar frugivore *Ateles* sp. did not show increase in DNE through their wear series (Pampush et al., 2018). However, Pampush et al. could not link this increase in *Alouatta* DNE (sharpness) with the lengths of the compensatory shearing crests. Without being able to directly link DNE to compensatory shearing crests, the underlying mechanism explaining how *Alouatta* teeth become sharper remains unclear, and the compensatory shearing crest hypothesis remains unconfirmed. While the DNE estimates of surface sharpness seemed to show trends consistent with many dental sculpting expectations (i.e., worn teeth showed higher DNE values), it remains unclear how this is operationalized within the morphology since the DNE values did not track enamel-dentine junction length in *Alouatta*.

With further scrutiny of the DNE measurement, Pampush et al. (2022) showed that in certain circumstances conventional total-surface DNE can be misleading when used to make functional inferences about diet (as is generally the aim of studies that analyze dental topography) if researchers do not account for exactly what features DNE is measuring on each surface, as well as differences in convexity/concavity ratios on dental surfaces. They suggested a modification of the measurement to only include the outward facing sharpness—the convex portion of the surface—in the assessment of functional surface sharpness and demonstrated how this approach brings the measurement into better alignment with observed dietary habits of extant primates. Additional study of early anthropoids found that total-surface DNE mischaracterizes their low, blunt-cusped molars as being equally sharp as those of extant primate insectivores—a finding that was corrected by using vDNE (i.e., convex-DNE) (Morse et al., 2023). These authors advocated that any future dental topography analyses in functional morphology studies should utilize vDNE

(Morse et al., 2023). Thus, vDNE offers what currently appears to be the best way of capturing the functional surface sharpness of a tooth without need for homologous landmarks. Applying these new techniques and perspectives provides an opportunity to continue exploring dental surfaces as dynamic morphologies. Given the prior attempts with *Alouatta*, it might be best to re-examine those surfaces in light of a new comparative sample from a primate with broadly similar dietary habits that could be expected to also exhibit dental sculpting.

The maroon leaf monkey of Borneo (*Presbytis rubicunda*) offers an interesting case study for exploring dental sculpting in primates and shedding further light on prior findings. A small-bodied member of the folivorous *Colobinae* clade (Napier, 1985), with a body size range of 5.5–7 kg (Mittermeier et al., 2013), these monkeys are roughly the same size as *A. palliata* (5.7–7.5 kg males; 4.7–6.4 kg females (Glander, 2006)). *P. rubicunda* tend to concentrate their diet on young leaves and the tough seeds of forest legumes (Davies et al., 1988), with cheek teeth that are described as having tall crests good for shearing (Lucas & Teaford, 1994; Wright & Willis, 2012). Colobines also have sacculated stomachs to digest the fibrous materials of their diet (Chivers & Hladik, 1980). Studies of *P. rubicunda* wear series compared with other sympatric cercopithecoids have shown some interesting results further underscoring the candidacy as a taxon utilizing dental sculpting. Teaford (1981, 1983) found that the enamel on *P. rubicunda* first molars was perforated relatively quickly, but that the species exhibits relatively less dental wear overall when compared to the cercopithecine *Macaca fascicularis* and another colobine, *Trachypithecus cristata*, suggesting that their moderately worn state is achieved fairly quickly and then maintained—consistent with a dental morphology that has improved performance after being "broken in" by macrowear. The goal of this paper is to use novel dental topography techniques to evaluate whether the formation of secondary morphology arises in *P. rubicunda*; and then marshal data on enamel thickness, and re-examined dental topography results from *Alouatta* (Pampush et al., 2016a; Pampush et al., 2018), to make informed speculations about how this process is operationalized within the primate dental morphology.

2 | MATERIALS AND METHODS

Following previously established protocols (e.g., Pampush et al., 2016a; Pampush et al., 2018; Spradley et al., 2017), 31 mandibles of maroon leaf monkeys (*Presbytis rubicunda*) with variably worn lower second molars selected to sample the widest possible range of wear states from the collection of the Harvard University Museum of Comparative Zoology (MCZ) and the American Museum of Natural History (AMNH) were micro-CT scanned. Scans of MCZ specimens were collected at the Harvard Center for Nanoscale Systems on a Nikon HMX ST 225 while those of AMNH specimens were collected at the Duke Shared Materials Instrumentation Facility on a Nikon XT H 225 ST, with scan resolutions of 25–45 μm across the sample. All specimens were visually inspected to ensure little or no postmortem damage to the second lower molars (e.g., no chips, cracks, or breakage) and for each mandible, the least-damaged second lower molar was chosen for analysis. The full inventory of specimens used in this study is available in SOM 1. The CT scans of the teeth are available through MorphoSource.org, grouped as a project associated with this paper. Reconstructed scans were exported as TIFF stacks, which were imported into Avizo 2021.1 (FEI Houston Hillsboro, OR) where the enameled crown of the second lower molar was segmented from the rest of the tooth root and mandible. During segmentation, any surface imperfections like postmortem fissures, which may interfere with topography measurements were digitally repaired. A surface was generated from the segmented tooth crown using Avizo's "Generate Surface" module without smoothing. This surface was then opened in the Avizo surface editor and cropped to the enamel cervix, so that only a surface representing the occlusal contours and enameled sidewalls remained. The raw surface was simplified and remeshed to 10,000 faces (Pampush et al., 2018)—the value used most consistently among dental topographic studies—and smoothed for 20 iterations with a lambda value of 0.6 in Avizo (Spradley et al., 2017) producing a conservative digital estimation of the surface morphology. Following processing, the digital surfaces were exported as PLY files and imported into molaR v5.3 (Pampush et al., 2016b; Pampush et al., 2022) for measurement within the R statistical computing environment (R Core Team, 2017). The analyzed surfaces are available within SOM 1.

