Adaptive wear-based changes in dental topography associated with atelid (Mammalia: Primates) diets

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Primates are generally characterized by low-crowned, brachydont molars relative to many other groups of mammals. This conservative architecture may create special challenges for maintaining dental functionality in the case of a diet requiring proficient shearing ability (e.g. folivory). One recent hypothesis, the ‘dental sculpting hypothesis’, suggests that some folivorous primates have dentitions that functionally harness macrowear in maintaining occlusal sharpness. We examined the relationships between four dental topography metrics [Dirichlet normal energy (DNE), orientation patch count rotated (OPCR), relief index (RFI) and occlusal relief (OR)] against macrowear [as measured by the dentine exposure ratio (DER)] in lower first molars of Ateles and Alouatta, which are two closely related platyrrhines with different diets (Alouatta is a folivore and Ateles a frugivore). We find support for the dental sculpting hypothesis, in that DNE increases with macrowear in the folivorous Alouatta but not in the frugivorous Ateles. Multiple contradictions between OPCR and the other variables suggest that this metric is a poor reflection of the molar form–function relationship in these primates. Distributions of relief measures (RFI and OR) confound expectations and prior observations, in that Ateles shows higher values than Alouatta, because these measures are thought to be correlated with dental shearing ability. We discuss the role that the relatively thicker enamel caps of Ateles might play in the distributions of these metrics.


INTRODUCTION

Worn mammalian teeth have presented an interesting challenge for functional anatomists. Regarding the general prevalence of and methodological difficulties posed by, worn teeth, Ungar & Williamson (2000: 2) remarked:

The fundamental fact that teeth wear has been the bane of dental functional anatomists for decades. Researchers have known for a very long
time that tooth form reflects function in living mammals, and they have conducted very elegant studies to demonstrate relationships between aspects of occlusal morphology and diet within various mammalian orders. Most such studies have been limited to unworn and slightly worn teeth. The problem with this is that teeth change shape as they wear, and natural selection does not stop when this happens.

These authors point to a potentially fertile area of research with these observations. In many mammalian taxa, worn teeth have been underrepresented in functional analyses (but see references below). Yet, as noted by Ungar & Williamson (2000), natural selection is continuously active throughout the entire dental life cycle, which often includes forms dramatically altered by dental wear. A natural follow-up observation is that mammals possess different modes of tooth wear (Fortelius, 1985; Janis & Fortelius, 1988; Janis, 1990). Differences in tooth wear modalities may reveal clues to how natural selection has shaped mammalian teeth to cope with and/or harness wear in maintaining or promoting dental functionality.

These questions and problems are likely to apply to all heterodont, unreplaced mammalian dentitions, but these issues might be especially acute in primates. Primates are generally characterized by low-crowned, brachydont teeth (Kay, 1975; Swindler, 2002) and long lifespans (Harvey et al., 1987) compared with many hypsodont or hypselodont mammals. This combination frequently results in older individuals with occlusal anatomies greatly modified from their original unworn forms (King et al., 2005; Cuozzo & Sauther, 2006; Morse et al., 2013; Ungar, 2015; Glowacka et al., 2016; Yamashita et al., 2016). Additionally, unlike taxa possessing hypselodont teeth, it has been proposed that the brachydont teeth of primates do not appear to be ‘designed to wear’ (M’Kirera & Ungar, 2003; Ungar & M’Kirera, 2003; Dennis et al., 2004; King et al., 2005; Ungar, 2005; Lucas, 2006; Berthaume, 2014; Godfrey et al., 2016; Glowacka et al., 2016; Pampush et al., 2016a).

In contrast, functional studies of ungulate and rodent dentitions have generally focused on worn but not senescent teeth (Brodie & Tobiasz, 1934; Baker et al., 1959; Fortelius, 1985; Janis & Fortelius, 1988; Fortelius & Solounias, 2000; Kaiser & Fortelius, 2003; Damuth & Janis, 2011; Saarinen et al., 2015). These ‘broken-in’ hypsodont teeth are said to exhibit a secondary morphology, distinct from the unworn primary morphology (Fortelius, 1985). In the case of ungulates and other hypsodont taxa, the secondary morphology of their occlusal surfaces is characterized by long, juxtaposed ribbons of enamel and dentine (and sometimes cementum), whose junctions form continuously sharpened edges (Fortelius, 1985; Popowicz & Fortelius, 1997; Fortelius & Solounias, 2000). These honed edges are presumed to be effective for cutting up fibrous plant material. Such high-crowned teeth interact with an abrasive diet to create and maintain sharpened occlusal blades throughout the tooth lifespan.

Primate teeth, in contrast, are not high crowned, nor does any primate possess teeth with interposed layers of enamel and dentine (Kay, 1975; Swindler, 2002) capable of producing an ungulate-like secondary morphology (with the possible exception of Theropithecus; see Jablonski, 1994). Nevertheless, several studies of macrowear on primate teeth have attempted to link wear-based changes in occlusal morphology to dietary characteristics (Janis, 1984; Anthony, 1994; Galbany et al., 2011; Morse et al., 2013; Yamashita et al., 2016), environmental agents (Rabenold & Pearson, 2011, 2014; Spradley et al., 2016) or more removed measures of reproductive fitness (King et al., 2005).

Recognizing both the methodological difficulties of working with worn teeth and the potential insights to be gained from studying them, Ungar & Williamson (2000) proposed using the tools and techniques of geographical information systems (i.e. topography) to side-step the macrowear-based obliteration of comparative landmarks. Since their seminal paper, many others have introduced topography-based techniques or performed studies on primates using dental topography. Additionally, Ungar and colleagues have continued to develop new tools for measuring dental topography (Ungar & M’Kirera, 2003; Ungar, 2005), such as measures of slope (a measure of average inclination of the surface), angularity (which they describe as the average relative change in slope over the surface) and relief index (a measure of three-dimensional (3D) surface area over the size of the two-dimensional (2D) planometric footprint).

Ungar and colleagues have applied these metrics to topographically dynamic cross-sectional wear series of great apes (M’Kirera & Ungar, 2003), howling monkeys (Dennis et al., 2004), platyrrhines (Ungar et al., 2018), cercopithecoids (Bunn & Ungar, 2009) and fossil hominins (Ungar, 2004). They have generally found that wear patterns within primate taxa tend to be stereotyped and that folivorous primates begin with and, despite wear, tend to maintain occlusal surfaces with relatively higher values of relief, sharpness and angularity compared with their more frugivorous relatives. Ungar (2015) later termed the maintenance of occlusal cutting ability, in the face of wear-based modification of brachydont teeth in more folivorous primates, ‘enamel sculpting’. (Ungar used the term ‘enamel sculpting’, but as one reviewer of a previous paper correctly pointed out, more than enamel is being sculpted in these situations. Therefore, hereafter,
we opt to use the more inclusive and accurate term, ‘dental sculpting’.

