



Sign-oriented Dirichlet Normal Energy: Aligning Dental Topography and Dental Function in the R-package *molAR*

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Abstract

Dirichlet normal energy (DNE) is a dental topography measurement aimed at capturing occlusal sharpness and has shown promise for its ability to sort primate molars according to perceived shearing ability. As initially implemented, this measurement does not differentiate concave versus convex contributions to surface sharpness. This is problematic because the DNE-signal derived from concave aspects of an occlusal surface measures a sharp ‘edge’ oriented inward towards the enamel dentine junction rather than outward towards food contact. The inclusion of concave DNE in dietary analyses of molars possessing deep occlusal sulci—such as those found among hominoids—inflates the perceived functional sharpness of these teeth. Concave-inflated DNE values can be misleading, being interpreted as indicating that a particular taxon is more adapted for processing fibrous food than is warranted. The modification of the DNE measurement introduced here ‘Sign-oriented DNE’ alleviates this problem by elimination of concave sharpness from analyses, allowing investigations to focus on features of occlusal surfaces plausibly linked to shearing, cutting, or shredding of food materials during Phases I and II of the masticatory power stroke. Convex DNE is just as effective at sorting non-hominoid primate molars into traditional dietary categories as the initial applications of the orientation-blind version of the measurement, and produces more theoretically coherent results from hominoid molars. Focusing on- and improving the connection between measurement and occlusal function will enhance the ability of dental topography to make meaningful contributions to our collective understanding of species’ dietary ecologies.

Keywords DNE · Crenulated enamel · Occlusal sulci · Enamel furrows · Dental sharpness · Curvature sign orientation

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Introduction

Originally introduced by Ungar and colleagues (e.g., Zuccotti et al. 1998; Ungar and Williamson 2000; Ungar and M’Kirera 2003), dental topographic (DT) analysis is a rapidly growing and diversifying approach aimed at studying the morphological, functional, and adaptive properties of mammalian teeth. Using scanned and digitized dental surfaces, DT measurements quantitatively characterize the surface topography of tooth crowns. Some prominent DT measurements include orientation patch count (Evans et al. 2007), relief index (Boyer 2008), average surface slope (Dennis et al. 2004), and the focus of this work: an estimate of surface sharpness known as Dirichlet normal energy (DNE, Bunn et al. 2011). DNE and other DT measurements offer many advantages over homology-based dental measures, such as shearing quotient (SQ; see: Kay and Simons 1980; Kay 1984; Anthony and Kay 1993; Strait 1993; Ungar and Kay 1995; Kirk and Simons 2000), or crown height (Williams and Kay 2001;

Damuth and Janis 2011). Paramount among the topography measurements' advantages is that they can be applied to teeth without requiring dental landmarks, as they are quantitative characterizations of whole or partial tooth surfaces. By side-stepping homology, these measurements can be applied to worn teeth (e.g., Ungar and Williamson 2000; Ungar and M'Kirera 2003; Pampush et al. 2018)—whose identifiable landmarks (discrete cusp tips and crests) are often obscured by wear—and they permit comparisons among clades that may not share homologous features (e.g., Evans et al. 2007; Harper et al. 2019; Selig et al. 2021). Generally speaking, DT measurements overwhelmingly derived their perceived usefulness from their ability to assign objective and distinct values to teeth supposedly possessing differing dietary adaptations (see below). The underlying assumption here is that within the context of mammalian mastication, DT measurements are reflective of the functional abilities of occlusal surfaces. However, uncritical acceptance of this assumption paves the way for misapplication or misinterpretation of DT measurements, particularly when applying them to teeth which are structurally distinct from reference samples. Before more thoroughly evaluating DNE, it is best to review what is understood about dental function and what might be learned about dental morphology from the use of DT measurements.

Associating Dental Topography and Dental Function

To date, there has been inconsistent and incomplete efforts made to connect dental topography measurement with models or assessments of tooth function. Stepping away from dental landmarks has hindered the interpretive footing of some DT measurements since modeling of how teeth move and interact during mastication has traditionally been framed around the interaction of various named features presumed to have functional relevance (e.g., cusp apices). Put differently, dental landmarks provide the essential vocabulary in characterizing exactly which and how parts of teeth are brought together to reduce food. Initial studies of mammalian masticatory movements were based on manipulation of dried skulls and jaws where researchers focused on how the cusps of upper and lower teeth might complement one another (Butler 1952, 1973; Mills 1955; 1963; 1967; Mills 1973). Models of mastication experienced a leap forward with the advent of cinefluorography and its application to mammals and primates exhibiting 'primitive' dental morphologies (Crompton and Hiiemae 1969, 1970; Kay and Hiiemae 1974a, b; Hiiemae 1978). Cinefluorographic recordings showed that mastication follows a rhythmic pattern arranged in two basic modes. Cycles in both modes consist of a closing movement in which the lower jaws are approximated, giving way to a power stroke when forces are applied between teeth and food. The two modes of mastication are distinguishable by the degree of occlusion in their

power strokes. In the initial mode, once a bite of food is separated and brought into the mouth, the upper and lower cheek teeth are closed around it, coarsely reducing the food, and mixing it with saliva in preparation for finer trituration. This so-called 'puncture-crushing' mode does not involve the direct occlusion of molars during its power stroke, and is not tightly constrained by—nor particularly informative of—the form-function relationship of molar structure. In a second subsequent 'chewing' mode of the power stroke, smaller food boluses are tightly pressed between teeth during the power stroke. During this second mode of mastication, precise contacts between the teeth guide and constrain masticatory movements. It is during this second operation of the power stroke—or intercuspal phase (Ross and Iriarte-Diaz 2014)—where molar form becomes relevant to masticatory function. It has been convincingly established that the complementary features of occluding molars work to reduce food while the mandibular molars are brought upward and medially, processing food between the interdigitating cusps (Crompton and Hiiemae 1970; Hiiemae and Kay 1972; Kay and Hiiemae 1974a; Hiiemae 1978, 1984). In primates and other mammals with conservative dental morphology, most or all of the features we identify as 'shearing' components come into occlusion during the initial upward and mediolingually-directed Phase I of the chewing power stroke (Crompton 1971; Kay 1975, 1977). When the teeth are fully interdigitated (in centric occlusion), the upper molar protocones (and hypocones, if present) are seated in the talonid and trigonid basins of the lower molars, respectively. Movement into this position is followed by a Phase II movement out of centric occlusion when the surfaces of the talonid and trigonid are dragged across the protocone and hypocone. The degree of force applied between the teeth during the two phases has been debated (Wall et al. 2006; Ross and Iriarte-Diaz 2014a, b), but certainly forces sufficient to produce a distinctive pattern of scratches on planar attrition wear surfaces are achieved during Phase II.

The adaptive significance of mammalian cheek-tooth morphology and mastication is realized with the observation that—not only are the varied forms seemingly optimized to efficiently triturate particular types of food materials—but that the morphological differences fit within the functional expectations for how chewing works (Butler 1939; Kay 1975; Lucas 2006). Early studies of primate molars established that species that feed on different proportions of fruit, leaves, and insects have different molar structure and that common adaptive patterns were acquired convergently in many clades. Primate frugivores have small teeth for their adult body size with relatively short molar crest lengths and crushing-grinding basins (Kay 1975). In contrast, leaf-eating species tend to have larger teeth for their adult body size with longer, sharper molar crests and larger crushing-grinding basins. These observations made with standard

dental measurements such as SQ have proven insightful, partly because these measures were intentionally designed to capture functionally relevant information based on models of how teeth interact during mastication, but also because they were explicitly linked to a performance metric: chewed food particle size (Sheine and Kay 1977, 1982; Kay and Sheine 1979). Since it is well established that the digestibility (extractable energy), especially of high-fiber plant materials is significantly improved when they are more finely triturated (McLeod and Minson 1969; Sheine and Kay 1977; Kay and Covert 1984), the connection between dental measures and performance allowed researchers to convincingly link their observations to adaptive scenarios (e.g., Kay 1984; Kay and Covert 1984; Anthony and Kay 1993; Kirk and Simons 2000; Allen et al. 2015).

In contrast to standard dental measures, the landmark-free approach which advantages the DT measurements also has the effect of disassociating them from models of tooth function and performance. Topography measurements are abstract expressions of surface-wide dental form that may segregate different morphologies, but do not necessarily follow a clear functional rationale. To be functionally insightful, measurements used to assess dental morphology must be correlated with performance outcomes—which is best assessed by chewed-food particle size and/or chew strokes or chewing time—but can also be inferred through other means. Otherwise, when detached from homology these measurements are unmoored abstractions of the morphology, wherein two dramatically different dental Baupläne with little-to-no clear resemblance might generate identical DT values. Outside of testing explicitly functional hypotheses, it is unclear what value DT measurements would hold in a phylogenetic context since the measures can disguise homoplasy as homology.

In practice, there may be three ways of showing or inferring that a DT measurement is capturing functionally relevant information about dental morphology to prove useful in testing adaptive hypotheses. First, a measurement could be experimentally grounded to a functional effect if it is shown to be correlated with chewed-food particle sizes or chewing time/chew-stroke count. This must be done using a set of dental morphologies whose disparity of forms at least encompasses the precision of the measurement, while also controlling for as many aspects of food material properties and chewing mechanics as possible. As mentioned above, we believe this to be the ideal approach for ecologically ground-truthing these measurements, and might be best achieved with a thoughtfully designed experiment on captive or opportunistically collected dead animals (e.g., Lanyon and Sanson 1986; Renaud and Ledevin 2017). Some progress has been made toward making these correlations. In gelada baboons (*Theropithecus*), Venkataraman et al. (2014)

studied food toughness and fecal particle size (FPS, as a surrogate for swallowed particle size) in the field, matched with age-graded topographic metrics on teeth from museum collections. They found that FPS is similar between prime and old adults in the wet season, when food fracture toughness was at a minimum, but older adults were less efficient (higher FPS) than prime individuals in the dry season when food toughness was highest. They linked these findings to DT measurements (declining relief index and orientation patch count; DNE was not measured) in older individuals. But this study did not directly compare occlusal topographies with FPS, limiting confidence in their results. A number of other studies on primates have reported on the relationships among FPS, age, and molar topography (Ungar 2004; Glowacka et al. 2016; Thiery et al. 2017) but none considers all three together, and clear documentation of the relationship between chewed-particle size and topography measurements has remained elusive.