Using molaR, two dental topography measures were collected. First, relief index (RFI) was collected following Boyer (2008), using molaR's RFI() function with default settings. Intra-specific studies have shown that RFI declines with dental wear proxies such as dentine exposure ratio (DER), making it a useful within-species surrogate for the state of wear, which does not rely on measuring dentine exposure (Glowacka et al., 2016; Morse et al., 2023). The inverse of RFI (RFI^{-1}) was used as a proxy for wear to make it more intuitively similar to that of traditional wear proxies such as dentine exposure, where an increase in the metric corresponds to greater specimen wear (Morse et al., 2023). Second, convex Dirichlet normal energy (vDNE, see: Pampush et al., 2022) was measured on the digital surfaces using the default arguments of the DNE() function in molaR v5.3. All surfaces and topography measures were checked for accuracy via 3D surface plotting and visual inspection with tools from the R package molaR v5.3.

In addition to the RFI topography measurement, two other measurements of wear reliant on dentine exposure were collected from scaled 2D occlusal surface photographs in ImageJ (Abràmoff et al., 2004). DER, measured as the area of exposed dentine on the occlusal surface divided by the total occlusal surface area, and scaled enamel-dentine-junction length (EDJL) measured as the perimeter of exposed dentine relative to the length of the tooth. The first measure (DER) is a traditional and commonly collected measure of wear, sometimes called percentage of exposed dentine (PED) (e.g., Galbany et al., 2011; Galbany et al., 2020; Kay & Cant, 1988; King et al., 2005; Ungar & Williamson, 2000). The second (EDJL) might predict the relative length of compensatory cutting edges on the hypothesis that the boundary between enamel and exposed dentine hones into an edge as sharp—or sharper—than the original, pristine crests (Anthony, 1994; King et al., 2005). All variables were checked for normality via Shapiro–Wilks test in R. Relationships were tested among the two wear proxies (RFI^{-1} and DER), the estimate of compensatory cutting-edge length (EDJL), and against vDNE using simple least squares regression in base R. Due to high levels of collinearity among the wear variables, we did not perform a multiple regression model and instead opted to explore each variable combination independently.

To further explore the relationship between dental morphology and dental sculpting, enamel thickness values were collected from the two least worn *P. rubicunda* specimens in our sample (MCZ-37368, and MCZ-35686). Using Avizo 2021.1, volume renderings of the scans of these two teeth were globally aligned and then digitally sectioned through the mesial (protoconid and metaconid) cusp pairs (Figure 1). 2D lines were drawn crossing the cervical margin and then photographs of these digital sections, including a scale bar generated in Avizo, were imported into ImageJ and the following variables were measured: area of the enamel cap, length of the enamel-dentine junction, and dentine area under the enamel cap above the cervical margin. From these measures a commonly used dimensionless thickness measure, relative enamel thickness (RET), was calculated as: $\frac{AET}{\sqrt{c}} \times 100$, where AET is the average thickness of the enamel cap in the section, and *c* is the area of the dentine below the enamel crown above the cervical margin (Andrews & Martin, 1991; Grine & Martin, 1988; Martin, 1985; Martin et al., 2003; Olejniczak et al., 2008; Pampush et al., 2013; Schwartz, 2000; Smith et al., 2005). To better contextualize the *P. rubicunda* enamel thickness values, RET and DER values were collected from the literature and opportunistically from digitized specimens in our collections following the protocols above. Finally, we provide some qualitative observations about the wear series in *P. rubicunda*.

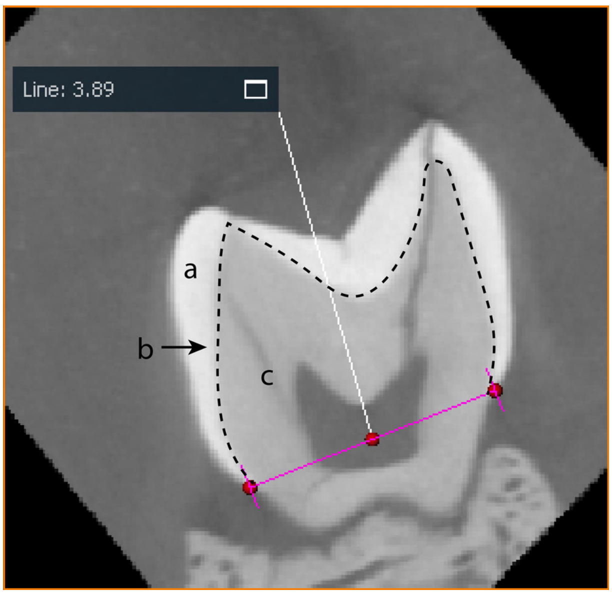

FIGURE 1 Digital cross-section of *Presbytis rubicunda* second mandibular molar (M_2) through the mesial cusp pair (protoconid and metaconid) of MCZ-37368. The line used for scaling was added in Avizo and is 3.89 mm long. a = the enamel cap, b = dashed line and is the enamel-dentine junction, c = the dentine area under the enamel cap. Left is buccal.