Other tools to examine occlusal morphology have since been developed and used effectively to distinguish among taxa with different diets. Orientation patch count rotated (OPCR), introduced and later refined by Evans and colleagues (Evans et al., 2007; Evans & Jania, 2014), has proven useful in understanding the presumed relative contribution of fibre in the diets of broad clades of mammals. Orientation patch count rotated works by counting the number of partitions formed on a tooth surface when grouped by common directional aspect (i.e. ‘patches’). The expectation is that boundaries among patches represent changes in surface orientation and, thus, constitute cutting edges. Therefore, an occlusal surface with more patches will usually result in more patch edges and, consequently, more available blades useful for shearing fibrous materials. In addition to studies of extant taxa (Bunn et al., 2011; Ledogar et al., 2013), OPCR has been applied to fossil taxa to gain general insights into palaeoecology (Wilson et al., 2012). However, one issue recently emerging from further investigations of OPCR is that it may have reliable discriminating power only when applied across vastly disparate dental morphologies (Pineda-Munoz et al., 2017). Additionally, it has been suggested that OPCR may find effective application only with true secondary morphology of hypsodont molars (Pampush et al., 2016a).

Dirichlet normal energy (DNE) is another topography measure that evaluates relative surface sharpness (see Bunn et al., 2011). Subsequent work has established its usefulness for grouping extant primate dental morphologies with commonly used heuristic dietary categories (Ledogar et al., 2013; Winchester et al., 2014) and for tracking dietary fibre content in great apes (Berthaume & Schroer, 2017). Building on these studies of extant taxa, DNE has been used to infer the diets of extinct species (Godfrey et al., 2012; Prufrock et al., 2016; López-Torres et al., 2018). Dirichlet normal energy is an integral measurement of the amount of bending energy on a surface (for a simple worked example of DNE, see supplementary materials provided by Pampush et al., 2016a). Surfaces with higher DNE values tend to be more angular and to possess more sharpened edges. As with other dental topography metrics, DNE is advantageous because researchers can forego reliance on consistent homologous landmarks, which are often obliterated with wear. Unlike other dental topography metrics, DNE directly measures the aggregate sharpness of a tooth surface, rather than assuming that the boundaries between patches are sharp (as with OPCR) or that high crowns are correlated with occlusal sharpness [relief index (RFI), see next paragraph].

One final metric used in this study, RFI, was originally introduced by Ungar & Williamson (2000). A modification of RFI was later proposed by Boyer (2008). In the original formulation, Ungar & Williamson (2000) cropped molar surface scans at the lowest point of the occlusal basin(s), then divided the 3D surface area of the cropped scan by its 2D planometric footprint. This calculation therefore provides a ratio relating the relative height of the cusps to the size of the tooth. Taxa with taller cusps and crests on their teeth have higher RFI values (M’Kirera & Ungar, 2003; Ungar & M’Kirera, 2003; Ulhaas et al., 2004; Allen et al., 2015). Boyer (2008) modified RFI in three key ways, aimed at comparing more disparate euarchontan tooth morphologies. First, he moved the cropping of the tooth surface to its cervical margin, thus including the entire tooth crown in the 3D area summation. Second, he took the square root of the ratio, to make area measures linear. Third, for allometric reasons, he transformed the resulting ratio with the natural logarithm. Like Ungar’s formulation, Boyer’s adaptation of RFI has shown some ability to distinguish teeth among the different dietary categories of primates (Ulhaas et al., 2004; Boyer, 2008; Winchester et al., 2014; Allen et al., 2015). To avoid confusion and to distinguish between the two measures of RFI, hereafter Ungar’s original version is referred to as ‘occlusal relief’ (OR), following some prior publications (Allen et al., 2015), whereas Boyer’s adaptation will retain the name ‘relief index’ (RFI).

Most workers have chosen to focus on establishing the dietary-signal reliability of dental topography as applied to unworn or slightly worn teeth. However, some projects have returned to the original vision of Ungar & Williamson (2000) by applying dental topography to worn teeth or wear series. In a recent paper, Glowacka et al. (2016) used dental topography measures, including slope, angularity and OPCR, to examine molar wear series of mountain gorillas. They found that gorilla molars maintained their shearing abilities despite considerable loss of occlusal surface material. Their findings support the concept of adaptive dental sculpting (sensu Ungar, 2015). Another study compared topographic slopes of molar wear series of mandrills and savanna baboons (Galbany et al., 2014) and reported that savanna baboons, which are more reliant on grasses and sedges than mandrills, maintained more angular and, presumably, better shearing occlusal surfaces as their teeth wore down.

Using DNE and other metrics, Pampush et al. (2016a) examined wear-induced topographic changes on the molars of mantled howling monkeys (Alouatta palliata). They found that DNE increased with higher levels of macrowear and argued that the observed phenomenon was an example of Ungar’s dental sculpting (see Ungar, 2015), whereby macrowear is harnessed either
to transform and/or to maintain the wearing occlusal surface of a brachydont tooth to remain effective in trituration. Maintaining, or even increasing, lifetime dental efficacy was interpreted as adaptive. Moreover, theoretical analysis allowed for the hypothesis that dental sculpting was a true evolutionary phenomenon associated with folivory and secondary morphology (Fortelius, 1985; Janis & Fortelius, 1988; Janis, 1990), then non-folivorous primates should have DNE values exhibiting relationships with macrowear … which are either: negative (i.e. DNE decreases with wear), weaker (i.e. smaller effect size), or non-significant (i.e. no pattern).

The objectives of the present study are to test the predictions of Pampush et al. (2016a) in comparing the interaction of dental topography with wear between Alouatta and its sympatric and more frugivorous relative, Ateles. Four topographic measures are used: DNE, OPCR, RFI and OR. Wear is assessed by measuring the relative amount of dentine exposure (i.e. DER; see Occlusal Surface Wear Measures below).

MATERIAL AND METHODS

Specimen preparation

Lower first molars ($M_1$) of Alouatta spp. ($N = 20$) and Ateles spp. ($N = 16$) with varying levels of macrowear were moulded from Duke University’s Glander Collection and the Smithsonian Institution. Many prior studies examining dental topography in primates have used lower second molars (Bunn & Ungar, 2009; Bunn et al., 2011; Ledogar et al., 2013; Winchester et al., 2014; Berthaume & Schroer, 2017). Pampush et al. (2016a) opted to use $M_1$ because among $M_1$, worn teeth were better represented. As this study is a follow-up to the findings of Pampush et al. (2016a), we opt to use $M_1$ again. Given a sample containing similar levels of wear, we would expect similar results from an analysis repeating our approach on $M_1$. All teeth were inspected for post-mortem damage, and specimens exhibiting cracks or chips were excluded from the sample. Individual specimen data, including species, recovery locality and raw topography measures, are detailed in the Supporting Information.

Moulds were made using Coltene President’s Jet (Coltene Group, Cuyahoga Falls, OH, USA) by extruding and thoroughly coating the moulding material over the cheek teeth. Casts were poured using Epotek 301 epoxy resin (Epoxy Technology Inc., Billerica, MA, USA), forming casts of the posterior mandibular tooth rows.