A second approach employs the comparative method, whereby topography measurements are inferred to be functionally relevant if they successfully differentiate dental morphologies. Currently this second technique is how most dental topography measurements derive their presumed efficacy—via demonstrations of their successful re-sorting of mammalian teeth into traditional heuristic dietary categories (e.g., insectivore, folivore, frugivore, etc.; see Evans et al. 2007; Winchester et al. 2014). With the specimens' dietary categories assigned a priori on the basis of field observations, such studies often show that these measurements are likely capturing functionally relevant properties of dental surfaces; possibly even quantifying the same features researchers have previously used to qualitatively sort teeth into dietary groups. However, in the case of some DT measurements, these inferences are based on the interpretation of patterns arising from uncertain processes; without clarity on precisely which tooth features are being measured and how these measures directly relate to masticatory function, dental topography is relegated to a black box operation that produces results constrained to analogy and lacking in functional insight. That is, even if the new measurement seems to identify patterns in teeth, those patterns need to correlate with function to be ecologically insightful. In contrast, classic and simpler measurements like SQ have already provided the core ecological insights and analogical frameworks these new DT measurements aim to make more 'objective,' and do so with clear underlying functional rationale. Without a clear correlation with some element of masticatory performance, the new dental topography measurements will remain hamstrung in their ability to speak to the functional capabilities of unusual occlusal morphologies (such as those encountered in wear series, or in extinct organisms for whom no straightforward modern analog exists), undermining their core purpose.

A third method relies on appealing to first principles while associating the measurements derived from teeth (e.g., sharpness as assessed with DNE) with the functional outcomes of their interactions with food materials (i.e., the ability of interdigitating tooth surfaces to reduce the particle size of chewed food). Through a deductive reasoning process starting with examination of the dental properties supposedly being captured by the various measurements, researchers might then conclude that the results of particular measurements must anticipate certain masticatory outcomes. Deductive logic of this kind, though largely theoretical, is still necessary for the attainment of measurement consistency, and for articulating the relationship between the measured features and functional outcomes.

Ultimately, to be useful in a dietary ecology context, these highly abstract measurements of dental morphology should be grounded to masticatory function using all three of the above stated approaches. They should: [1] correlate with a performance metric, [2] effectively capture observable patterns among study specimens, and [3] offer clear underlying functional rationale(s). Until there is clarity and certainty regarding the value of these measurements in functional terms (if at all), researchers employing DT measurements should remain skeptical of the biological interpretations arising from any surprising or incongruous dental topography findings. In other words, if the DT measurement values from a particular taxon do not conform to *a priori* expectations (e.g., molars with apparently blunt cusps yielding surprisingly high values of sharpness), researchers would be better served to question the measurements themselves (or the protocol for producing them), rather than attempting to rewrite the known feeding ecology of the taxon under consideration.

In this paper, we introduce an important modification to how the dental topography measurement DNE is expressed, by labeling and sorting the surface according to the orientation (concave vs convex) of its curvature. This is operationalized in a revision to the R package *molAR* (Pampush et al. 2016a), and is expected to produce a more coherent link between the DNE measurement and functional sharpness of occlusal surfaces. In presenting sign-oriented DNE, we explore four interrelated goals. [1] First, decompose the calculation of DNE and assess the components' associations with dental performance. As will be shown below, while there is solid rationale to consider DNE the best estimate of *functional* occlusal sharpness among the current suite of DT measurements, not all aspects of its final summation can be deductively linked to masticatory performance. In particular, the concave-oriented component of total surface sharpness is likely confounding the link between DNE measurement values and realized dental performance and should be eliminated from the measurement in future applications. [2] Second, reanalysis of previously published primate dental surfaces will show that the isolated convex DNE component

retains its correlations with diets high in fiber/exoskeleton consumption. The proposed modification to DNE not only better aligns the measure with current models of chewing mechanics but should also improve its precision since concave, non-masticatory edges are eliminated from the final summation of specimen DNE values. [3] We demonstrate below that this proposed modification to the DNE measurement is non-trivial by examining great ape (Hominoidea) molars in comparison to other primate teeth. It will be observed that not all primates (let alone mammals generally) possess similar ratios of convex to concave dental surface curvature, such that the concave surface contribution to the final DNE surface values cannot be dismissed as commonly held 'noise' when making adaptive comparisons or interpretations. Furthermore, we will argue that without convincingly connecting concave DNE to the same measurement objectives as convex DNE, the comingling of these two components into one value produces functional and interpretive incoherence. [4] Fourth, and finally, we examine the effects and interaction that scaling, scanning, and processing of teeth into digital surfaces has on the ratio between concave and convex components of DNE values. We will examine whether the differences among the digital surfaces analyzed here are non-allometric products of the underlying morphology or artifacts of the digitization process for completing the measurements. It is our expectation that these analyses and alterations to the DNE calculation will make it more consistent and reliable across the varied dental morphologies of mammalian taxa, and guide researchers in applying DNE for meaningful ecological and evolutionary insights.

Methods

Measurement Background and Decomposition of Dirichlet Normal Energy (Goal 1)

When viewed from first principles (*à la* deductively), not all purported measurements of topographic surface sharpness—a valuable property of teeth to measure given its expected link with the ability to slice through tough or crack-arresting materials (Lucas 2006)—are similarly effective and/or consistent in a dietary ecology framework. Orientation patch count (OPC), for instance, is designed to count the number of 'breakage sites'¹ on a molar and is coarsely correlated with the proportion of fiber in a species' diet across broad mammalian groups (Evans et al. 2007).

¹ 'Breakage sites' are defined by van der Glas et al. (1992: p. 105) as "part of the occlusal surface of the post-canine teeth which is suitable for the breaking of particles of a particular size." Most dental morphologists take this to mean the outward facing crests and cusps of molars.

Ecologists have taken this to mean that the count of breakage sites tracks the cutting ability of teeth (e.g., Evans and Janis 2014), since dietary fibers are generally work-limited for breakdown (Strait 1997; Lucas 2006). That is, fibrous materials need to be cut with continuous application of force, whereas stress-limited materials will catastrophically fail when enough force is applied. While the comparative analyses seem to demonstrate the efficacy of OPC, considering the calculation of the measurement—which begins by sorting contiguous aspects of the tooth surface according to whichever direction the feature faces within an eight compass directions framework (see Evans et al. 2007; Evans and Janis 2014)—suggests that it is set up to analyze lophodont teeth. In fact, OPC has proven most effective when deployed in clades possessing lophodont taxa, and it does not seem to correlate with dietary fiber content among clades possessing more basal tribosphenic designs (Pineda-Munoz et al. 2017). One might interpret this to mean that the measurement seems to work when the boundaries between patches are sharp edges associated with crests, but begins to come apart when teeth lack crests. For instance, even a simple hemisphere has an OPC value of eight (because some part of the hemisphere will face each of the 8-compass directions) but at best has only one ‘breakage site’ at the apex of the hemisphere. This limited functional correspondence likely explains the success of the measurement in certain applications (e.g., Evans et al. 2007; Evans and Janis 2014) while OPC’s use among bunodont dentitions has yielded fewer insights (e.g., Winchester et al. 2014).

On the other hand, Dirichlet normal energy (DNE)—even as conventionally implemented—is one of the more promising measurements because of the way it characterizes dental surfaces. DNE is a unitless and directionless, assessment of surface sharpness. It follows that if DNE is indeed measuring sharpness in a functionally meaningful way, then we would expect animals routinely consuming tough foods like fibrous leaves and other plant parts (or insect exoskeletons) to have overall sharper occlusal surfaces—and correspondingly higher DNE values—as has been previously demonstrated with some comparative studies (e.g., Winchester et al. 2014). Furthermore, when DNE is mapped onto a model tooth surface, the areas exhibiting the greatest Dirichlet energy density tend to correspond to the portions of the tooth making functional contact during Phase I occlusion (see chewing mechanics above). Together, these observations suggest that DNE is capturing functionally relevant properties of a dental surface.

The DNE of a surface is estimated with the formula:

$$DNE = \sum e(p) \times area(p) \quad (1)$$

where $e(p)$ is the Dirichlet energy density about point p given by the formula:

$$e(p) = \left(\frac{1}{r_a}\right)^2 + \left(\frac{1}{r_b}\right)^2 \quad (2)$$

As can be seen from the underlying Dirichlet energy density calculation, sharpness is estimated for each point on the analyzed surface by summing the two squared reciprocal radii of osculating circles (r_a and r_b) found in the planes of principle curvature about each point. Point-based sharpness values are summed over the entire surface to give a ‘total surface’ DNE measure (for visuals and worked example, see SOM of Pampush et al. 2016b).

Particularly relevant to the underlying calculations in the DNE measurement is the use of osculating circle radii to assess sharpness. The use of osculating circles appears to be one of the more successful approaches researchers have found to quantify sharpness (e.g., Popowicz and Fortelius 1997; Evans et al. 2005; Hainsworth et al. 2008), a property which has otherwise proven surprisingly difficult to measure (for review see Reilly et al. 2004). In one standout study of knife blades, Hainsworth et al. (2008) demonstrated a relationship between osculating circle radii and performance (see also: McCarthy et al. 2010). While controlling for the force involved and the material being penetrated, Hainsworth et al. (2008) measured the osculating circle radii of blade edges before using the knives in a series of stabbing experiments. From their results Hainsworth et al. (2008) note two key findings: First, they show that osculating circle radii (i.e., morphology measurement) are correlated with knife penetration (i.e., performance measurement), meaning that the measurement can be used to predict functionality. The second point their data makes is the way the two measurements are correlated. They show that the smaller the osculating circle radius (i.e., the finer the knife edge) the deeper the stabbing depth—interestingly—in a negative correlation which resembles the formula $y = -\sqrt{x}$ (see Fig. 10 in Hainsworth et al. 2008). These results can be algebraically manipulated to present a positive linear correlation between osculating circle radii and stabbing penetration by taking the reciprocal of the radii and squaring them. This mirrors the manipulation occurring within the Dirichlet energy density measurement (Eq. 2) with the minor difference that Dirichlet energy density is measuring sharpness in two dimensions (two orthogonal radii) instead of one. If sharpness is quantified in this manner and summed across all points on the surface, it produces Eq. 1 from above. Therefore, one can interpret DNE as a natural surface-wide extension of the osculating circle approach to measuring sharpness.