Finally, digital *A. palliata* surfaces published previously by Pampush et al. (2018; 2016a), and Morse et al. (2023) were re-analyzed alongside the *P. rubicunda* specimens. The vDNE metric—developed since the *Alouatta* specimens were first analyzed—as well as measures of enamel thickness were taken from the scanned *Alouatta* teeth to contextualize these new findings in *P. rubicunda*.

3 | RESULTS

Results of the linear least-squares regressions between our estimate of surface sharpness (vDNE) and two wear proxies (DER and RFI^{-1}), as well as our estimate of surface blade length (EDJL) in *P. rubicunda* are presented in Table 1. Our estimate of surface sharpness, vDNE, is positively correlated with both estimates of wear (DER, $p < 0.001$; and RFI^{-1}, $p < 0.001$). vDNE is also positively correlated with EDJL ($p = 0.002$). For comparison, the same correlations performed in *A. palliata* from Morse et al. (2023) are presented in Table 2. Correlations among the wear variables (DER and RFI^{-1}) as well as between EDJL and the wear variables are presented in Table 3. As expected, the two wear variables track one another (DER vs RFI^{-1}, $p < 0.001$), as well as predict the relative length of exposed enamel-dentine junction (EDJL, $p < 0.001$). Again, the same analyses performed in *A. palliata* from Morse et al. (2023) correlating DER, RFI^{-1}, and EDJL among each other are presented in Table 4. Raw values of DER, RFI^{-1}, EDJL, and vDNE for each specimen is provided in SOM 1.

TABLE 1 Linear regression models of vDNE versus wear variables in *Presbytis rubicunda*.

Variable	Coefficient	DF	*t*-value	r^2	*p*-value
DER	79.395	1, 29	4.123	0.347	<0.001
EDJL	7.605	1, 29	4.379	0.377	<0.001
RFI^{-1}	52.140	1, 29	3.326	0.251	0.002

Abbreviations: DER, dentine exposure ratio; EDJL, enamel-dentine-junction length; RFI, relief index; vDNE, convex Dirichlet normal energy.

TABLE 2 Linear regression models of vDNE versus wear variables in *Alouatta palliata*.

Variable	Coefficient	DF	*t*-value	r^2	*p*-value
DER	103.040	1, 17	2.444	0.217	0.025
EDJL	25.971	1, 17	2.624	0.246	0.018
RFI^{-1}	72.013	1, 17	2.164	0.169	0.045

Abbreviations: DER, dentine exposure ratio; EDJL, enamel-dentine-junction length; RFI, relief index; vDNE, convex Dirichlet normal energy.

TABLE 3 Linear regression models of wear variables and enamel-dentine-junction length in *Presbytis rubicunda*.

Variable	Coefficient	DF	*t*-value	r^2	*p*-value
DER versus EDJL	0.137	1, 29	9.134	0.733	<0.001
DER versus RFI^{-1}	0.528	1, 29	6.132	0.549	<0.001
RFI^{-1} versus EDJL	0.154	1, 29	5.032	0.448	<0.001

Abbreviations: DER, dentine exposure ratio; EDJL, enamel-dentine-junction length; RFI, relief index; vDNE, convex Dirichlet normal energy.

TABLE 4 Linear regression models of wear variables and enamel-dentine-junction length in *Alouatta palliata*.

Variable	Coefficient	DF	*t*-value	r^2	*p*-value
DER versus EDJL	0.020	1, 17	0.354	0.051	0.727
DER versus RFI^{-1}	0.561	1, 17	4.289	0.491	<0.001
RFI^{-1} versus EDJL	1.046	1, 17	1.403	0.051	0.179

Abbreviations: DER, dentine exposure ratio; EDJL, enamel-dentine-junction length; RFI, relief index; vDNE, convex Dirichlet normal energy.

TABLE 5 Enamel thickness table.

Species	Source	*N*-tooth type	RET species weighted-$\bar{X}$
Alouatta palliata	This study	2-M_1	7.958
Cacajao calvus	Martin et al., 2003	1-M_2	9.84
Chiropotes satanas	Martin et al., 2003	2-M_2	10.35
Gorilla gorilla	Shellis et al., 1998 Martin, 1985	1-M_2 4-M_2	10.59
Erythrocebus patas	Shellis et al., 1998	2-M_2	12.28
Papio cynocephalus	Shellis et al., 1998	1-M_2	12.43
Presbytis rubicunda	This study	2-M_2	12.503
Macaca mulatta	Shellis et al., 1998	3-M_2	13.15
Pan troglodytes	Smith et al., 2005	9-M_2	13.40
Theropithecus gelada	Shellis et al., 1998	3-M_2	14.66
Cebus capucinus	Dumont, 1995	3-M_1	15.13
Pongo pygmaeus	Smith et al., 2005	8-M_2	16.33
Cercocebus torquatus	Dumont, 1995 McGraw et al., 2012	3-M_1 1-M_2	17.86
Lophocebus albigena	Dumont, 1995 McGraw et al., 2012	2-M_1 1-M_2	18.32
Cercocebus atys	Daegling et al., 2011	3-M_2	19.66
Sapajus apella	This study	4-M_2	20.133

Average RET values for 16 extant anthropoids taken from the literature are presented in Table 5, including the data collected from our digital sample of *P. rubicunda* and *A. palliata* teeth. Note that the *A. palliata* specimens are the thinnest of this diverse set, while the *P. rubicunda* fall out with a roughly average RET.