Mesh generation and preparation

Tooth casts were scanned using the Duke University Shared Materials and Instrumentation Facility (SMIF) microCT (a Nikon XTH 225 ST). Scanning parameters were set at approximately 125 kV, 106 µA and an approximate voxel size of 20.6 µm for each cast. Meshes were segmented in Avizo 8.1 (FEI Visualization Sciences Group, Berlin, Germany), using the ‘Segmentation Editor’ to define materials that included the occlusal surfaces and the sidewalls of the $M_1$s to the cervical margin, following standard DNE and OPCR preparation procedures (Ledogar et al., 2013; Winchester et al., 2014; Pampush et al., 2016b). Minor defects in the casts created during the moulding and casting process were repaired using the interpolation tools in the Segmentation Editor of Avizo.

Once the relevant portions of the tooth scans were isolated and retriangulated into surfaces (using the ‘Generate Surface’ dialog in Avizo), the meshes were retriangulated in the Avizo ‘Surface Editor’ module to eliminate minor artefacts created during the reconstruction process, following the recommendations of a published methodological investigation (see Spradley et al., 2017). Raw surfaces were down-sampled to ~20 000 faces using the ‘Simplification Editor’, then further down-sampled to ~10 000 faces using the ‘Remesh Surface’ tool, with interpolation set at ‘smoothly’.

Unpublished experiments (JD Pampush, PE Morse, JP Spradley) since the publication of Spradley et al. (2017) have shown the remeshing operation to be of great importance to avoid producing a surface with extremely disparate polygon mesh face sizes upon simplification. These same unpublished experiments show that the two-step down-sampling with remeshing is more likely to generate consistent surfaces than either one-step down-sampling or down-sampling without remeshing the surface. Surfaces with highly irregular distribution of face sizes tend to be particularly prone to the measurement-distorting effects of outlier faces. Additionally, the two-step down-sampling and remeshing procedure used here follows the recommendations provided in the Avizo User’s Guide (https://www.fei.com/software/avizo-user-guide) and conforms to the procedures of prior publications (Guy et al., 2013). In previous studies, it has been reported that the ~10 000 face count is optimal for teeth of the size of the taxa investigated here (Winchester et al., 2014; Pampush et al., 2016a; Spradley et al., 2017).

In other studies, protocols using higher face counts have been implemented, but it is unclear that larger face counts add more biologically relevant detail to the analyses, and without open access to the study surfaces it can be difficult to validate the results using different retriangulation protocols (Berthaume & Schroer, 2017; Spradley et al., 2017; Thiery et al., 2017).

After cropping and down-sampling of the surfaces, each surface was smoothed in Avizo with the ‘Smooth Surface’ function for 25 iterations with a lambda value...
of 0.6. In other studies, slightly different procedures for smoothing have been used. Our procedure was chosen based on the investigation of methods by Spradley et al. (2017), which showed other variations of the smoothing protocol to be prone to introduction of surface artefacts. The resulting surfaces were exported from Avizo as PLY files. The processed PLYs are available on MorphoSource (http://morphosource.org/) under the project heading ‘Pampush et al. Atelidae Adaptive Dental Topography Dynamics.’

**TOPOGRAPHIC ANALYSES**

Prepared occlusal surface meshes were imported into R (R Core Team, 2017). The R package molaR (Pampush et al., 2016b) was used to calculate DNE, OPCR and RFI on each tooth mesh. DNE was calculated using the ‘Vertex Exclusion’ criterion of molaR, thereby excluding boundary faces, which are defined as any PLY face with at least one vertex on the boundary of the surface mesh, from the final summation of the surface DNE value. It is important to implement boundary exclusion because faces on the edge of a mesh frequently have erroneous Dirichlet energy density values owing to highly inaccurate boundary vertex normals (Pampush et al., 2016b; Spradley et al., 2017).

The top one-tenth of 1% (i.e. 1/1000th) of all Dirichlet energy density faces was excluded from the total surface DNE summation, in keeping with prior DNE calculation protocols (Winchester et al., 2014; Pampush et al., 2016a, b). Surfaces were visually inspected with the molaR DNE plotting function (DNE3d) to be certain that all significant outlier faces were removed. For surfaces exhibiting clear outliers after the top 0.1% exclusion, individual face values were explored closely to determine a more appropriate outlier exclusion parameter. In the most extreme cases, the outlier exclusion criterion was extended to the top 0.15% of all faces (resulting in the removal of an additional five faces for some specimens).

OPCR was calculated on each tooth surface using molaR. The settings engaged for OPCR included eight different calculating positions, each set 5.625° apart from the adjacent positions. Minimum PLY-face count for OPCR inclusion was set at three, consistent with prior studies (Evans et al., 2007; Evans & Janis, 2014; Pampush et al., 2016b; Winchester, 2016).

RFI was calculated using the RFI function in molaR, whereas OR was calculated using a combination of Avizo and ImageJ (Abramoff et al., 2004). In calculating OR, meshes were first cropped to the lowest point in the occlusal basin, then opened in Avizo and visualized in orthographic projection, with a uniform background colour and a dynamic scale bar. Meshes were aligned orthogonal to the occlusal surface, and the Avizo ‘headlight’ was turned off, making the tooth mesh appear as a flattened footprint. The magnification of the footprint was adjusted to a standard length so that the footprint of each mesh would be represented by an approximately equal number of pixels, thereby standardizing the error introduced by approximating the smooth footprint edge with square pixels. A scene picture normal to the occlusal plane was imported into ImageJ to estimate the planometric area. Three-dimensional area was measured in Avizo using the ‘Measure and Analyze’ dialog.

**OCCLUSAL SURFACE WEAR MEASURES**

Wear on the occlusal surfaces was measured using DER. Following the protocol described by Spradley et al. (2016), scaled 2D occlusal views of the teeth were sketched, with emphasis on the boundary of the occlusal surface and the areas of exposed dentine, using a camera lucida mounted on a Wild M5 binocular microscope at ×12 magnification by a single observer (J.D.P.). The occlusal drawings were digitally scanned and then analysed in ImagoJ (Abramoff et al., 2004). Dentine exposure ratio (sometimes called PED ‘percentage of exposed dentine’, M, wear ratio or wear index) was calculated in the usual way (Kay & Cant, 1988; Kay et al., 2002; Elgart, 2010; Morse et al., 2013; Glowacka et al., 2016; Pampush et al., 2016a) as:

\[
\text{DER} = \frac{DA}{TA}
\]

where \(DA\) is the total area of exposed dentine and \(TA\) the two-dimensional footprint area of the occlusal surface. This is a slight departure from other studies in that DER is proportional rather than a percentage; however, equivalent values can be achieved by multiplying our DER by 100.

**STATISTICAL ANALYSES**

Each of the variables (DER, DNE, OPCR, RFI and OR) was tested for normality using a Shapiro–Wilk test (Shapiro & Wilk, 1965) within each taxon (Supporting Information, Table S1). Non-normally distributed variables were Z-rank transformed using the R package GenABEL (GenABEL project developers, 2013). Owing to the lack of normality among some of the measures, distributional comparisons between *Ateles* and *Alosaatta* for each of the non-transformed variables were conducted with Kruskal–Wallis tests (Kruskal & Wallis, 1952). Given that the samples come from several species of each genus, intrageneric differences were tested for each of the variables (Supporting Information, Table S2). The relationships between macrowear (as measured with DER) and the four topography metrics (RFI, OR, DNE and OPCR) were tested with ordinary least-squares regression (Galton,
occclusal relief (OR) and relief index (RFI). Dirichlet normal energy (DNE), orientation patch count rotated (OPCR), and OR between Alouatta (blue) and Ateles (red). The DER distributions were consistently non-normal, but no other variables were consistently non-normal. No intrageneric differences exceeded the Bonferroni threshold for significance.