Examining the underlying DNE calculation provides some insights into the expected performance of the measurement, with two items particularly worth noting. (1) The measurement does not account for the orientation of the surface sharpness, since an osculating circle can be placed

above or below the surface and simply has to trace the curve at the measurement point. As the reciprocal radii are always squared to produce the Dirichlet energy density measure, the positive or negative signs of the radial values are eliminated (Dirichlet energy density is always expressed as an absolute value). (2) While squaring of the reciprocal radii linearize their relationship to performance, it also has the mathematical effect of relegating most of the surface to irrelevance in the final summation. Put differently, in a surface composed of irregular curvatures (like a tooth with sharp cusps and crests, but relatively gently-curving walls and basins) a small amount of the surface area accounts for the vast majority of the total DNE value. In concert, the orientation blindness and the emphasis on relatively small portions of the surface to define the total DNE value require researchers to be particularly cognizant of what exactly it is they are measuring, especially if they plan to use those results to draw ecological or adaptive inferences.

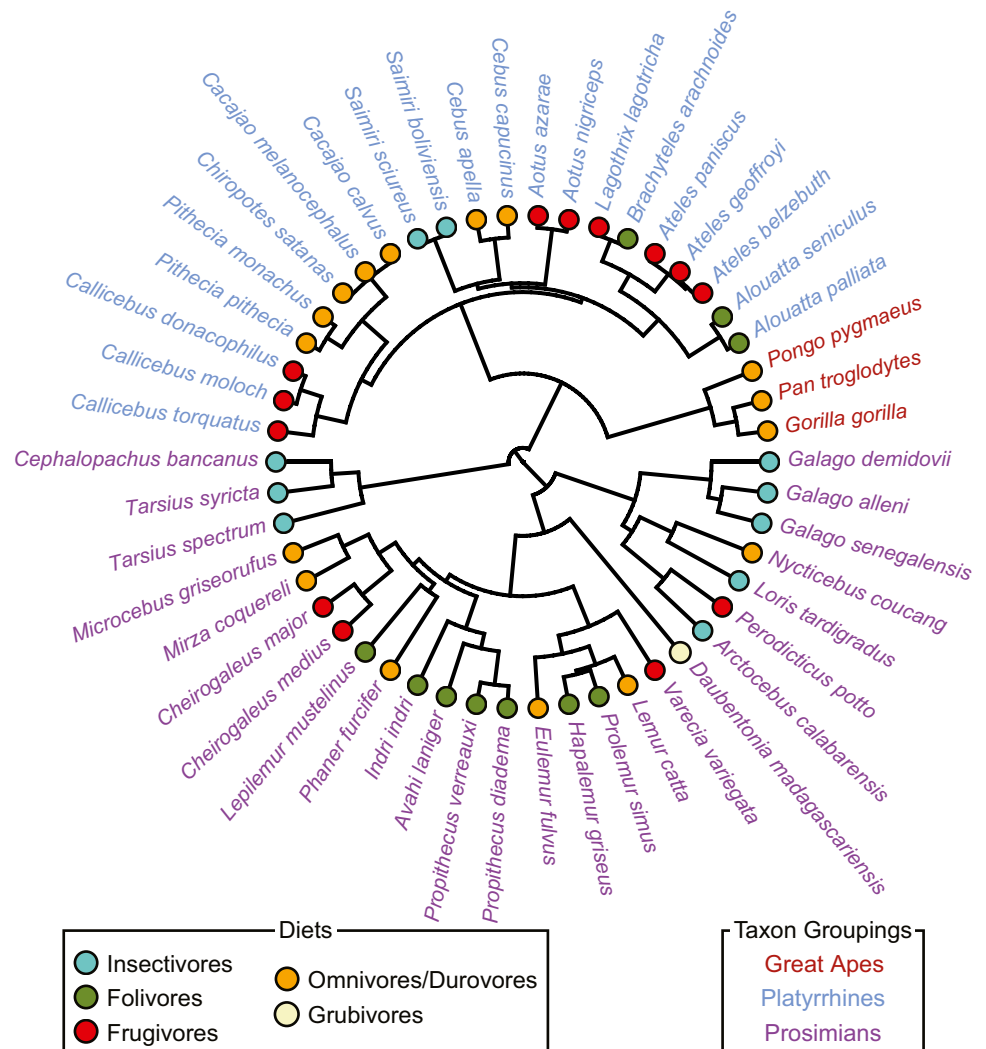
From the perspective of tooth shearing ability, a major flaw in the conventional application of DNE as a measure of surface sharpness is its inability to distinguish concave from convex components of sharpness. If DNE's utility as a dietary signal is derived from its capturing of occlusal sharpness in a *functional* context (as opposed to a strictly morphological assessment), then occlusal sulci, the often deep and sharp grooves on tooth surfaces, may be creating an interpretive problem. As currently implemented, infolded creases such as occlusal sulci are summed as sharp elements just as are ridges and crests even though the 'sharp' component of these grooves is oriented towards the inner dentine of the tooth. With the current understanding of mastication, it is hard to imagine how deep and sharp sulci could assist in slicing up food. Due to this lack of accounting for sharpness orientation, conventional DNE measurements of tooth surfaces that combine sharp crests with crenulations and/or deep sulci may misinform functional/adaptive interpretations. During normal mastication, dietary materials are unlikely to make contact with- or be deformed by- the nadirs of the deep occlusal sulci, and in the event that they do, during these interactions they are being 'cupped' not 'split' as they are at cusp tips or along crests and shearing ridges. Thus, when sharp, deep sulci are present to a high degree, scholars may interpret high values of DNE as pointing to elevated cusp and ridge sharpness, when instead the occlusal 'sharpness' measured by DNE is disproportionately derived from inwardly-directed, sharply concave occlusal sulci. This may lead to the understandable misinterpretation that a species is adapted to masticate higher levels of dietary fiber than its teeth are actually equipped to efficiently process—provided DNE is being used as a proxy for functional masticatory surface sharpness.

A simple solution is at hand to better align DNE as a functionally relevant measurement of masticatory morphology: Investigated surfaces can be partitioned into concave and convex components (described below), allowing researchers to disregard the concave aspect of DNE and focus their functional interpretations on the outwardly sharp convex DNE value. The convex component of the DNE summation represents the aspect of the tooth expected to make direct contact with food materials, and therefore actually be used in food breakdown.

Software and Data Collection

The R package `molaR` is a suite of tools for performing dental topographic analyses (Pampush et al. 2016a). The package allows researchers to measure the following from PLY-format files (McHenry and Bajcsy 2008) that represent dental surfaces: Dirichlet normal energy (DNE), orientation patch count (OPC), orientation patch count rotated (OPCR), surface slope (m), and relief index (RFI). The package also contains tools for performing analyses of measurement accuracy and quality, as well as visualization of these measures on digital surface models. The updated version `molaR` 5.0 contains a modification to the `DNE()` function incorporating a new user-adjustable argument `kappa`, which enables users to set the inflection point for defining the concave versus convex portions of the occlusal surface (for specific details of the calculation, and for an extreme example of sign-oriented DNE applied to a convex-dominated tooth, see Online Resources 1 and 2). The default value of `kappa` is set at 0, meaning that the function will partition the surface into concave and convex portions according to a neutral or zero measurement of curvature. Users can adjust `kappa` anywhere between -2 to 2, with negative values biasing the boundary towards concave curvature values, meaning that `kappa` = -1 will result in a reduced area being defined as concave, while `kappa` = 1 will have an enlarged area of the surface designated as concave. The new `DNE()` function separately aggregates the concave and convex contributions to the total DNE value, as well as the surface area measurements, for the analyzed surface. As is standard when applying DNE to dental surfaces (e.g., Bunn et al. 2011; Winchester et al. 2014; Pampush et al. 2016a), PLY faces with a vertex on the boundary, and those faces with Dirichlet energy densities above the 99.9th-percentile are excluded from the final DNE summation (though users can adjust these parameters in the `molaR` `DNE()` function). Therefore, the function otherwise makes no changes to the way DNE is calculated—the total DNE of a surface is constant regardless of the value of `kappa`—but this novel parameter permits deeper insight into the relative contributions (concave or convex) to total DNE.

Fig. 1 Radial plot of phylogenetic tree used in analyses, downloaded from 10k Trees (Arnold et al. 2010). Colored points at end of each tip indicate species' dietary category. Colored text of binomina indicates grouping used for analyses



Additionally, users can adjust *kappa* to isolate the most concave or convex portions of a surface for more detailed analysis.

Surfaces derived from dental scans of 234 minimally worn lower second molars (M_2) were analyzed for this study. The sample includes 100 strepsirrhine specimens, 8 tarsiers specimens (i.e., 'prosimians'; 26 total species) and 107 platyrrhine specimens (21 species) from the data set of Winchester et al. (2014), downloaded from <https://MorphoSource.org> (Fig. 1, Online Resource 3; Boyer et al. 2016). These surfaces were combined with unworn lower second molar surfaces of the hominoids *Gorilla gorilla* ($N=6$), *Pongo pygmaeus* ($N=6$), and *Pan troglodytes* ($N=7$) either downloaded from *MorphoSource.org* or from *human-fossil-record.org* (Online Resource 3). In preparation for measuring DNE, all surfaces were processed uniformly following protocols detailed elsewhere (e.g., Pampush et al. 2016b; Spradley et al. 2017), whereby the M_2 tooth crown was digitally segmented away

from adjacent teeth as well as its roots using *Avizo* 9.5 (FEI Houston, Hillsboro, OR). Occlusal surface damage was digitally repaired during segmentation. If the damage was so extensive as to obscure the original surface contours the specimen was discarded. Digital surfaces were generated without smoothing from the segmentation results. After cropping to the enamel cervix, surfaces were simplified and remeshed to ~10,000 faces, smoothed 20 iterations in *Avizo*, and exported as PLY files for analysis in R following previously published recommendations (Spradley et al. 2017).