The wear patterns in *P. rubicunda* second molars follow a stereotyped sequence (refer to Figure 2): (1) the sequence begins with an unworn tooth except for occasional small perforations in the lingual cusps (metaconid and entoconid), although these perforations are inconsistent and do not tend to expand until much later in the wear-series. (2) Perforations (dentine lakes) first appear on the buccal cusps (protoconid and hypoconid) at the junction between the cusp and transverse crest. (3) Buccal cusp perforations expand into lingually pointed chevrons along the adjacent crests, while fingers of dentine are exposed in the trigonid and distal basins in a kind of converging "E" shape. (4) Chevrons of exposed dentine migrate further lingually across the transverse crests as more dentine is exposed in the trigonid and distal basins. The two dentine pools between the buccal cusps coalesce at later stages of wear, although the talonid basin remains at least partly enameled. (5) Dentine pools fully coalesce: Only a coherent rim of enamel remains around the crown, with fingers of enamel penetrating into the central trigonid basin of the tooth tracing the outlines of the former transverse crests. Enamel in the interposed basins is mostly worn away, yet, despite extreme enamel loss the highest observed DER values are only at ~0.45, whereas *P. badius* and *A. palliata* have shown DER values above 0.80 (Morse et al., 2013; Pampush

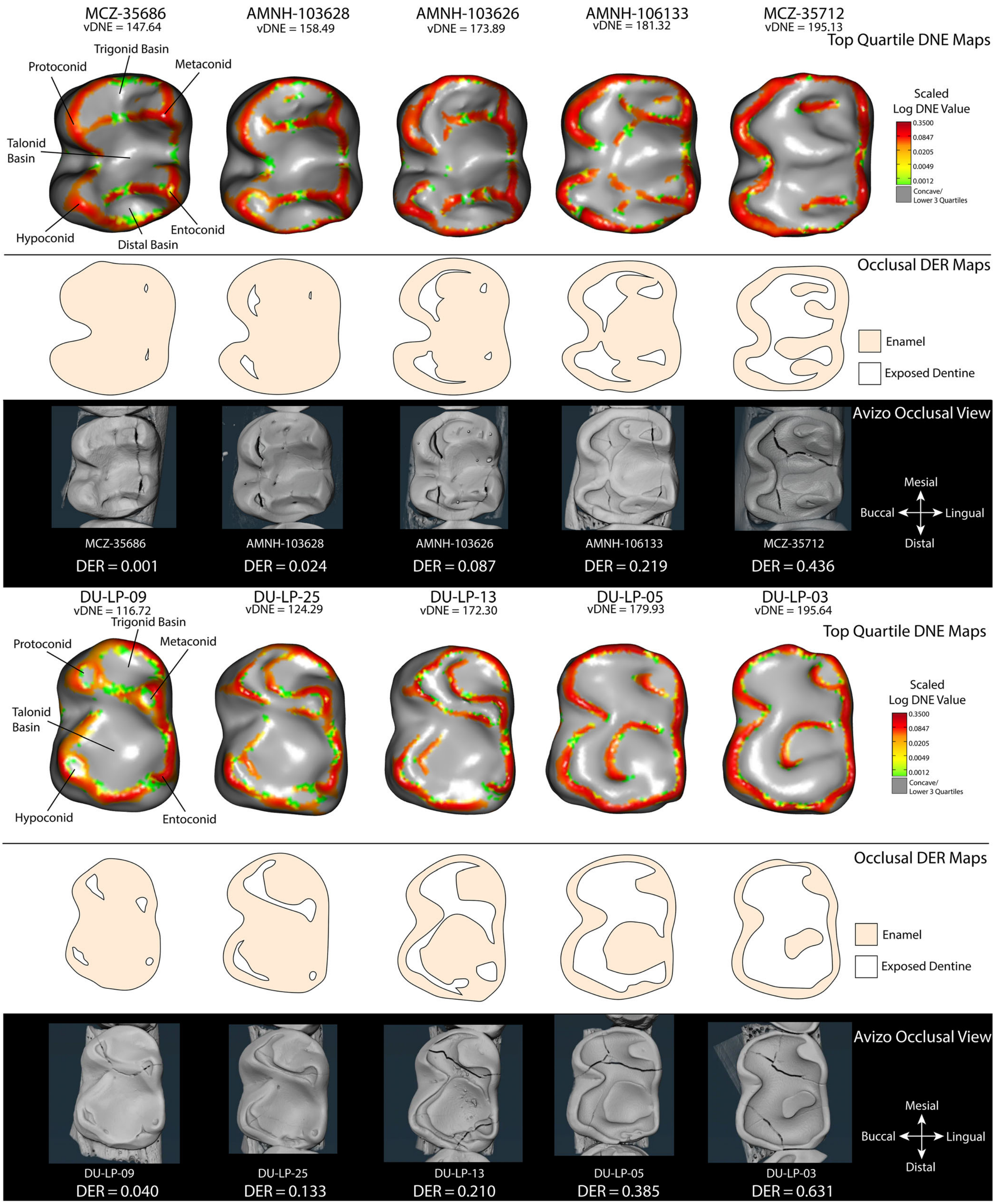

FIGURE 2 Maps of surface features depicting the five representative teeth marked maroon and blue in Figure 3. Top set of figures are of *Presbytis rubicunda* and bottom set are of *Alouatta palliata*. Top row in each set depicts convex Dirichlet normal energy (vDNE) surface maps showing only the top quartile of convex faces. Note that the highest areas of sharpness are found around the rim of the occlusal surface as well as along the transverse lophs and area of exposed enamel-dentine junction. While only making up 25% of the total surface, these aspects of the teeth account for more than 70% of the total vDNE on each surface. Second row in each set shows cartoon depictions of dentine exposure on the occlusal surface. Bottom row in each set is of occlusal views of the scanned surfaces taken from Avizo 2021.1.