The results of Kruskal–Wallis tests for differential DER in Ateles Alouatta are shown in Table 2. All the measures except OR are significantly different between the taxa, with Alouatta showing expectedly higher values of DNE, DER and OPCR than Ateles. Alouatta exhibits lower values of RFI than Ateles (Table 2; Fig. 1). Results of the regression analyses comparing DER with the topography metrics are presented in Table 3. DNE has a significant positive linear relationship with DER in Alouatta but does not in Ateles (Figs 4, 5). The original fitting of a linear model to DER and OPCR in Alouatta returned no significant relationship (Table 3). However, a post hoc quadratic fitting of OPCR vs. DER in Alouatta is significant (Table 4). Contrary to Alouatta, in Ateles OPCR has a significant positive linear relationship with DER (Table 3; Figs 6, 7). RFI has a significant negative correlation with DER for both Ateles and Alouatta (Fig. 8), whereas OR shows a significant negative correlation with DER in Ateles but not Alouatta (Fig. 9).

### RESULTS

Summary statistics for each of the measurements for both Ateles and Alouatta are presented in Table 1. Violin plots illustrating the untransformed distributions of the topography metrics (i.e. DNE, OPCR, RFI and OR) are shown in Figure 1. A violin plot showing distributional differences in DER is shown in Figure 2, and Figure 3 highlights specimens exhibiting differential DER for both Alouatta (blue) and Ateles (red). The DER distributions were consistently non-normal, but no other variables were consistently non-normal. No intrageneric differences exceeded the Bonferroni threshold for significance.

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### DISCUSSION

**Dirichlet normal energy and macrowear in Atelidae**

In a previous study aiming to understand macrowear-induced dental topography dynamics of Alouatta, Pampush et al. (2016a) showed that occlusal surface sharpness (as measured with DNE) increased with macrowear (as measured with DER) in mantled howling monkeys (A. palliata). They speculated that this phenomenon of increasing DNE with macrowear was an adaptive emergent property of the primate trait complex including: brachydonty, folivory, long lifespan and a diet capable of inducing tooth wear. Following the secondary morphology ideas of Fortelius and Janis (Fortelius, 1985; Janis & Fortelius, 1988; Janis, 1990; Fortelius & Solounias, 2000; Karme et al., 2016) and the dental sculpting concept of Ungar (M’Kirera & Ungar, 2003; Ungar & M’Kirera, 2003; Ungar, 2008, 2015), Pampush et al. (2016a) suggested that the thinner enamel of howling monkeys (Olejniczak et al., 2008) is arranged in such a way as to promote occlusal sharpness with macrowear. This might be achieved by promoting perforations of the thin enamel cap, thereby creating exposed enamel–dentine junctions where the enamel edge is continuously sharpened (Kay, 1981; Lanyon & Sanson, 1986; King et al., 2005; Ungar, 2008). Such an arrangement might result in harnessing (rather than circumventing or forestalling) the effects of dietary wear and converting the potential liability posed by tooth wear into an asset to promote and prolong their masticatory efficiency.

Two components of the results presented here reinforce the original conclusions of Pampush et al. (2016a). First, a re-evaluation of a partly overlapping sample of howling monkey molars shows the same correlation between macrowear and DNE (Table 3; Fig. 4). Second, a sample of spider monkey molars collected and analysed in a similar manner shows no statistical trend between DNE and macrowear (Table 3; Fig 4). These dual observations are consistent with the hypothesis that macrowear-induced increases in DNE (i.e. dental sculpting) are specific to folivorous primates (Pampush et al., 2016a) and are consistent.
with findings of cusp sharpness in apes (Berthaume, 2014).

The finding of a positive correlation between DNE and macrowear in Alouatta but not Ateles is important for two reasons. First, high DNE can be reasonably associated with increased masticatory cutting efficiency, which should be selected for in folivores but not in frugivores (Bunn et al., 2011; Winchester et al., 2014). The finding that DNE increases and is not simply maintained as howling monkey molars wear suggests that the enamel is arranged, either via thickness distributions or heterogeneity of tissue types, or both, to produce exposed boundaries between enamel and dentine where the enamel is sharpened for cutting (Kay, 1981; Ungar, 2008). Second, if DNE showed a positive correlation with macrowear in a non-folivorous brachydont primate, then it would be possible to conclude that primate occlusal surfaces, in general, sharpen with macrowear or that high levels of macrowear create artefacts on primate occlusal surfaces, intimating a false sharpness picked up by the measurement. Either of these scenarios would throw into question whether the observed macrowear-DNE phenomenon seen in howling monkeys is, in fact, an adaptation specifically for mastication of a more fibrous, tougher diet.

The DNE macrowear findings for Ateles spp. and Alouatta spp. presented here are generally in agreement with findings in other primates, in studies using different topographic approaches. Examinations of mountain gorilla molars, which did not use DNE, have consistently concluded that gorillas maintain surface sharpness as their teeth wear (M’Kirera & Ungar, 2003; Glowacka et al., 2016). We suspect that the finer DNE measurement of this sample would detect an increase in surface sharpness with wear, as seen in howling monkeys; such a finding would be particularly expected given

Figure 1. Violin plots of topography measurement distributions in Ateles spp. (red) and Alouatta spp. (blue). The width of the coloured area represents the density of the variable distribution. White dots indicate the distributional average. Black rectangles and lines show interquartile distances.
Figure 2. Violin plot of dentine exposure ratio (DER) distributions comparing *Alouatta* (in blue) and *Ateles* (in red). The width of the coloured area represents the density of the variable distribution. White dots indicate the distributional average. Black rectangles and lines show interquartile distances.

Figure 3. Three-quarters buccal view of *Alouatta* (in blue) and *Ateles* (in red) right lower first molar surfaces and occlusal views of their corresponding planometric footprints, with *Alouatta* in orange and *Ateles* in gold. Mesial is at the top and buccal to the right. Surfaces are all presented at the same scale. Planometric footprints depict areas of exposed dentine in translucent grey.
the highly folivorous nature of the diet of mountain gorillas (Schaller, 1963; Fossey & Harcourt, 1977; Watts, 1984, 1996; Taylor, 2006). A study by Berthaume & Schroer (2017) found that higher DNE values were associated with higher-fibre diets among African apes, although they did not explicitly investigate the effects of macrowear on the measurement. Apart from great apes, the DNE macrowear findings here shadow previous dental topography findings in Alouatta (Dennis et al., 2004) and in platyrrhines generally (Ungar et al., 2018), although once again, these studies did not use DNE and therefore did not explicitly detect increases in sharpness with macrowear. DNE should be used to study variably worn molars in other primate groups with closely related folivores and non-fo livores, such as hominoids (e.g. Gorilla, Pan), strepsirrhines and cercopithecoids, to explore the phylogenetic extent of dental sculpting more thoroughly.