Several different types of data were collected from each of the digitized dental surfaces and specimens. Sign oriented DNE was measured on each dental surface in *molar* 5.0 with the contributions from the concave and convex areas of the tooth partitioned using the default *kappa* value of 0 (see Online Resource 1 for technical details of curve orientation assignment). The partitioned tooth surface area was also measured. DNE ratio (DNE-R) and surface area ratio (SA-R) were both calculated as concave portion divided by convex

Table 1 Mean DNE values

Group	Diet/Genus	Mean Total DNE $\pm$ SD	Mean Convex DNE $\pm$ SD	Mean Concave DNE $\pm$ SD	Mean Convex Area $\pm$ SD	Mean Concave Area $\pm$ SD
Prosimians	Folivory	237.55 $\pm$ 48.47	185.88 $\pm$ 35.42	51.66 $\pm$ 16.58	34.99 $\pm$ 23.781	12.38 $\pm$ 7.15
	Frugivory	155.44 $\pm$ 35.15	129.93 $\pm$ 30.27	25.50 $\pm$ 11.04	28.21 $\pm$ 15.67	9.47 $\pm$ 6.79
	Insectivory	278.75 $\pm$ 53.50	221.33 $\pm$ 39.25	57.42 $\pm$ 15.71	11.12 $\pm$ 4.84	4.53 $\pm$ 1.92
	Omnivory	205.37 $\pm$ 30.73	169.22 $\pm$ 25.49	36.15 $\pm$ 8.26	19.28 $\pm$ 13.46	6.72 $\pm$ 4.72
Platyrrhines	Folivory	202.94 $\pm$ 24.63	153.11 $\pm$ 22.15	49.82 $\pm$ 8.62	92.07 $\pm$ 12.46	27.21 $\pm$ 4.12
	Frugivory	174.80 $\pm$ 28.71	136.22 $\pm$ 17.85	38.56 $\pm$ 12.74	36.05 $\pm$ 18.34	10.42 $\pm$ 5.10
	Durophagy/Omnivory	147.39 $\pm$ 21.96	119.26 $\pm$ 14.95	28.13 $\pm$ 9.86	29.95 $\pm$ 5.98	8.41 $\pm$ 1.65
	Insectivory	214.49 $\pm$ 20.81	163.67 $\pm$ 13.68	50.82 $\pm$ 9.56	13.25 $\pm$ 1.23	4.35 $\pm$ 0.62
Apes	<i>Gorilla</i>	291.21 $\pm$ 77.44	168.99 $\pm$ 34.28	122.22 $\pm$ 44.97	422.03 $\pm$ 37.69	122.41 $\pm$ 13.66
	<i>Pan</i>	211.77 $\pm$ 40.01	143.38 $\pm$ 23.93	68.39 $\pm$ 17.99	213.39 $\pm$ 20.57	49.92 $\pm$ 1.99
	<i>Pongo</i>	227.16 $\pm$ 53.48	139.52 $\pm$ 26.91	87.63 $\pm$ 27.81	291.03 $\pm$ 61.98	63.92 $\pm$ 15.12

portion. Additional DNE parameters for outlier and boundary exclusion were left at their default values (Pampush et al. 2016a). Each of the non-hominoid taxa was assigned into a traditional heuristic dietary category (i.e., insectivore, folivore, frugivore, etc.) following the same designations used by Winchester et al. (2014) when they originally published these surfaces. Additionally, three different scaling measures were collected; species mean body mass for all available taxa was recovered from the literature, tooth length was taken directly from the surfaces themselves, and scanning resolution (in millimeters) was recorded for each specimen.

To investigate the dietary signal from the isolated convex component of DNE, the Winchester et al. (2014) data set was

reanalyzed comparing convex DNE with traditional dietary categories using a phylogenetically controlled Markov-chain Monte Carlo sampled generalized linear model (MCMCglmm) through the R package MCMCglmm (Hadfield 2010). The advantage of using the MCMCglmm rather than a simple phylogenetically controlled least-squares regression (i.e., PGLS; see Grafen 1989), is that in the former, data entries do not need to be reduced to species averages and instead individual specimen measures can be used as we have done here.

A series of additional MCMCglmms were performed to investigate scaling allometry of concave DNE and the DNE-R. Logit-transformed DNE-R was compared with

Table 2 Ratio Values

Group	Diet/Genus	Concave/Convex DNE Ratio (DNE-R)	Concave/Convex Surface Area Ratio (SA-R)
Prosimians	Folivory	0.227	0.353
	Frugivory	0.196	0.336
	Insectivory	0.259	0.408
	Omnivory	0.213	0.348
Platyrrhines	Folivory	0.325	0.295
	Frugivory	0.283	0.289
	Durophagy/Omnivory	0.235	0.281
	Insectivory	0.311	0.328
Apes	<i>Gorilla</i>	0.723	0.290
	<i>Pan</i>	0.476	0.233
	<i>Pongo</i>	0.628	0.219

Notes: Heat-map table shows higher values with darker cell backgrounds and lower values with paler cell backgrounds.

log-transformed tooth length, log-transformed body mass, and scanning resolution in models incorporating all taxa, and within each of the taxonomic groupings. In keeping with prior dental topography studies that have grouped strepsirrhines and tarsiers from this data set together into the ecomorphological (and now systematically defunct) category ‘prosimians’ (Boyer 2008; Bunn et al. 2011; Winchester et al. 2014), we employ this nomen and compare these taxa with platyrrhines and hominoids. The phylogenetic tree used for these analyses was downloaded from 10 k trees (Arnold et al. 2010) and reflects the modern cladistic systematic consensus that there are two basal clades of primates, Strepsirhini and Haplorhini, the latter consisting of anthropoids and

tarsiers. All MCMCglmm analyses employed a sampling rate of 50, a burn-in of 3,000, and were iterated 250,000 times. All MCMCglmm posterior distributions were tested for convergence using the R package *coda* (Plummer et al. 2006).

In addition to the MCMCglmm, non-phylogenetically controlled ANOVAs were performed examining logit-transformed DNE-R and SA-R sorted by taxonomic groupings to gain insights into potential grade effects using base R functions (R Core Team 2017). Finally, logit-transformed DNE-R and SA-R were compared with diet in phylogenetically controlled ANOVAs within prosimians and platyrrhines using the R package *phytools* (Revell 2012).

Fig. 2 **A** and **B**: Summary pie charts showing average convex and concave contributions to subsets of the sample. Platyrrhines and prosimians are sorted by dietary categories following Winchester et al. (2014). Apes (plotted with red) are grouped according to genus. **A**. Convex and concave proportions of surface DNE. **B**. Convex and concave proportions of M_2 surface area. Note the significantly larger percentage of concave DNE derived from ape molars, despite smaller percentage of concave surface area as compared to the other primates analyzed here. **C**. Overlaid boxplots of conventional (i.e., ‘Total’) DNE that incorporates DNE from the concave portions of the tooth crown (in faded colors) and convex DNE (in bolder colors).

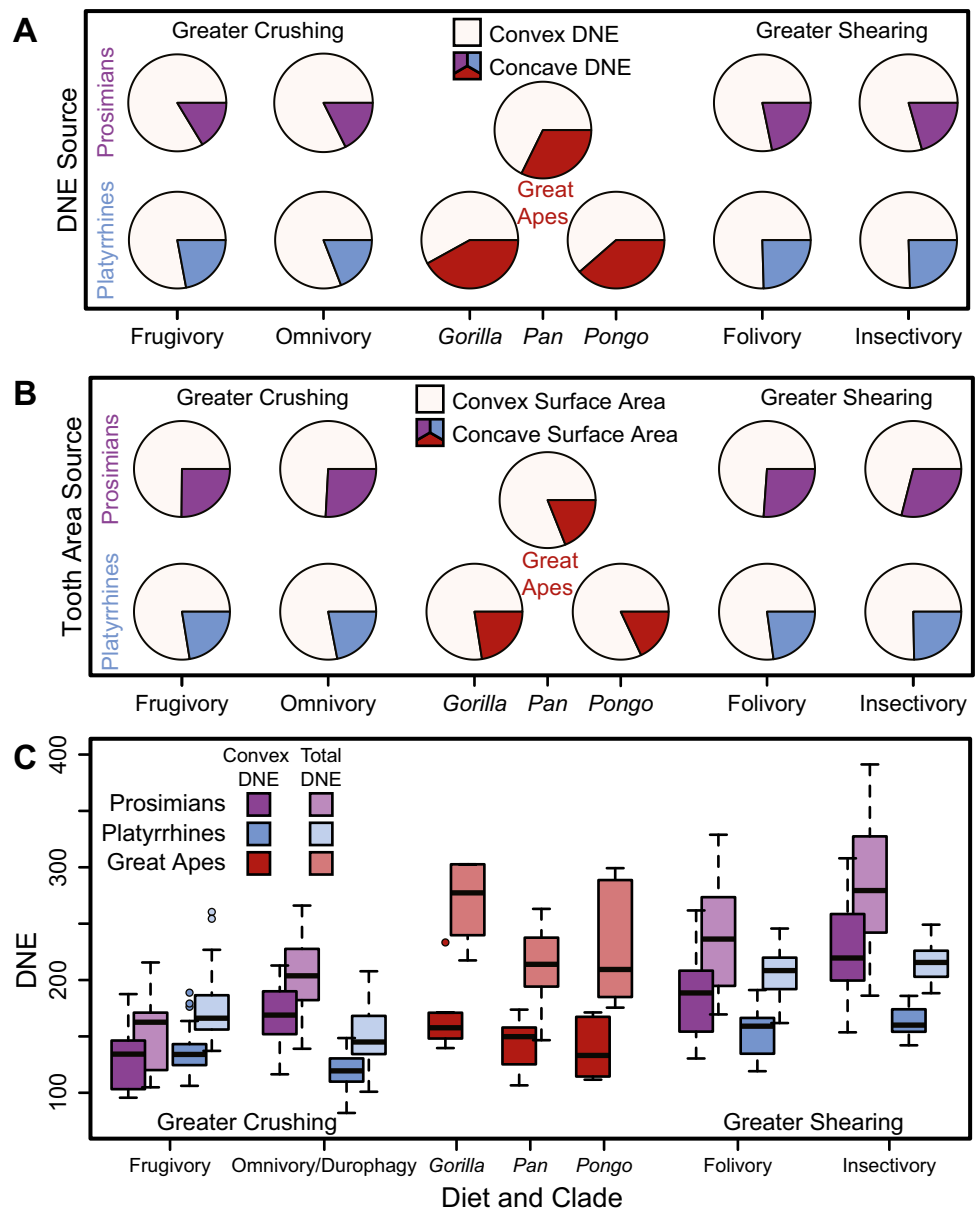


Table 3 Phylogenetically controlled MCMCglmm results comparing convex DNE with diet using Winchester et al. (2014) sample