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et al., 2016a). In these most worn teeth, the observed sharpness is primarily associated with the narrow rim of the enamel encircling the occlusal surface. Qualitatively, this wear pattern is very similar to the one described in *P. edwardsi* (King et al., 2005), although that taxon appears to exhibit relatively more wear on their molars, and has not been measured for vDNE and EDJL.

4 | DISCUSSION

The teeth of *P. rubicunda* seem to demonstrate dental sculpting. Regardless of the chosen wear variable (DER or RFI^{-1}), as the teeth of *P. rubicunda* in our cross-sectional sample show higher levels of wear, their estimated surface sharpness—as measured with vDNE—tends to increase (Table 1, Figure 3). When compared with an additional measurement—scaled enamel-dentine junction length (EDJL)—which is an estimate of the relative length of the "compensatory shearing blades" (see: Anthony, 1994; King et al., 2005), vDNE is once again positively correlated (Table 1, Figure 3) suggesting that it is the exposed enamel-dentine junctions that are contributing most to this increase in surface sharpness. Examining the interaction between DER and EDJL (Table 3, Figure 4), shows a predictable curve where higher rates of DER correlate curvilinearly with higher values of EDJL, which both correlate with higher vDNE values. Specimens, which fall off the curve, have lower EDJL values and correspondingly lower vDNE values. Unlike the DER:EDJL relationships observed in prior studies (e.g., Morse et al., 2013), the *P. rubicunda* specimens never exhibit a decline in EDJL. This is likely the product of not having extremely worn specimens in the sample despite exhaustive attempts

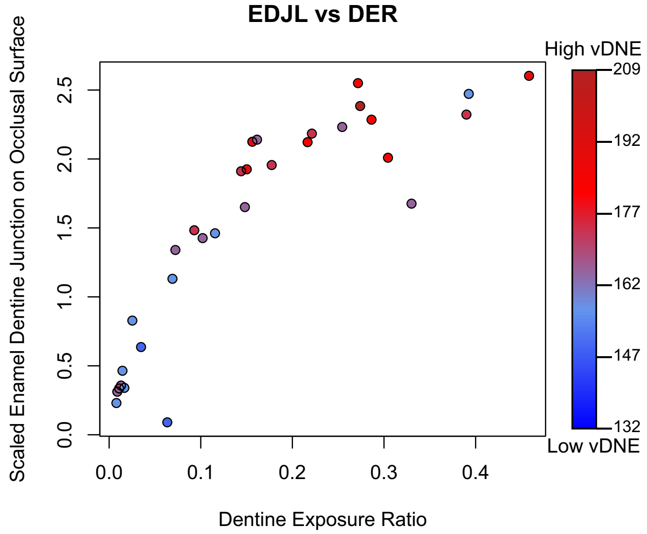

FIGURE 4 Scatter plot of scaled enamel-dentine junction length (EDJL) against dentine exposure ratio (DER) and color scaled for convex Dirichlet normal energy (vDNE).