**ORIENTATION PATCH COUNT ROTATED AND MACROWEAR IN ATELIDAE**

The observed relationships between macrowear and orientation patch count rotated among Ateles and Alouatta are somewhat unexpected. OPCR is thought to be a problematic measure to use in primates, as Winchester et al. (2014) had shown that it does a poor job of segregating primate molars into heuristic dietary categories. Many previous studies have asserted that higher OPCR values indicate a greater ability to shear fibrous foods (Evans et al., 2007; Evans & Janis, 2014), arguing that higher OPCR is indicative of more surface complexity, resulting in more ‘shearing tools’ on the occlusal surface. Therefore, it might be expected that OPCR would increase with macrowear in Alouatta, in a way mirroring how DNE interacts with macrowear; if both are stand-ins for cutting efficiency, then the measures should be collinear. Pampush et al. (2016a) previously reported no relationship between OPCR and macrowear in Alouatta, yet the new OPCR results presented here offer additional insights. First, in the sample of variably worn Alouatta molars, OPCR shows a parabolic, not linear, relationship with macrowear (Tables 3 and 4; Fig. 6). This parabolic association was potentially present in the sample analysed by Pampush et al. (2016a), however these authors did not test for it (see fig. 5 of Pampush et al., 2016a).

Regardless, this parabolic relationship between OPCR and macrowear in Alouatta generally conforms to the life-cycle expectations for a tooth exhibiting some kind of secondary morphology (sensu Fortelius, 1985); that is, the pristine form starts with a lower OPCR value (presumably, therefore, being less shearing efficient), moderate and intermediate levels of macrowear result in higher OPCR values during the animal’s prime of life, followed by inevitable dental senescence with high levels of macrowear and a fall-off of OPCR values.

Although the relationship between OPCR and macrowear conforms to expectations that OPCR may be measuring the shearing ability in Alouatta, the lack of a relationship between OPCR and DNE contradicts this conclusion (Table 5; Fig. 10). In a post hoc test, we used a linear model correlating OPCR and DNE in Alouatta, finding no significant relationship between these alternative measures of shearing ability. Instead, we suggest that the parabolic relationship

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**Table 2.** Kruskal–Wallis tests for mean differences between taxa

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\chi^2$</th>
<th>d.f.</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>DNE</td>
<td>20.725</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>DER</td>
<td>10.339</td>
<td>1</td>
<td>0.001</td>
</tr>
<tr>
<td>RFI</td>
<td>11.388</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>OPCR</td>
<td>12.378</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>OR</td>
<td>3.293</td>
<td>1</td>
<td>0.069</td>
</tr>
</tbody>
</table>

Alouatta possesses consistently higher Dirichlet normal energy (DNE), dentine exposure ratio (DER) and orientation patch count rotated (OPCR) values than Ateles, and consistently lower relief index (RFI).

---

**Table 3.** Correlations of wear with topography metrics

<table>
<thead>
<tr>
<th>Model vs.</th>
<th>Taxon</th>
<th>Coefficient</th>
<th>$F$-statistic</th>
<th>d.f.</th>
<th>$r^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>DNE vs. DER</td>
<td>Alouatta</td>
<td>0.681</td>
<td>15.590</td>
<td>1.18</td>
<td>0.434</td>
<td>0.001</td>
</tr>
<tr>
<td>DNE vs. DER</td>
<td>Ateles</td>
<td>0.425</td>
<td>3.102</td>
<td>1.14</td>
<td>0.123</td>
<td>0.100</td>
</tr>
<tr>
<td>RFI vs. DER</td>
<td>Alouatta</td>
<td>−0.817</td>
<td>36.08</td>
<td>1.18</td>
<td>0.648</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>RFI vs. DER</td>
<td>Ateles</td>
<td>−0.873</td>
<td>44.9</td>
<td>1.14</td>
<td>0.745</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>OPCR vs. DER</td>
<td>Alouatta</td>
<td>0.087</td>
<td>0.140</td>
<td>1.18</td>
<td>0.047</td>
<td>0.713</td>
</tr>
<tr>
<td>OPCR vs. DER</td>
<td>Ateles</td>
<td>0.746</td>
<td>17.570</td>
<td>1.14</td>
<td>0.525</td>
<td>0.001</td>
</tr>
<tr>
<td>OR vs. DER</td>
<td>Alouatta</td>
<td>−0.186</td>
<td>0.651</td>
<td>1.18</td>
<td>0.018</td>
<td>0.430</td>
</tr>
<tr>
<td>OR vs. DER</td>
<td>Ateles</td>
<td>−0.768</td>
<td>20.17</td>
<td>1.14</td>
<td>0.561</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

The DER values were Z-rank transformed to normality. DER, dentine exposure ratio; DNE, Dirichlet normal energy; OPCR, orientation patch count rotated; OR, occlusal relief; RFI, relief index.
Figure 4. Bivariate plot of the lower right first molar dentine exposure ratio (DER) vs. Dirichlet normal energy (DNE) in Alouatta (in blue) and Ateles (in red). DER and DNE show a significant positive correlation in Alouatta, but are not correlated in Ateles. Labelled points correspond to the tooth surfaces depicted in Figures 3, 5, and 7.

Figure 5. Surface plots of the lower right first molars of Alouatta (top row) and Ateles (bottom row) viewed from the distobuccal perspective, with mesial at the top of the figure. Surfaces are coloured for Dirichlet energy density (DED). Warmer colours are areas of higher DED. Note the warmer surface of the Alouatta molars, particularly around the exposed enamel-dentine junctions.

between OPCR and macrowear might be capturing an increase in surface complexity, distinct from surface sharpness (i.e. DNE), as the enamel cap is initially perforated (increasing surface tissue heterogeneity) and before the dentine pools link up, which would serve to re-homogenize the occlusal surface and reduce complexity. The non-significant results of the linear model indicate a decoupling of surface complexity (OPCR) from integral surface sharpness (DNE) in variably worn teeth of *Alouatta* and imply that one of these measures is not directly capturing occlusal cutting efficiency. Given the construction of the two metrics, it seems more likely that DNE captures cutting efficiency, because it measures integral surface sharpness directly, whereas OPCR is built on the assumption that all boundaries between individual patches serve as ‘breakage sites’ (Evans et al., 2007). Given the context and application of OPCR, showing a relationship between higher food fibre content and larger OPCR values (Evans et al., 2007), ‘breakage sites’ might reasonably be interpreted as ‘cutting edges’. Thus, this implicit assumption in OPCR can be shown to be especially precarious when one considers a perfectly smooth hemisphere, which in the normal calculation of OPCR will exhibit eight patches. These eight patches presumably portend eight cutting edges (Spradley, 2017). Intuitively, however, it is known that a smooth hemisphere, much like the bowl-shaped talonid basin of a primate molar (Fig. 7), will have no blade-like edges conferring an efficient shearing ability. Dirichlet normal energy, in contrast, does not weight all occlusal surface elements equally, but instead the estimates of curvature for surface features are given exponentially increasing scores, i.e. areas of high curvature (high sharpness) are weighted much more heavily than the surfaces of a rounded cusp (Pampush et al., 2016a; Spradley, 2017).