	Posterior Mean	l-95% CI	u-95% CI	eff. Sample	<i>p</i>
(Intercept)	129.083	82.515	181.224	5294	<0.001
Folivory	40.014	2.953	76.822	5160	0.0352
Frugivory	19.053	-16.629	50.935	5479	0.2757
Grubivory	-57.463	-146.868	27.158	5813	0.1951
Insectivory	87.303	46.187	128.102	4940	<0.001
Omnivory	34.236	-8.181	76.016	4940	0.1081

Posterior Mean = average posterior effect size, l-95% CI = lower confidence interval on effect size, u-95% CI = upper confidence interval on effect size, eff.Sample = effective sample size, *p* = probability

Results

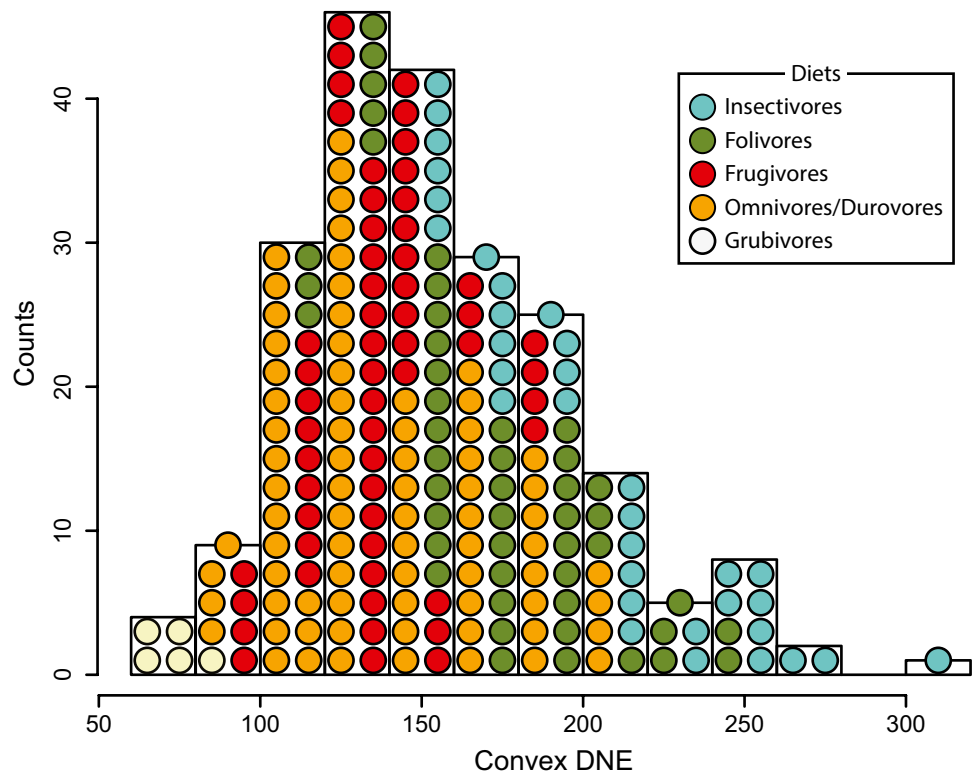
Summary statistics describing the mean values of DNE, convex DNE, concave DNE, convex surface area, and concave surface area (with $kappa=0$) are organized by taxonomic group and diet in Table 1. The DNE ratio (DNE-R) and surface area ratio (SA-R)—both defined as concave/convex—are presented in heat-map style in Table 2, illustrating that while the hominoids have much higher DNE-R values, they possess relatively low SA-R values. Pie charts organized by taxonomic group and diet visually present these ratios in Fig. 2A, B. All raw data, including the surface files used to perform these calculations are available in Online Resource 4.

Table 4 MCMCglmm results of size analyses

Model	post.coef (95CI range)	eff.sample	pMCMC
All Specimens	0.5144	5440	0.002
DNE-R ~ Tooth Length	(0.166–0.846)		
Prosimians	0.2611	4940	0.285
DNE-R ~ Tooth Length	(-0.223–0.739)		
Platyrrhines	0.3078	5990	0.291
DNE-R ~ Tooth Length	(-0.264–0.888)		
Apes	2.369	4335	0.002
DNE-R ~ Tooth Length	(1.066–3.632)		
All Specimens	0.1353	4940	0.055
DNE-R ~ Body Mass	(-0.007–0.267)		
Prosimians	-0.022	4940	0.790
DNE-R ~ Body Mass	(-0.187–0.141)		
Platyrrhines	0.080	4940	0.630
DNE-R ~ Body Mass	(-0.275–0.399)		
Apes	0.8736	5711	0.006
DNE-R ~ Body Mass	(0.385–1.416)		

post.coef = posterior correlation coefficient. eff.sample = effective sample size. pMCMC = MCMC specific probability

Examination of convex DNE's diet-based sorting ability shows (as expected) that insectivores and folivores tend to have higher convex DNE values than those of frugivores and omnivores, reflecting their overall sharper cusps and crests (Table 3). These trends are visualized in the colored histogram in Fig. 3, and the differences between conventional

Fig. 3 Histogram of entire dental sample's convex DNE distribution. Colored circles represent individual specimens and their dietary category. Apes are included among omnivores

(i.e. total) DNE and convex DNE are shown in the box plots of Fig. 2C.

Multiple MCMCglmm results are presented in Table 4, describing the statistical relationships between DNE-R and two measures of size, tooth length and average species body mass. MCMCglmm models in these analyses employed the entire data set as well as specific examinations of the taxonomic groupings. The overall distributions of tooth length and average species body mass are visualized against logit-transformed DNE-R in Fig. 4A, B. Three of these models returned significant correlations: DNE-R is significantly correlated with tooth length across all specimens, and DNE-R is also significantly correlated with tooth length within great apes, but not within the other groups. Finally, DNE-R is significantly correlated with average species body mass within great apes, but not within or across the other groups.

Significant correlations exist between DNE-R and scan resolution across all specimens and within great apes, as well as between concave DNE and scan resolution across all specimens and within apes. Table 5 presents the results of MCMCglmm analyses comparing scanning resolution with

two measures: DNE-R and concave DNE. Like the other set of MCMCglmm analyses, these use several different specimen partitions—across all specimens, and then within each of the groupings (i.e., prosimians, platyrrhines, and great apes). The relationship between scan resolution and logit-transformed DNE-R is plotted in Fig. 4C, and between scan resolution and concave DNE in Fig. 4D. In both cases, these significant relationships appear to be driven by gorillas, which required much lower resolutions during scanning due to their significantly larger size than even the other apes.

In a post hoc analysis aimed at investigating the relationship between scanning resolution against concave DNE and DNE-R, we scanned a single maxillary molar (M^2) of *Pan troglodytes* at three different resolutions (9, 18, and 36 μm), and then subjected the different scans to the previously described processing regime of simplifying, remeshing, and smoothing to end up with three different ~10,000 face PLY files. DNE-R (concave/convex) for these surfaces is highest for the 9 μm resolution scan at 0.875, followed by a precipitous drop off to a DNE-R of 0.514 at the 18 μm scale. The 36 μm scan has a DNE-R of 0.431 as

Fig. 4 Scatter plots comparing logit-transformed DNE-R (ratio of concave to convex DNE) with measures of taxon size and scanning resolution. **A.** Log-transformed average species body mass, collected from the literature. **B.** Log-transformed tooth length measured from the digital surfaces. **C.** Logit-transformed DNE ratio (concave/convex) with scanning resolution. **D.** Concave DNE against scanning resolution. The platyrrhines and prosimians were all scanned at either 10 or 18 μm resolutions, whereas apes required lower scanning resolutions due to their larger size