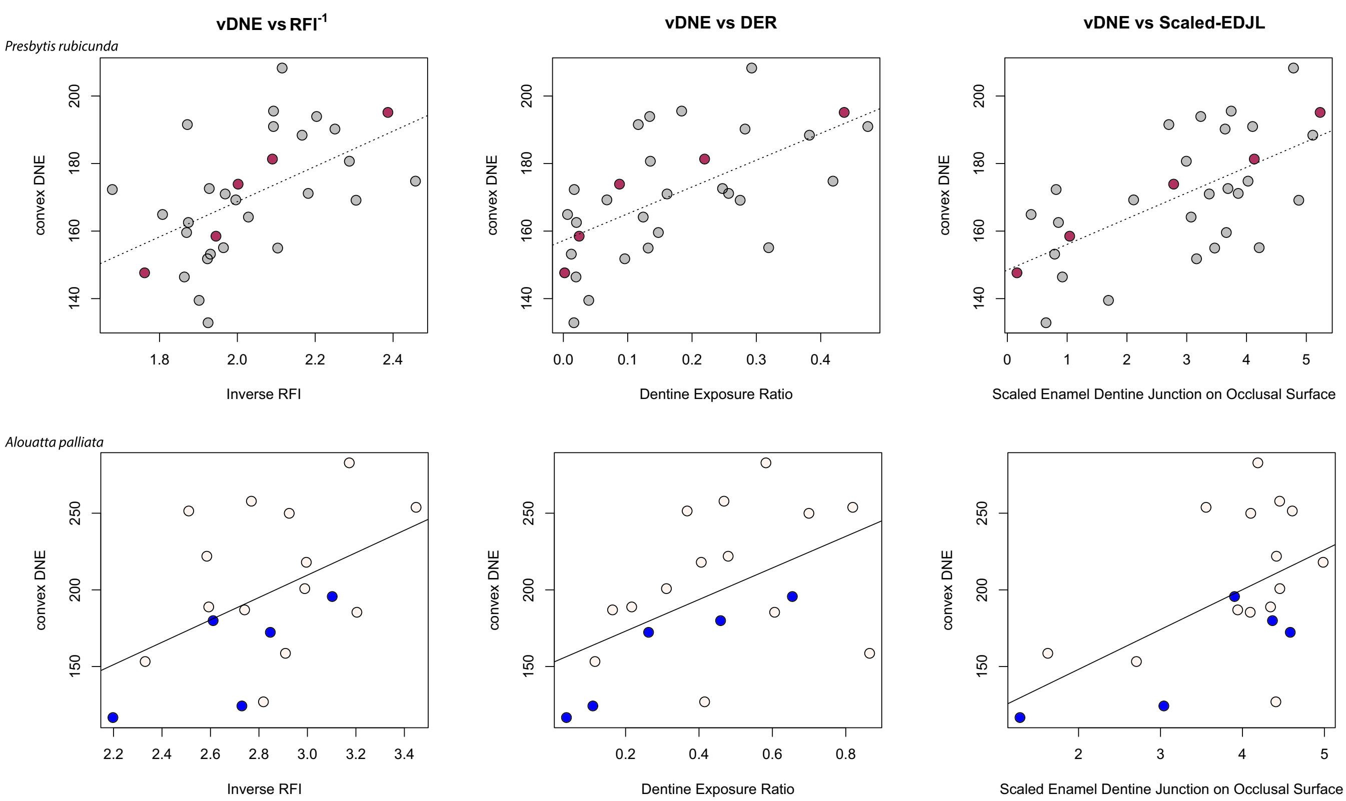

FIGURE 3 Scatter plots of convex Dirichlet normal energy (vDNE) against two measures of wear; inverse relief index (RFI^{-1}) and dentine exposure ratio (DER); as well as against the scaled estimate of compensatory shearing crest length (EDJL). Top row of figures shows *Presbytis rubicunda* and bottom row shows *Alouatta palliata*. Maroon and blue highlighted points are the same teeth depicted in Figure 2.

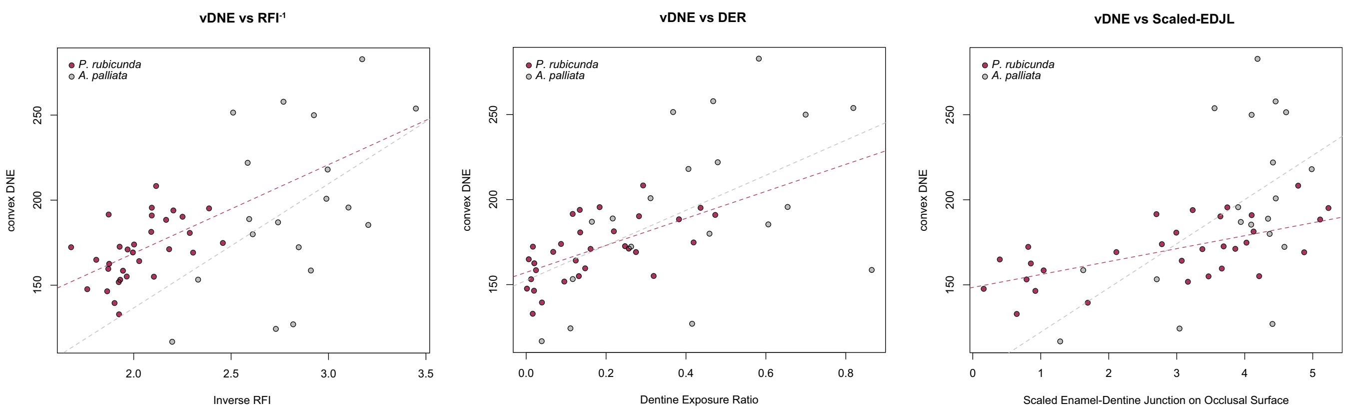

FIGURE 5 Scatter plots of convex Dirichlet normal energy (vDNE) against two measures of wear; inverse relief index (RFI^{-1}) and dentine exposure ratio (DER); as well as against the scaled estimate of compensatory shearing crest length (EDJL) for both *Alouatta palliata* (gray) and *Presbytis rubicunda* (maroon).