The surprising OPCR findings in *Ateles* underscore the dubious nature of the application of OPCR to primates in several ways (see also Winchester et al., 2014). First, there is a positive linear relationship between OPCR and macrowear in *Ateles* (Table 3; Fig. 6). Second, an unplanned comparison of OPCR and DNE in *Ateles* shows a significant positive

**Figure 6.** Bivariate plot of dentine exposure ratio (DER) vs. orientation patch count rotated (OPCR) in *Alouatta* (in blue) and *Ateles* (in red) lower first molars. DER and OPCR show a significantly positive linear correlation in *Ateles* and a parabolic correlation in *Alouatta*. Labelled points correspond to the tooth surface depicted in Figures 3, 5, and 7.

**Table 4.** Quadratic fit for orientation patch count rotated vs. dentine exposure ratio in *Alouatta*

<table>
<thead>
<tr>
<th>Model</th>
<th>d.f.</th>
<th>Coefficient</th>
<th>$\chi^2$</th>
<th>$r^2$</th>
<th>$P$-statistic</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quadratic fit for</td>
<td>2,17</td>
<td>0.977</td>
<td>−14.798</td>
<td>0.381</td>
<td>6.848</td>
<td>0.007</td>
</tr>
<tr>
<td>OPCR vs. DER</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
relationship between the two measures (Table 5; Fig. 10), although there remains a non-significant relationship between DNE and macrowear in Ateles. These dual findings are consistent with the interpretation derived from Alouatta that DNE and OPCR do not equally reflect shearing ability and cast doubt on the biological relevance of the positive association between OPCR and macrowear in Ateles. Furthermore, even if the relationship between macrowear and OPCR is not spurious in Ateles, it seems unlikely that spider monkeys would exhibit adaptive dental sculpting, which is presumed to complement a folivorous diet, given what we know about their ecology (van Roosmalen, 1985; Wallace, 2005; González-Zamora et al., 2008). Spider monkey diets are generally composed of large quantities of fleshy fruit, which are unlikely to require sharp occlusal cutting surfaces to process effectively. Instead, the bulbous rounded cusps observed in Ateles cheek teeth are more suited for mashing fruit (Lucas, 2006). These bulbous rounded cusps are present in the newly erupted, pristine morphology of Ateles cheek teeth (Rosenberger, 1992; Anthony & Kay, 1993), and therefore the construction of their teeth is probably adapted to avoid occlusal surface modification in prolonging their dental lifespan (see below).

This unexpected constellation of wear-induced topography dynamics suggests a role for the relatively thicker enamel of Ateles; their thick enamel caps (see Olejniczak et al., 2008) are seemingly adaptations to resist wear and maintain the primary morphology (sensu Fortelius, 1985) of the occlusal surface (Pampush et al., 2013). Given enough time,
the enamel cap will eventually become perforated with increased levels of macrowear, which would increase OPCR as the occlusal surface becomes more heterogeneous. As macrowear proceeds, it would be expected that the linking up of exposed dentine pools would re-homogenize the surface. One potential explanation for the linear, as opposed to parabolic, relationship between macrowear and OPCR in *Ateles* is the lack of more heavily worn specimens, ultimately resulting from their thicker enamel.

**Figure 8.** Bivariate plot of dentine exposure ratio (DER) vs. relief index (RFI) in *Alouatta* (in blue) and *Ateles* (in red) lower first molars. DER and RFI show a significant negative correlation in both taxa, i.e. RFI decreases with wear in both species, but RFI is consistently greater in *Ateles* compared with *Alouatta* (*Tables 1 and 3*). Labelled points correspond to the tooth surfaces depicted in *Figures 3, 5, and 7*.

**Figure 9.** Bivariate plot of dentine exposure ratio (DER) vs. occlusal relief (OR) in *Alouatta* (in blue) and *Ateles* (in red) lower first molars. The OR declines significantly with increased DER in *Ateles* but not in *Alouatta*. Labelled points correspond to the tooth surface depicted in *Figures 3, 5, and 7*.
The fact that in *Ateles* OPCR is correlated with both DNE and macrowear, yet DNE and macrowear are not correlated, might be explained by the proposed sequence of stages (see Fig. 11):

1. Pristine teeth are rounded, bunodont molars, with low DNE and OPCR.
2. Wear eventually perforates the enamel cap, introducing higher surface complexity and therefore increased OPCR, while the initial holes in the enamel are ringed with sharp edges, linking increased OPCR to tentatively increased DNE.
3. Initially formed sharp edges around enamel perforations are quickly rounded down with additional wear, yet the higher surface complexity is maintained. Therefore, the relationship between exposed dentine and high DNE is not maintained, yet a tangential relationship between OPCR and DNE is produced.
4. As wear progresses, the sequence of stages 2 and 3 is repeated, until occlusal enamel loss is so great that there is no additional room for new perforations, only the expansion of current perforations and the linking up of dentine pools.

This proposed sequence accounts for the relationships between the three measures (OPCR, DNE and macrowear (DER)) in *Ateles*. In this scenario, DNE increases in *Ateles* are an artefact of initial enamel perforations, not the product of continued honing on exposed enamel–dentine junctions as suggested for *Alouatta*. This accounts for the lack of correlation between macrowear and DNE.

Contrasting the DNE and OPCR results in *Alouatta* and *Ateles* suggests that OPCR is not closely measuring the shearing efficacy of these primate molars, but instead measuring only the generalized complexity of their teeth. This conclusion is reinforced by the observation of the high OPCR values of crenulated pitheciine molars (Ledogar *et al.*, 2013; Winchester *et al.*, 2014), which are not thought to be adapted for folivory (Rosenberger, 1992). Furthermore, features nearer the cervix than the occlusal surface, such as large

---

**Table 5.** Dirichlet normal energy vs. orientation patch count rotated in *Ateles* and *Alouatta*

<table>
<thead>
<tr>
<th>Model</th>
<th>Taxon</th>
<th>Coefficient</th>
<th>F-statistic</th>
<th>d.f.</th>
<th>$r^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>DNE vs. OPCR</td>
<td><em>Alouatta</em></td>
<td>0.4186</td>
<td>3.83</td>
<td>1,18</td>
<td>0.129</td>
<td>0.066</td>
</tr>
<tr>
<td>DNE vs. OPCR</td>
<td><em>Ateles</em></td>
<td>0.5846</td>
<td>7.27</td>
<td>1,14</td>
<td>0.295</td>
<td>0.017</td>
</tr>
</tbody>
</table>

DNE, Dirichlet normal energy; OPCR, orientation patch count rotated.

**Figure 10.** Bivariate plot of Dirichlet normal energy (DNE) vs. orientation patch count rotated (OPCR) in *Alouatta* (blue) and *Ateles* (red). The DNE and OPCR are correlated in *Ateles* (dashed red line), but not in *Alouatta* (dashed blue line). For complete correlation results, see Table 5.
or complex cingula, might serve to increase OPCR without adding any more ‘tools’ to the occlusal surface. In the cases of *Ateles* and *Alouatta*, introducing tissue heterogeneity to the occlusal surface (via dentine pools) does serve generally to increase surface complexity (i.e. OPCR) but does not necessarily result in a sharper surface (as measured with DNE) and is therefore a dubious reflection of shearing ability. In taxa that exhibit more explicit forms of secondary morphology, such as rodents and ungulates, OPCR might more closely track presumed shearing efficiency (*Evans et al.*, 2007; *Evans & Janis*, 2014; *Pineda-Munoz et al.*, 2017). The findings presented here, however, suggest that OPCR is not a particularly useful metric for diagnosing the form–function relationship in primate molars (see also: *Bunn et al.*, 2011; *Winchester et al.*, 2014). Therefore, researchers should be cautious when inferring dietary information in brachydont, extinct taxa on the basis of OPCR values (*Boyer et al.*, 2010).