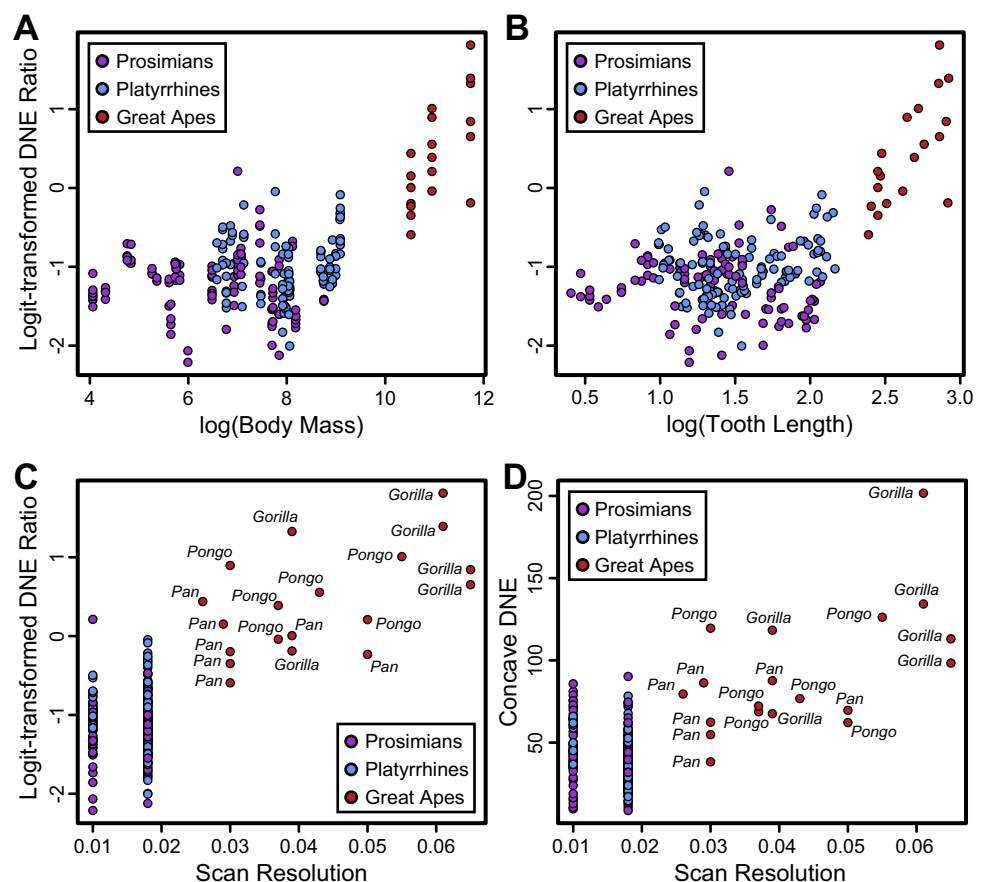


Table 5 MCMCglmm results of resolution analyses

Model	post.coeff (95CI range)	eff.sample	pMCMC
All Specimens DNE-R ~ Scan Resolution	14.868 (3.130–25.837)	4940	0.012
Prosimians DNE-R ~ Scan Resolution	–4.630 (–27.994–20.506)	4940	0.702
Platyrrhines DNE-R ~ Scan Resolution	–28.417 (–126.821–76.203)	4940	0.567
Apes DNE-R ~ Scan Resolution	26.555 (4.173–50.032)	787.4	0.039
All Specimens concave DNE ~ Scan Resolution	894.97 (437.88–1405.28)	4940	< 0.001
Prosimians concave DNE ~ Scan Resolution	–421.47 (–1258.91–445.14)	4940	0.342
Platyrrhines concave DNE ~ Scan Resolution	–2007.579 (–5519.13–1327.141)	4940	0.227
Apes concave DNE ~ Scan Resolution	1621.22 (319.49–2827.97)	3480	0.020

post.coeff = posterior correlation coefficient. eff.sample = effective sample size. pMCMC = MCMC specific probability

the relationship appears to level-off (see Online Resource 5 for plots and Online Resource 6 for table of raw values). From this analysis it is safe to conclude that as scanning resolution decreases, the amount of concave DNE contained in digitized models of teeth decreases much more quickly than does the amount of convex DNE. Thus, if any of the specimens scanned for these analyses would be biased with methodological inflation of concave DNE it would be the specimens scanned at the finest resolution. Therefore, the relatively inflated concave DNE values observed in these great ape molars in our sample are unlikely to be an artifact of lower scanning resolution.

Conventional ANOVAs comparing logit-transformed DNE-R and surface area ratios across the taxonomic groups indicates significant differences among these groupings (Table 6). This is suggestive of a grade shift between great apes and the other taxa within this sample. Furthermore, phylogenetically-controlled ANOVAs examining logit-transformed DNE-R and SA-R within the prosimian and platyrrhine groupings show only one significant relationship to diet, among prosimians and DNE-R (Table 7). These additional ANOVAs further suggest that the increase in DNE-R and SA-R is not a product of diet, but rather suggests historical contingency in the *Baupläne* of these primate molars.

Table 6 ANOVA of Ratios Comparing Phylogenetic Groups

Model	DF	F-value	P-value
DNE-R ~ Phylogenetic Group	2	130.8	< 0.001
SA-R ~ Phylogenetic Group	2	54.55	< 0.001

Discussion

Utility of Convex DNE for Studies of Dietary Ecology (Goal 2)

Conventional Dirichlet normal energy is regarded as a proxy for surface sharpness (Bunn et al. 2011; Winchester et al. 2014; Pampush et al. 2016b), a property expected to correlate with fibrous and tough diets in primates (Kay 1975; Lucas 2006). However, when decomposed and critically assessed for their functional implications, not all components of the conventional DNE measurement can be deductively associated with a *functionally* sharp occlusal surface (i.e., a surface consisting of blades that might be expected to interact with and cut food). Notably, concave components of the occlusal surface can consist of very sharp and deep crevices; such concave features are oriented towards the enamel dentine junction and would not be expected to directly interact with a food bolus. Obviously,

Table 7 Phylogenetic ANOVA of Ratios Comparing Diets within Phylogenetic Groups

Model	F-value	P-value
Prosimians DNE-R ~ Diet	7.738	0.044
Prosimians SA-R ~ Diet	7.393	0.051
Platyrrhines DNE-R ~ Diet	1.345	0.710
Platyrrhines SA-R ~ Diet	2.186	0.506

this presents an explanatory challenge to researchers using conventional DNE to ascribe dietary characteristics from occlusal surfaces. Rather than arguing that concave sulci have a functional shearing role during mastication, a more plausible stance is to argue that concave DNE contributes ‘noise’ when the measurement is used as to assess a tooth’s shearing ability. Concave ‘noise’ of this kind is likely to play a role to some degree among nearly all mammalian molars, since complex mammalian cheek teeth are almost always characterized by both crevices and crests. For the continued application of DNE among primates, it is reassuring to note that the isolated convex component of DNE—measured from the portion of the occlusal surface oriented toward food contact—is correlated with fibrous diets needing masticatory cutting, supporting Winchester et al.’s (2014) general conclusions (Table 3, Figs. 2C and 3). The reanalyzed Winchester et al. (2014) data set of prosimian and platyrrhine primates shows that insectivorous and folivorous taxa from both groups exhibit higher convex DNE values than their more frugivorous or omnivorous/

durophagous relatives (Figs. 2C and 3). Close inspection of the regions of the molars that produce the highest levels of convex DNE show that they are associated with ‘shearing crests’ used in Phase I of the chewing power stroke (Fig. 5), further underscoring that convex DNE is capturing functionally relevant information. It should be noted however, that the prosimians and platyrrhines contained in the Winchester et al. (2014) data set all exhibit fairly similar ratios of convex to concave DNE (DNE-R Table 2). Thus the switch to analyzing only the convex DNE component had little to no effect on the relative arrangement of measured specimen values—and therefore pertinent dietary inferences—of these taxa. Given these results, conventional DNE analyses which have previously looked at prosimians, platyrrhines, and other close relatives are unlikely to gain new ecological insights with this revision to the DNE measurement, even if the measure is now more theoretically consistent with current models of tooth function (e.g., Ledogar et al. 2013; Winchester et al. 2014; López-Torres et al. 2018; Selig et al. 2019, 2021). However, this new

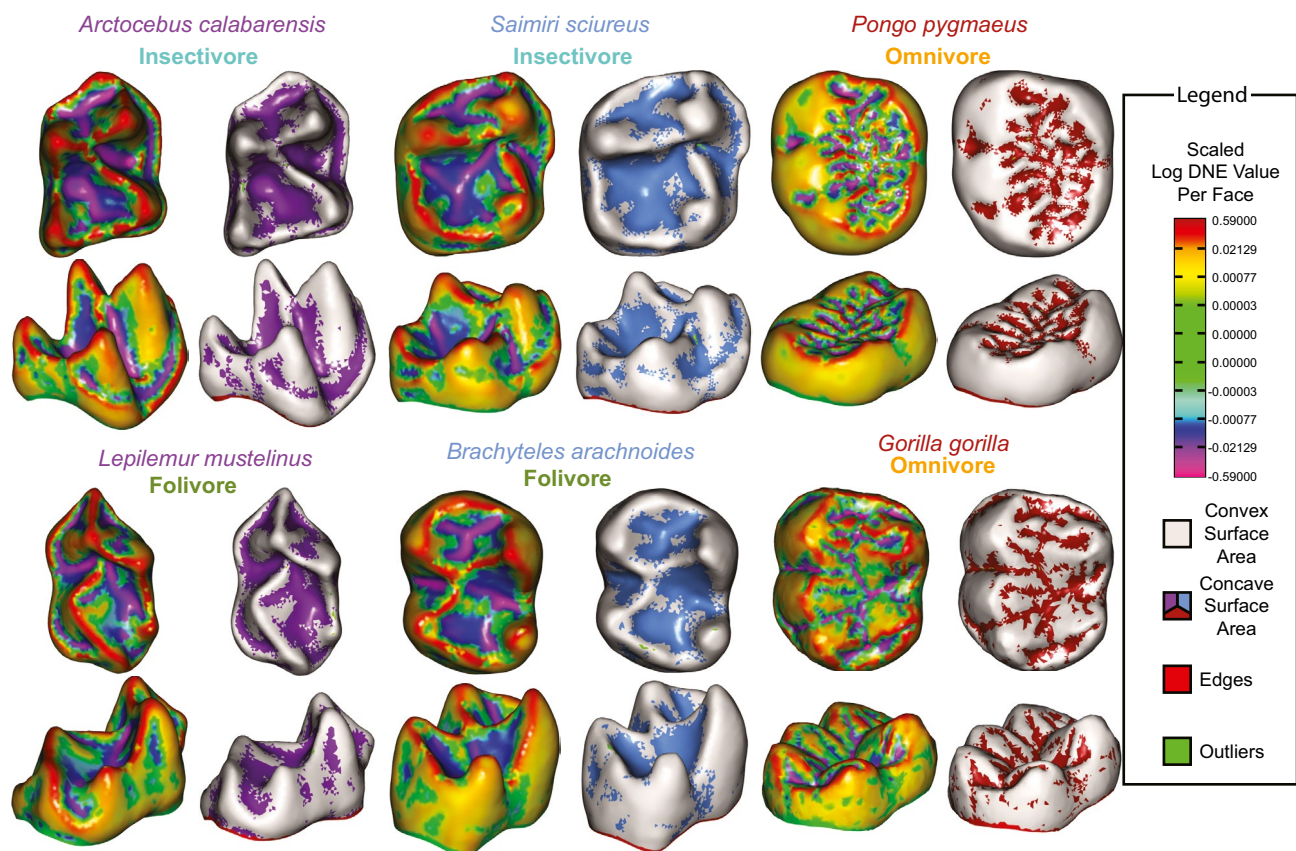


Fig. 5 M_2 models of representative specimens from each taxonomic grouping, in occlusal and oblique perspectives. Left images in each pair illustrate sign-oriented DNE (scaled consistently among all specimens) in log-scale to improve visualization of surface curvature. Right images in each pair illustrate convex and concave regions of the M_2 surfaces. Note that in contrast to prosimian

and platyrrhine folivores and insectivores, these *Pongo* and *Gorilla* M_2 s show both relatively lower, more rounded cusps, and smaller, more discretized concave regions corresponding to grooves and sulci. The narrow nature of these concave regions accounts for the relatively lower concave area observed in ape molars (Fig. 2B), but also generates high DNE values (Fig. 6)

approach does appear to have implications for analyses of great ape molars (see below), and potentially other taxa characterized by different ratios of concave to convex DNE.