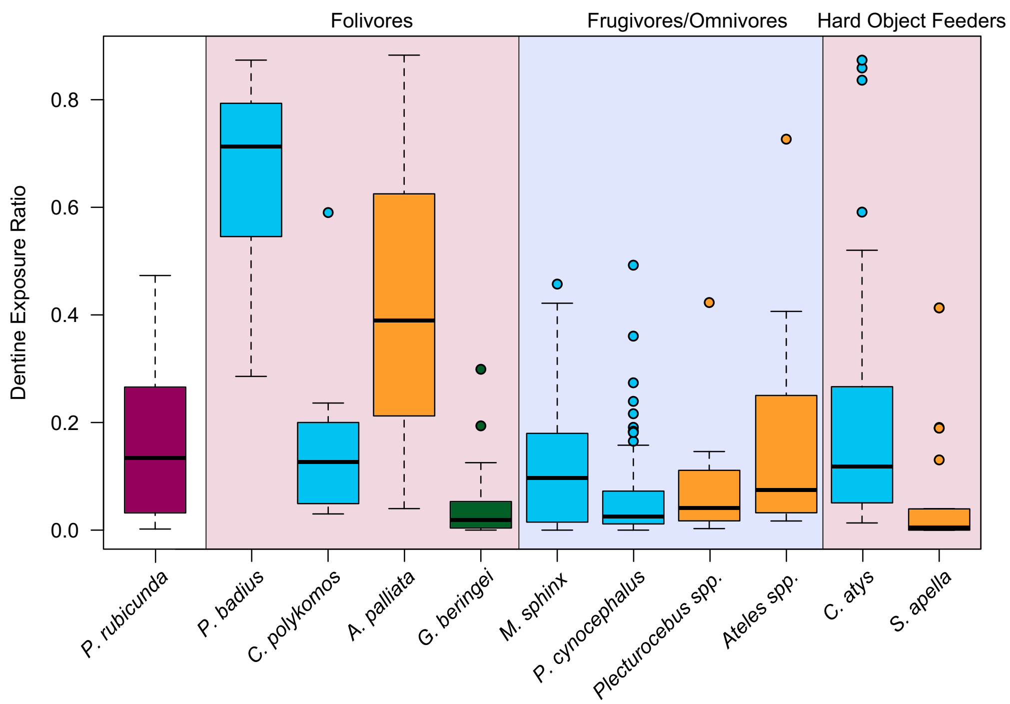

FIGURE 6 Box plots of Dentine exposure ratio of *Presbytis rubicunda* (depicted in maroon) and other taxa taken from the literature. Catarrhine monkeys are colored in blue, platyrrhine monkeys colored in orange, and great apes depicted in green. Taxa are organized left to right on the basis of their traditional heuristic dietary classifications (i.e., Folivores, Frugivores, and Hard Object feeders). *P. rubicunda* set apart in maroon at the left. Data from the following sources: *Piliocolobus badius*, *Colobus polykomos*, and *Cercocebus atys* from Morse et al., 2013. *Plecturocebus* sp. and *Sapujus apella* from Morse et al., 2023. *Papio cynocephalus* from Galbany et al., 2011. *Mandrillus sphinx* from Galbany et al., 2014. *Gorilla beringei* from Galbany et al., 2016. *Alouatta palliata* and *Ateles* sp. from Pampush et al., 2018.

to sample the entire wear-range of the species. To be clear, we suspect extremely worn samples to exist, we just have not been able to find any in the many museum collections we have visited. Together this paints a compelling picture that macrowear generates new cutting edges on the occlusal surface of *P. rubicunda* molars via honing of the exposed enamel-dentine junctions into cutting features, confirming—at least in this species—the compensatory shearing crest hypothesis (see Anthony, 1994; King et al., 2005).

While there is a clear and explainable relationship between EDJL and surface sharpness in *P. rubicunda*, consistent with the compensatory shearing crest hypothesis, Pampush et al. (2016a) failed to show the same relationship between DNE (note, not vDNE) and EDJL in *A. palliata*, a finding confirmed again using vDNE (Table 2). Despite this, the *A. palliata* sample presented by Pampush et al. (2016a) and reanalyzed for vDNE by Morse et al. (2023) shows that sharpness increases on these teeth as they wear (using DER and RFI^{-1} as wear

TABLE 6 Measures of average length and breadth of *Alouatta palliata* first lower molars and *Presbytis rubicunda* second lower molars used in this study.

Species	N	$\bar{X}$ length (mm)	$\bar{X}$ breadth (mm)	$\bar{X}$ occlusal area (mm^2)
Alouatta palliata	10	8.21	6.40	52.54
Presbytis rubicunda	31	5.62	4.99	28.04

proxies). This suggests that *A. palliata* is engaging in dental sculpting via a mechanism other than a simple increase in compensatory shearing crest length, which is further supported by the more chaotic distribution of *A. palliata* specimens in plots of vDNE vs. the wear proxies (DER and RFI^{-1}) and EDJL (Figures 2 and 5). There are other morphological differences between *P. rubicunda* and *A. palliata*, which suggest that the two species are arriving on dental sculpting through different processes and morphological configurations. For one, *A. palliata* has some of the thinnest RET measured in any primate (RET = 7.95), whereas *P. rubicunda* shows RET values (RET = 12.50) near the middle of the pack (see Table 5). The much thinner enamel of *A. palliata* might account for the significant differences in DER values between the two species (Figure 6). Although it should be underscored that the samples of *A. palliata* and *P. rubicunda* used in this study were acquired quite differently, and represent different tooth positions. The majority of the *A. palliata* sample is derived from Duke University's Glander Collection, which was amassed through opportunistic collections of deceased individuals found at the La Pacifica field site in Costa Rica (see Glander, 1975; Glander et al., 1991). Documentation associated with the MCZ and AMNH indicate that almost all of the *P. rubicunda* specimens in their collections were wild-shot in Borneo during several specimen collecting expeditions in the 1930s. Thus, the Glander collection is analogous to a "cemetery" population, whereas the specimens from the MCZ and AMNH are "catastrophic assemblages" and more likely to be "snapshots" of the living population, potentially accounting for the differences in DER (see Wood et al., 1992). Additionally, Pampush et al. (2016a) had opted to use first molars in their initial study so as to increase the range of wear sampled. Since that study, it has become standard to use second lower molars and so perhaps the *A. palliata* specimens are more worn compared to the *P. rubicunda* presented here because the data are taken from different tooth positions, although it is worth noting that these species have differing numbers of adult teeth, and in terms of places from most mesial they occupy the same rank. Furthermore, despite being very similar in body size, *A. palliata* possesses much larger postcanine teeth than *P. rubicunda*. Post hoc data on tooth size collected from the specimens scanned for this study are presented in (Table 6), demonstrating the larger molar size of *A. palliata* compared to *P. rubicunda*. Perhaps the morphological arrangement *A. palliata* has acquired to produce dental sculpting is one where enlarged occlusal surfaces with exceptionally thin enamel are allowed to stochastically perforate and hone any available enamel edges into cutting surfaces (see Figure 2). Bolstering this speculation, some prior researchers have noted that there seems to be strong selection for tooth size in *A. palliata* (DeGusta et al., 2003). Finally, unlike *A. palliata*, *P. rubicunda* possesses classic cercopithecoid bilophodont molars. The wear pattern seen in *P. rubicunda* molars has enamel perforations, which trace along the transverse lophs of the tooth from buccal to lingual. The bilophodont structure of these teeth may be the reason for the clear linear relationship between the scaled enamel-dentine junction length measure and vDNE, and may also account for the lack of clear relationship in those variables in *A. palliata*.