**RELIEF AND MACROWEAR IN ATELIDAE**

Occlusal relief and RFI, which are very similar measurements, both decline with greater levels of macrowear in *Ateles* (*Table 3; Figs 8, 9*). This is to be expected, because both measures are essentially ratios of the aggregate height of the tooth crests and crown, over the occlusal footprint. As the primary morphology is rounded down, the size of the planometric footprint remains fairly stable, resulting in decreases in both OR and RFI. Thus, both measures are greatly impacted by enamel and dentine tissue loss, which inevitably occurs with macrowear.

RFI in *Alouatta* behaves in a similar manner to that of *Ateles*, whereas OR shows a departure from expectations (*Table 3; Figs 8, 9*), with OR scores maintained throughout the wear cycle in *Alouatta*. Although this is somewhat surprising, given both the findings in *Ateles* and the negative correlation observed between macrowear and RFI in *Alouatta*, this finding does correspond to some previous studies. Ungar and colleagues had previously noted that although occlusal relief generally declines with wear in all taxa, higher OR values are maintained throughout the wear cycle in folivorous taxa compared with non-folivorous taxa (*M’Kirera & Ungar*, 2003; *Ungar*, 2015; *Ungar et al.*, 2018). However, the departures in behaviour between the relief measures compared with *Ateles*, and between RFI and OR within *Alouatta*, beg the question: what is different about OR in *Alouatta* as opposed to *Ateles*?

We note that OR is heavily dependent on the depth of the lowest point of the occlusal surface (typically, the talonid basin) with respect to the height of the sidewalls of the tooth. This is because OR takes the planometric area (i.e. 2D area) of the tooth to be equal to the area captured by a transverse plan intersecting the lowest point of the occlusal basin(s). If the talonid basin is sufficiently shallow, or the sidewalls sufficiently curved, such that the lowest point on the occlusal surface is well above the widest portion of the vertical sidewalls of the tooth, then the planometric...
areas of unworn teeth will be reduced dramatically. We observe this to be the case among our sample of *Alouatta*, but not in *Ateles* (Fig. 12). The relationship between OR and macrowear is expected to shadow that of the relationship between RFI and macrowear, so long as the point of reference (the lowest point on the occlusal surface) is relatively fixed. In thick-enamelled *Ateles* (Olejniczak et al., 2008) this appears to be the case, as the enamel at the bottom of the talonid basin is rarely perforated. This contrasts with thin-enamelled *Alouatta* (Olejniczak et al., 2008), in which the enamel of the talonid becomes perforated with even moderate amounts of macrowear (Fig. 3). Therefore, the lowest point on the occlusal surface in *Alouatta* is not fixed, but rather likely to be altered to some degree with macrowear. This difference in the taxa, again pertaining to enamel thickness, is likely to explain why OR and macrowear have a non-significant relationship in *Alouatta* and a negative correlation, as predicted, in *Ateles*.

In exploring these proposed relationships, we ran correlations of the OR planometric footprint area and the OR 3D surface area against DER for both *Alouatta* and *Ateles* (Table 6; Figs 13, 14). Although none of these correlations was significant, *Ateles* generally conformed to expectations, i.e. the planometric footprint area of *Ateles* stayed relatively stable, whereas the 3D surface area exhibited a negative trend (although not significant). This combination accounts for the expected negative relationship between OR and DER in *Ateles*. In *Alouatta*, in contrast, a negative correlation between 3D surface area and DER is absent, and these teeth exhibit a high degree of variance in the planometric footprint area. Levene’s tests comparing relative variances showed *Alouatta* to have significantly greater variance in 2D planometric footprint area compared with *Ateles*, but this was not the case for 3D area (Table 7). Together, these results suggest that the shape of the *Alouatta* tooth sidewalls and the thin enamel that allows talonid basin perforations (and therefore shifts the transverse plane intersecting the lowest portion of the occlusal basin) introduce significant amounts of OR–2D area variance. This added variance prevents the expected negative OR–DER correlation, suggesting.

![Figure 12](https://example.com/figure12.png)

**Figure 12.** Three-quarters and occlusal views of unworn right lower first molars of *Alouatta* (top row) and *Ateles* (bottom row) teeth. Grey surfaces indicate the area of the tooth surface that remains after transverse cropping at the lowest point of the occlusal basin, after the occlusal relief (OR) measurement protocol. The array of red points shows portions of the tooth surface removed from the OR measurement. Note the considerably larger planometric footprint area removed from the *Alouatta* molar compared with *Ateles*.
that the observed maintenance of OR with macrowear is an artefact of the measurement.

**DISTRIBUTIONAL DIFFERENCES IN MACROWEAR BETWEEN *ALOUATTA* AND *ATELES***

The sampled molars examined in this study show *Alouatta* to have relatively higher levels of macrowear (DER) than *Ateles* (Table 2; Fig. 2). There are several factors to consider when evaluating this result. The collections from which these teeth are drawn were composed in significantly different ways. The Glander Collection, from which the majority of the howling monkey molars are sampled, is a ‘cemetery’ collection of individuals that died without human intervention and were opportunistically collected by K. Glander over many years of intensive study (K. Glander, pers comm). In contrast, the entirety of the *Ateles* sample, and some of the *Alouatta* (see Supporting Information, Table S4 for specific details), are drawn from the Smithsonian Collection and were presumably wild shot, probably constituting a distinctly different demographic from that typically seen in a cemetery population (see: *Wood et al.*, 1992; *Cohen, 1994; Wright & Yoder, 2003*). This suggests that more of the Smithsonian sample is composed of animals taken in the prime of life, whereas the Glander Collection might be composed primarily of much older individuals.

Despite differences in the constitutions of the two collections, we do not have sufficient reason to suspect that the difference in collection procedures introduced significant differences in the distributions of *Ateles* vs. *Alouatta* macrowear measures. For one thing, a *t*-test comparison of the DER values shows no differences between the *Alouatta* derived from the different collections (Fig. 15; *t* = 1.39, *P* = 0.1819). If anything, the Smithsonian-derived *Alouatta* have higher levels of macrowear. Rather, what seems more plausible is that differences in enamel thickness between the two taxa (*Olejniczak et al.*, 2008) produce the observed differences.
The relatively thicker enamel of spider monkeys might be an adaptive response to prevent significant accumulation of macrowear, whereby they are capable of maintaining their primary morphology (mostly unaltered) well into late adulthood (Pampush et al., 2013). Alternatively, the thinner enamel of howling monkeys is likely to promote secondary shearing crest development, as Kay has long argued (Kay, 1981). Although differences in the collection procedures cannot be ruled out totally, it seems more likely that the differences in DER distributions are the result of enamel thickness, and therefore an honest reflection of the ecology of these animals, rather than demographic disparity.