Taxonomic Differences and the Functionality of Concave DNE (Goal 3)

In contrast to the measures taken from prosimians and platyrrhines, great ape molars tend to exhibit large amounts of highly concentrated concave DNE (i.e., DNE arising from the concave areas of the occlusal surface; Table 1, Fig. 2A). This concave DNE contribution is particularly striking among apes because of the relatively small amount of surface area it is derived from (for examples of surfaces see Figs. 2A, B and 5). In the case of great apes, this concave DNE contribution is likely confounding the interpretive power of the conventional (i.e., total-surface) DNE measurement (Fig. 6) because the sharp edges of these concave features are oriented inward towards the enamel-dentine junction, and are certainly not being used to shred, slice, or cut food. When the outsized concave contribution to total DNE is included during dietary interpretation of great apes, they cluster with primate folivores (Fig. 2C). Such a finding could be interpreted as indicating that great ape occlusal surfaces are relatively sharp compared with other primates, and suggestive of adaptation for shearing-based mastication of highly fibrous or mechanically tough diets. However, this interpretation does not square with the ecologically well-characterized great ape diets typically full of fruit, nuts, herbaceous vegetation, and occasionally meat (e.g., Watts 1984; Nishihara 1995; Pruetz 2006; Taylor 2006; Kanamori et al. 2010). Mountain gorillas, on the other hand, are known to be highly folivorous (Schaller 1963; Fossey and Harcourt 1977; Watts 1984), but were not analyzed here; our sample is composed of western lowland gorillas characterized by more frugivorous diets (Doran et al. 2002; Doran-Sheehy et al. 2009). When the ape molars are assessed for only convex DNE, their measures fall out with the convex DNE measurements of the platyrrhines and prosimian species Winchester et al. (2014) labeled as omnivores (Fig. 2C). This omnivore designation reflects not only the reported diversity of great ape diets, but likely the current precision of the DNE measurement when trying to characterize dietary adaptation on generalized occlusal morphologies.

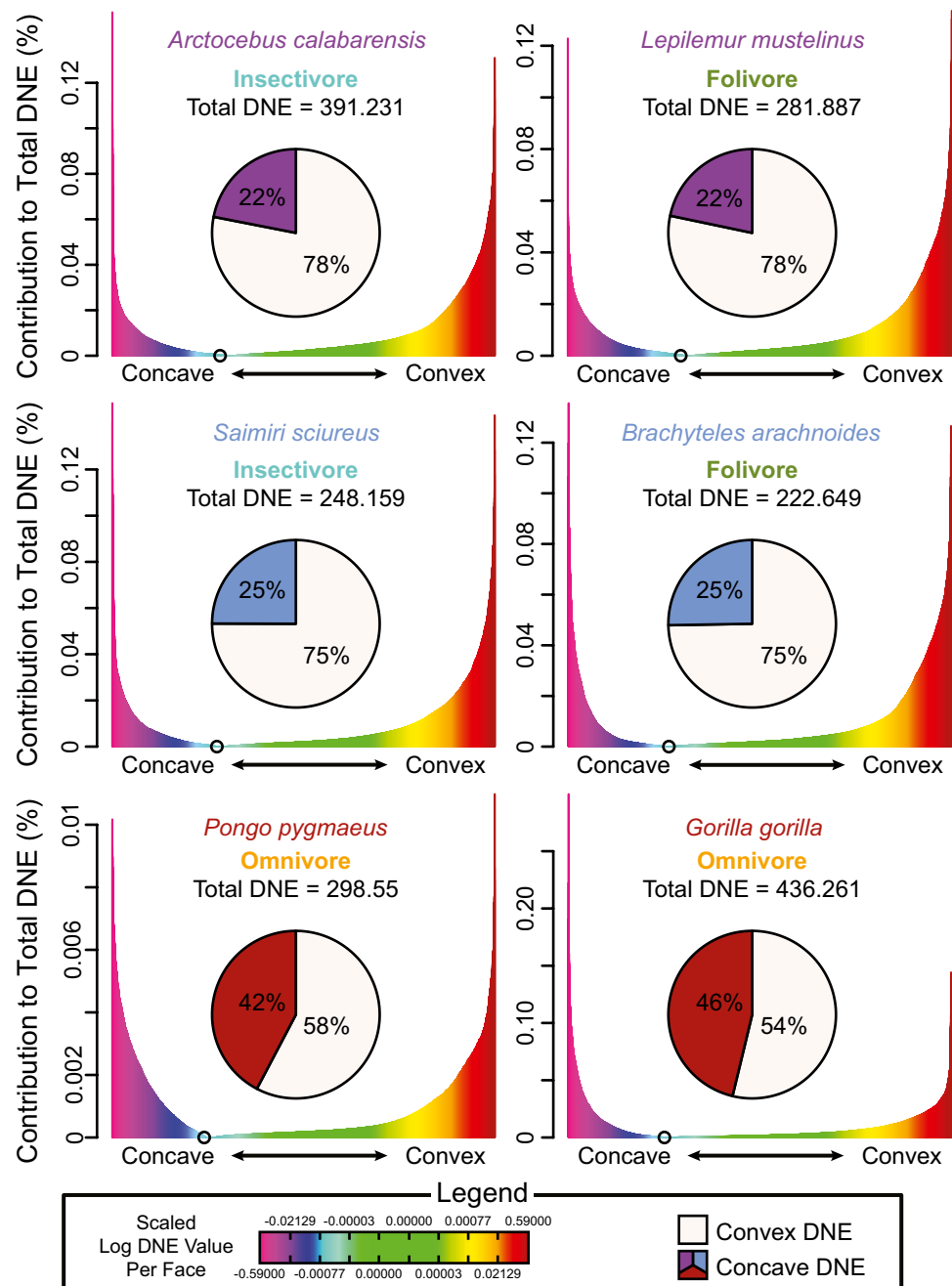
The preponderance of sharp sulci on ape teeth begs the question as to whether there might be some relationship with tooth function or if their presence is related to how tooth enamel develops. Regarding the morphogenesis of the ape occlusal sulci (and therefore the measured concave DNE), Butler (1956) noted that sulci normally correspond in position to valleys in the surface of the dentine. He suggested that they may be greatly exaggerated in depth owing to a localized failure of enamel formation, an epiphenomenon

of the restriction of the vascular supply to the ameloblasts lying in the depths of the sulcus. If Butler is correct, deep sulci would be an example of fabrication noise (Seilacher 1973). In keeping with Butler's (1956) model, for the comparatively thick-enameled primates like *Homo*, *Australopithecus*, *Paranthropus* or *Pongo* (Grine and Martin 1988; Shellis et al. 1998) the deep occlusal sulci are possibly the spandrellic consequence of the evolution of thicker enamel driven by the need to overcome stresses directed normal to the occlusal plane and/or exposure to dietary abrasives and wear (Kay 1981; Vogel et al. 2008; Pampush et al. 2013). In such a scenario, the enamel thickness of the cusps is the principal target of selection and the thickening of the cuspal enamel should prove sufficient by itself to achieve functional competence with or without the accompanying sulci. However, this potential process cannot explain the presence of all great ape deep occlusal sulci because not all have evolved thickened molar enamel (Molnar and Gantt 1977). Indeed, many Miocene apes have thick enamel without deep occlusal sulci (Alba et al. 2010). Another complication is the degree to which dentine surface complexity is echoed in the outer enamel surface, a relationship with considerable variation among primates, and particularly so among the great apes (Skinner et al. 2010). Further research is needed to determine the potential functional value of the highly crenulated occlusal basins often found, for example, in *Pongo* and the platyrrhine *Chiropotes* (Vogel et al. 2008; Ledogar et al. 2013). Whatever the ultimate cause, our results indicate that the concave DNE contributed from the sulci and inward crenulations of hominoid molars should not be viewed as tooth sharpness, as it relates to the ability of teeth to cut through tough foods.

The occlusal sulci on hominoid (including human) molars are not necessarily functionless morphogenic byproducts, although as noted above, that remains a distinct possibility. Yet, before applying an abstract and complex measurement like DNE in the study of occlusal sulcus morphology, it is worth asking some basic questions to better frame ecological hypotheses so as to consciously avoid the sharpshooter fallacy² (see Evers 2017). What function do the sulci serve other than to separate the tooth into discrete cusps and crests? How exactly should researchers use a measurement like DNE to functionally assess concavely oriented sulci

² As explained by Evers (2017), the sharpshooter fallacy arises when particular outcomes are assessed without proper context and perceived patterns are erroneously assumed to be linked to some underlying cause. This fallacy is illustrated with a parable about a poor marksman who shoots without aiming at a barn and later paints targets around the bullet holes. Researchers can fall victim to this fallacy if they indiscriminately apply complex measurements like DNE to morphologies without specific expectations for what they are trying to measure.