Teaford (Teaford, 1981, 1983) observed some of these same patterns in *P. rubicunda* wear series; indeed, even using many of the same specimens. He noted that the buccal cusps are the first to perforate and expand from continued wear. This might suggest that the buccal and lingual cusps have different roles in that the lingual cusps are used more in puncture crushing, while the buccal cusps are more often engaged in shearing actions (Teaford, 1983), but this remains speculative. It may also be reflective of shearing during Phase I occlusion (Janis, 1990; Ungar, 2015), wherein the mandibular molars approach the maxillary molars in an upward and lingual direction, dragging transversely across the upper molar surface. Thus, the observed wear pattern on these teeth suggests that foods are sheared primarily in Phase I of occlusion, as supported by jaw movement and force transmission studies of another cercopithecoid monkey by Wall et al. (2006).

It has been proposed that thin enamel on the molars of some primates may be an adaptation to folivory, since rapid perforation could permit exposed enamel-dentine junctions to act as accessory shearing crests (Kay, 1981; Rensberger, 1973; Schwartz, 2000; Ungar & Williamson, 2000; Walker & Murray, 1975). When compared to other extant anthropoids for which RET data is available, *P. rubicunda* has a RET value roughly average among primates (Table 5). Many of the taxa with reported RET values possess thinner enamel than *P. rubicunda*, and some of these taxa are folivorous, but not all. At present, many of the more thinly enameled primate species do not have enamel thickness values reported in the literature. It will be revealing to explore RET in a larger sample of closely related taxa with differing diets, and to connect these findings to changes in dental topography through wear series.

5 | CONCLUSIONS

The relationships presented here between wear and surface sharpness in *P. rubicunda* molars serve as examples of dental sculpting and secondary morphology in this folivorous primate. As enamel is perforated on the occlusal surface—according to our measure of surface sharpness (vDNE)—sharper and longer shearing crests are added. This provides support for the hypothesis that some primates use these exposed junctions between enamel and dentine (so called "compensatory shearing crests") to cut fibrous materials in their diets, and further suggests that at least some primate taxa embrace macrowear to extend, or even enhance, the functionality of their dentition. The presumption is that many primate folivores tend to have thin enamel to facilitate the perforation of enamel and elongation of enamel-dentine junctions on the crown surface, and yet, *P. rubicunda* possess RET values roughly average among those other primates reported in the literature. Despite this, *P. rubicunda* manages to perforate its enamel relatively quickly (in terms of its lifespan) and the species does so with a stereotyped pattern (based on the specimens we examined). Interestingly, while *P. rubicunda* perforate the enamel on their occlusal surfaces relatively quickly (as compared to other similar species) they then maintain a moderate level of wear for a long duration, indeed, it is difficult to find specimens with extreme states of wear in which more than half of the occlusal enamel is lost. This may suggest that these animals have particular portions of their occlusal surfaces that are set up to be perforated, and others, which will maintain enamel coverage for long durations as a potential mechanism for the maintenance of their dental functionality. This may be an example of a primate clearly engaging in dental sculpting (termed "enamel sculpting" by Ungar, 2008) to form secondary morphology (sensu Fortelius, 1985).

AUTHOR CONTRIBUTIONS

James D. Pampush: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); software (equal); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Paul E. Morse:** Conceptualization (equal); data curation (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); software (equal); visualization (equal). **Richard F. Kay:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); software (equal); supervision (equal); validation (equal); visualization (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

All the raw data as well as the digital surfaces made to calculate the topography values are available in R-data object SOM 1. Within SOM 1, dat is a dataframe containing all raw data, DNEsurfaces contains the DNE objects produced by the molaR 5.3 function DNE(), which includes the raw digital surfaces. The original MicroCT scans are available on MorphoSource.org in a project titled with this manuscript.

ORCID

James D. Pampush https://orcid.org/0000-0003-0867-8310
Paul E. Morse https://orcid.org/0000-0003-3318-3862
Richard F. Kay https://orcid.org/0000-0002-4219-7580

ENDNOTE

[i] ArcGIS is a software program first released in 1982 by Esri LLC. The letters GIS stand for "geographic information system" and the term "Arc" is a legacy of the original beta program "ArcInfo" where "arc" is a reference to the spatial map connection between two data points. This software is commonly used in archeological, ecological, and geographical studies.

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