**Distributional Differences in Dirichlet Normal Energy and Orientation Patch Count Rotated Between Ateles and Alouatta**

As both DNE and OPCR are proposed measures of molar shearing efficiency, it is unsurprising that Alouatta has consistently higher values than Ateles in both measures (Table 2; Fig. 1), despite our scepticism that OPCR measures shearing ability in primates. Alouatta starts with relatively higher levels of DNE on the pristine molars, a finding consistent with previous studies (Winchester et al., 2014), but the difference in DNE values widens as both sets of teeth take on higher levels of macrowear (Fig. 4). The widening difference in DNE values can be attributed to dental sculpting (Ungar, 2015). The results are slightly different for OPCR, wherein Alouatta begins with marginally higher OPCR values, which rapidly increase with moderate levels of macrowear separating the two genera (Fig. 6). However, OPCR continues to increase in Ateles with macrowear, whereas in later stages of macrowear, Alouatta OPCR begins to decline, resulting in similar OPCR values at higher levels of macrowear (Fig. 6). These higher values of DNE and OPCR in Alouatta generally reflect the sharper edges of the molars and the greater surface tissue heterogeneity, respectively, than those of Ateles.

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**Figure 14.** Plot of three-dimensional (3D) surface area, used in the occlusal relief (OR) measurement, against dentine exposure ratio (DER) for Alouatta (in blue) and Ateles (in red). Neither relationship is statistically significant (see Table 6), and Ateles and Alouatta exhibit similar variances in 3D area (see Table 7).

**Table 7.** Levene test for unequal variance

<table>
<thead>
<tr>
<th>Measure</th>
<th>Coefficient of variation</th>
<th>d.f.</th>
<th>F-statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Two-dimensional area</td>
<td>Alouatta = 13.527</td>
<td>1,34</td>
<td>11.43</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Ateles = 8.053</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Three-dimensional area</td>
<td>Alouatta = 16.450</td>
<td>1,34</td>
<td>2.70</td>
<td>0.109</td>
</tr>
<tr>
<td></td>
<td>Ateles = 12.767</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Perhaps the most unexpected finding of this research is the observation that Ateles, which is a documented frugivore (van Roosmalen, 1985; Anapol & Lee, 1994; Wallace, 2005; González-Zamora et al., 2008), possesses higher OR and RFI values than Alouatta (Table 2; Fig. 1). Although only RFI is significantly different between the two taxa (Table 2), the fact endures that average values of OR remain higher in Ateles than in Alouatta (Table 1). This observation holds even when considering only the least-worn specimens of either taxa in our sample (Figs 8, 9); therefore, this result cannot be attributed to differences in macrowear. Other studies have consistently found that more folivorous taxa tend to have higher RFI and OR values (M’Kirera & Ungar, 2003; Ungar & M’Kirera, 2003; Boyer, 2008; Bunn & Ungar; 2009; Winchester et al., 2014), consistent with the hypothesis that more folivorous taxa require taller crests and cusps for shearing fibrous materials. Allen et al. (2015), in contrast, noted that RFI and OR were roughly equivalent in Ateles and Alouatta, or that Ateles had slightly higher values, depending on which teeth were examined (see table 2 of Allen et al., 2015). They argued that shearing quotient was a more effective measure of the ability of a primate to triturate fibrous foods than either OR or RFI, in agreement with the earlier findings of Winchester et al. (2014).

Findings by Allen et al. (2015) and those reported here comparing Ateles and Alouatta relief measures might be explained by considering allometry. Howling monkey molars are considerably larger in size than are spider monkey molars (Fig. 3; Plavcan, 1990), despite howling monkeys being smaller in body size (Smith & Jungers, 1997). There might be some allometric effect in which the size of the planometric footprint grows faster than the relative 3D area of the tooth surface (Fig. 3). Some kind of allometric effect may be picked up in the measure, which is why RFI and OR discriminate among teeth adapted for different diets relatively better among prosimians than platyrrhines (see Winchester et al., 2014: fig. 2). Alternatively, information might be gleaned from the observation that RFI is significantly different between the taxa, whereas OR is not (Table 2). The RFI calculation procedure calls for cropping the tooth surface mesh at the dental cervix, therefore incorporating the sidewalls of the tooth in the calculation (Boyer, 2008). The OR calculation, in contrast, includes the tooth only above the lowest portion of the occlusal basin (i.e. the ‘triturating’ portion of the tooth; Ungar & Williamson, 2000; M’Kirera & Ungar, 2003; Ungar & M’Kirera, 2003). Thus, at least according to the OR calculation, the two taxa have relatively equal cuspal clearance, whereas RFI consistently indicates Ateles to possess relatively higher cusps. Finally, as Winchester et al. (2014) and Allen et al. (2015) show, there is considerable overlap of RFI values (and OR values) when comparing platyrrhine folivores and frugivores. Thus, selecting a folio–frugivore pair of platyrrhines to compare RFI/OR values, particularly in worn teeth,
might result in values transposed from expectation. Put differently, although RFI and OR might show a general ability to distinguish molar morphology by diet among large collections of primate species, owing to the considerable overlap in molar morphologies between dietary categories, these measures are unreliable in one-on-one comparisons and might become less informative in worn specimens. Paleontologists should take note when using these measures.

CONCLUSION

We compared changes in lower first molar dental topography measures (DNE, OPCR, RFI and OR) with a measure of macrowear (DER) in the lower first molars of two similarly sized atelid genera (Ateles and Alouatta). Consistent with prior hypotheses, Alouatta showed increases in DNE with increasing macrowear (DER), whereas Ateles did not, indicating that Alouatta molars might be ‘designed’ to wear (i.e. dental sculpting). This hypothesis should be explored further in other primate groups with closely related folivores and non-folivores. OPCR showed a parabolic trend with macrowear in Alouatta and a positive trend with macrowear in Ateles, the latter of which we discount for reasons given above. When examining the relationship between OPCR and DNE, we note unexpected statistical associations, leading us to question the utility of OPCR in diagnosing primate occlusal function. The examinations of RFI and OR show some departures from expectations. Both RFI and OR are observed to be relatively higher in Ateles than in Alouatta; a finding that cannot be dismissed by greater levels of macrowear in Alouatta, and one confounding interpretations of the utility of the metrics for diagnosing folivory. This finding might be the product of measurement idiosyncrasies or could reveal that these two taxa, in particular, betray the folivore–frugivore dichotomy (as other works have shown). Trends between RFI and OR with macrowear fit expectations in Ateles, i.e. RFI and OR both decrease with greater levels of macrowear. RFI shows a decrease with macrowear in Alouatta, whereas OR does not. We speculate that this is a result of a more fluid planometric footprint area in Alouatta, arising from the shifting location of the transverse cropping plane used in the OR measurement.

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REFERENCES


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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** Taxon-specific tests for normality.

**Table S2.** Kruskal–Wallis tests of intrageneric interspecific differences.

**Table S3.** Breusch–Pagan tests for regression heteroscedasticity.