Fig. 6 Bar plots showing the relative contribution to total DNE from each face on the surface of the representative specimens illustrated in Fig. 5. Face DNE values are ordered from most concave to most convex and colored consistently with the DNE plots in Fig. 5. Open circle along x-axis represents the inflection point where surface orientation transitions from concave to convex (i.e., neutral or 'flat' orientation). Pie charts embedded in the plots show the relative contributions to DNE from the concave and convex portions of each surface. Note the relatively steep slopes of the prosimian and platyrrhine concave faces, while the apes show much shallower slopes, indicating the larger number of concave faces making significant contributions to total DNE



within their ecological hypothesis? Perhaps the sulci serve as 'stress sinks' during crushing actions, acting in concert with buttressing features like the 'protostylid' and 'trigonid crest' to protect the non-renewable enamel from cracks and catastrophic failure as some have speculated (e.g., Benazzi et al. 2013). If this is the case, then before applying DNE (or any other abstract topographical measurement) it is worth examining what kind of sulcus morphology would best accommodate this role and how concave DNE might correlate with that morphology. One way to approach this is to use the optimality criterion (Parker and Maynard Smith 1990), which argues that a morphology is well suited to counter

particular loading regimes if it evenly distributes stress throughout the structure, thereby avoiding the production of failure points. It is well known that enamel cracks form from concentrated stress (Lucas 2006; Lucas et al. 2008), and sharp deep sulci engender stress concentrations during loading (Benazzi et al. 2013). Cracks, even in deep sulci, expose the underlying dentine to bacterial colonization and the development of dental caries. In fact, deep occlusal sulci are associated with dental caries with or without cracks in the enamel (Brown 1970). All other things being equal, a better morphology for countering masticatory crushing loads would involve parabolic shaped cusps and sulcal basins

which would more evenly distribute stresses (Lucas 2006; Constantino et al. 2011). As this work has shown, sharp deep sulci correlate with high concave DNE values, and thus transitively, high concave DNE should correlate with the production of large stress concentrations in sulci during heavy masticatory loading. Given the framework of this functional hypothesis, concave DNE should be *negatively* correlated with enabling stress dissipation during hard object feeding. Furthermore, if sharp, deep occlusal sulci are stress-sinks for crushing hard foods, then these features should be associated with other adaptations for hard-object feeding like thick enamel. The taxon possessing the largest average concave DNE in our sample is the relatively thin-enameled *Gorilla gorilla*, not the thick-enameled hard-object feeder *Pongo pygmaeus* (Schwartz 2000). These observations run counter to the expectations of the stress-sink hypothesis, suggesting that this hypothesis is poorly framed and/or that DNE is not an appropriate tool for assessing occlusal sulci's functional role(s)—assuming occlusal sulci are more than just spandrels.

Considering the above, when applying conventional DNE to a dental surface we find ourselves at something of an interpretive impasse. Convex DNE measures outward facing sharpness, plausibly linked to cutting ability and correlated with dietary toughness and fiber content, while concave DNE measures inward facing sharpness which is likely engendering stress concentrations that are seemingly maladaptive for crushing loads and have no plausible functionality for shearing. Given this framing, we see no value in combining these two sources of DNE into a single measurement, since they are likely tracking very different functional (or even fabrication) consequences of the dental morphology, one directed outward toward the food bolus and the other inward to the internal structure of the tooth. Additionally, it has been shown that concave and convex DNE are not necessarily correlated across taxa, and if comingled into a single measurement, researchers cannot discern whether they are measuring outward or inward oriented sharpness. Perhaps deep occlusal sulci have some functional role only realized with sufficient dental wear, but such a hypothesis is yet to be articulated or tested. Until there is some demonstrable functional benefit for sharp concave sulci included in the functional complex associated with shearing, researchers using DNE as a sharpness proxy to study feeding ecology and adaptation are best advised to disregard concave DNE and focus on the convex DNE component.

Effects of Scaling and Digitization on DNE Ratios (Goal 4)

While measures of convex DNE align the great apes with other primate omnivores, a central question remains, why do these great ape molars show such radically higher values of

concave DNE and therefore significantly different DNE-R than their prosimian and platyrrhine relatives (Table 2, Figs. 2 and 6)? Despite the mathematical proofs indicating that the DNE measurement is unitless (see Bunn et al. 2011; Pampush et al. 2016a), the size disparity among the taxa of this study naturally points towards two inter-related forms of allometric scaling concerns: methodological and biological. Methodologically, to produce faithful digital models of their molars, the specimens in this study were necessarily scanned at different resolutions. It is therefore possible that the increased relative amount of concave DNE among great apes is the byproduct of different scan resolutions. The non-ape teeth used in this study were scanned at resolutions of 10 and 18 μm , but the apes were scanned at lower 23–65 μm resolutions. There are detectable trends between DNE-R and concave DNE with scan resolution across the entire sample (Table 5, Fig. 4), however closer inspection of these results suggests that this relationship is driven by the gorilla sample. Gorillas exhibit not only the largest size of any of the specimens in the sample, but also exhibit the largest DNE-R values (concave to convex, Table 2). Within only the prosimians and platyrrhines, both of which have specimens scanned at 10 and 18 μm resolutions, there are no differences in the DNE-R or quantities of concave DNE (Table 5, Fig. 4). The findings within the non-ape sample in which some specimens have been scanned at roughly half the resolution of others, suggest that the inflated concave DNE measures characteristic of great apes are not the result of scanning differences. Moreover, a lower scan resolution should cause features such as narrow crests and sulci to be represented as blunter rather than sharper edges on digitized surface models—the reverse of our findings. Indeed, in our *post-hoc* analysis of an upper molar of a chimpanzee scanned at three different resolutions, both convex and concave DNE were observed to decrease with coarser resolutions, but the concave DNE does so much more dramatically than does the convex DNE component (Online Resources 5 and 6).

Having discounted a methodological origin for our observations, we conclude that there is something biologically different about great ape molars apart from their size, which is producing these concave DNE results. The other size-based analyses presented in Table 4, and Fig. 4 support this suggestion. In a pattern very similar to the resolution analyses, when compared with tooth length, DNE-R is significantly correlated across the whole data set as well as within the apes but not within any other subsets of the specimens (Table 4, Fig. 4B). The analyses of species body mass averages against DNE-R (Fig. 4A) showed significant correlation within apes, but not within prosimians, within platyrrhines, or across the specimens generally. Additionally, the non-phylogenetically controlled ANOVAs comparing DNE-R and SA-R among the three groups confirm that apes stand apart from the other primates analyzed here

(Table 6). In concert, these findings suggest that DNE-R results are not the product of scaling problems associated with producing the measurement nor the result of some sort of primate-wide scaling phenomenon; rather they seem to be related to the biology of great ape dental structure alone. Researchers might speculatively associate the higher levels of concave DNE found on great ape molars with processes of evolving relatively thicker enamel (Molnar and Gantt 1977), developmental interactions with the underlying dentine surface—which is typically more complex in apes (Skinner et al. 2010)—or to a functional stress-dissipating role (Benazzi et al. 2013), but as discussed above, further research is required to explore these hypotheses and their consequences before drawing informed conclusions.

Conclusions

Dirichlet normal energy (DNE) is one of several new and potentially useful dental topographic measurements with relevance for understanding tooth function and inferring dietary behavior in extinct primates. This study analyzes DNE's ability to provide functionally relevant insights when employed in dietary ecology studies of primate (and mammalian) cheek teeth. Following the deductive decomposition of the measurement into its concave and convex components, we propose a modification to the DNE measurement whereby the concave and convex portions of the occlusal surface are partitioned into their separate contributions to the total surface-wide DNE measure. The interpretive consequences of this refinement are explored, and several major conclusions reached: (1) DNE's value is found in its ability to capture functional properties of occlusal surfaces (specifically the ability to reduce the size of food particles by shearing and/or cutting), and should be employed in the context of *functional* dietary ecology hypotheses. (2) The value of DNE as a functional signal is undermined by considering the combined concave and convex contributions to total surface-wide DNE. These separate components of occlusal morphology have distinct (and uncorrelated) functional consequences, the former being associated with the ability of teeth to comminute food and the latter of uncertain significance but possibly related to attenuating internal stresses or an artifact of enamel growth. Therefore, combining the two produces incoherence in the functional interpretation of DNE values. (3) In the specific case of great apes and (speculatively) other mammals exhibiting similar occlusal features on their molars (e.g., some bears, bunodont artiodactyls, sea otters etc.), sharply grooved and inwardly oriented sulci or furrows contribute 'sharpness' components whose function has not been established and may not be relevant to the ability of the tooth to cut tough foods, and therefore add 'noise' to the functional utility of the total DNE signal,

potentially misleading inferences about the diet of investigated taxa. (4) Consideration of convex DNE in isolation retains and refines the validity of previous findings regarding relationships between occlusal sharpness and consumption of dietary fiber, whether that be chitinous insect exoskeletons or cellulose plant fiber, while also aligning those taxa with sharply concave surfaces (i.e., great apes) with the functional expectations the measurement was originally intended to reflect. (5) Methodologically, large quantities of concave DNE do not appear to be artifacts of the scanning and digitization process, but rather seem to be derived from something distinct about the morphogenesis of particular mammalian teeth. Given these findings, this refinement to DNE should help researchers using it to bring new insights to dietary-reconstruction debates involving molars with deep occlusal sulci, such as those found among hominins.

Dental topography measures offer great promise for bringing new insights to our collective understanding of the function and adaptation of molar teeth, particularly in the integrated context of dental lifespans. However, researchers need to articulate their questions carefully while incorporating the assumptions and accounting for the capabilities of these abstract quantifications of morphology in their studies, and resist being seduced by the 'objectivity' the derived numerical values seem to present. The presented refinement and discussion of DNE here should help researchers effectively and intelligently deploy this measurement, and the other dental topography measurements should be similarly explored for improvements, coherence, and proper application.

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Data Availability Statement The updated version of the R-package `molaR` (5.0) is archived with CRAN (Comprehensive R Archiving Network) and is available free to download and use. Please cite this paper when using Sign-Oriented DNE from `molaR` 5.0. All raw data used to complete these analyses is available with the Supplementary Online Material (Online Resource 4), including the complete set of dental surfaces from which the DNE measurements were derived. See the Online Resources Cover Page (Online Resource 7) accompanying this article for more information.

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