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Journal of Mammalian Evolution

Sign-Oriented Dirichlet Normal Energy: Aligning Dental Topography and Dental Function in the R-package molaR.

--Manuscript Draft--

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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

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	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.

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Dear Dr. Croft,

Thank you for reconsidering our manuscript, "Sign-Oriented Dirichlet Normal Energy: Aligning Dental Topography and Dental Function in the R package molaR" (JOMM-D-21-00070R2), for publication. We feel that our first revision addressed all of the major suggestions/critiques of the two reviewers, and the paper was made much stronger for it. In this second round of revisions, we have further adjusted our language to accommodate some of the new criticisms from Reviewer 2 (R2), but take issue with apparent differences in opinion between us and this reviewer, with capitulation to their perspective fundamentally undermining our central critique of the field of dental topography—something that we consider essential to the manuscript's aims. R2 states:

This paper appears to have two main objectives: improve the DNE method, and defend the functional interpretation of DNE. The first one is very easy, and I am completely convinced that it is valuable. The second objective appears to generate many tangents in the paper that are not particularly necessary and are generally overly long.

I think the manuscript is currently poorly set out, including extensive and sometimes repeated discussions on topics that are really only tangentially related. It appears that the majority of the text added to the Introduction is not particularly informative for the main focus of this manuscript, and can safely be shortened or removed. A lot of the material added in the Methods is also a literature-based review of DNE and would be more relevant in the Introduction or Discussion, and can be significantly shortened, retaining only the modification of the calculation of DNE.

R2 correctly diagnoses the two main thrusts of this paper: [1] to critically assess and improve the DNE measurement in light of tooth functionality, and [2] to make clear that given its detachment from homology, DNE's (and dental topography measurements in general) utility is as an estimate of the tooth's functional abilities. It is surprising to see the reviewer ready to accept the clear benefits of the first goal, but to miss the obvious connection with the second. Indeed, these two goals are deeply intertwined, since the rationale for the DNE improvement is based on the measurement being useful in a functional context. R2 seems to find our critique of prior implementations of DNE and dental topography generally as "tangential" despite their foundational importance for our study in the first place. This appears to be in direct opposition to the assessment of Reviewer 1 (R1), who previously requested that these aspects of the manuscript be expanded. Given what appears to amount to a disagreement in opinion about the utility of dental topography as an approach (as R2 states, "The Results and Discussion section are good" and offers no comments or edits in this portion of the manuscript), we think R2 should be encouraged to publish a critique of this paper rather than blocking us from clearly and fully laying out our argument and position. As we have already addressed a large number of edits from both reviewers in our first round of revisions and R1 is pleased with our current revision, we advocate that the pages of the literature—not confidential peer-reviewed comments—is where the debate between R2's interpretation of dental topography and our own should take place.

Because we need to make several points at length to defend the construction of our manuscript, some of R2's comments are addressed here before the regular table of comments.

Best regards,
James D. Pampush

Reviewer 2:

A lot of the material added in the Methods is also a literature-based review of DNE and would be more relevant in the Introduction or Discussion, and can be significantly shortened, retaining only the modification of the calculation of DNE.

R2 dismisses our deductive analysis of DNE as 'a literature review,' a stance we take issue with and to which we must respond.

The original paper defining DNE for use in dental topography (Bunn et al. 2011) contains only a very technical and somewhat opaque description of the DNE measurement. After describing their surface preparation, they write (pg. 250-251):

The Dirichlet energy is defined to be the extent to which the normal map expands in orthogonal directions: if u and v denote orthonormal direction on the surface, and n(p) denotes the normal at point p on the surface, then locally the normal map expands as $e(p)=\|n_u\|^2 + \|n_v\|^2$, where n_u and n_v denote the derivatives of the normal n in the directions u and v, and $\| \bullet \|$ denotes the Euclidean norm (length) of a vector. The function over the tooth surface e(p) is called energy density. The global measure of curviness is then defined by summing up these local energies over the tooth surface: $E = \int_M e(p)dvol(p)$., where we integrate with respect to the surface area dvol(p).

In case the directions u and v are not orthonormal, the energy density is calculated by $e(p) = tr(G^{-1}H)$, where $G = \begin{pmatrix} \langle u,u \rangle & \langle u,v \rangle \\ \langle u,v \rangle & \langle v,v \rangle \end{pmatrix}$, and $H = \begin{pmatrix} \langle n_u,n_u \rangle & \langle n_u,n_v \rangle \\ \langle n_u,n_v \rangle & \langle n_v,n_v \rangle \end{pmatrix}$ and $\langle \blacksquare, \blacksquare \rangle$ denotes the Euclidean inner-product (dot product). In the discrete surface case, we first approximate the normal of the surface at the each vertex as the normalized average of the normals of its adjacent triangular faces. We then use the previous equation for calculating the energy density in each triangle (assuming that the map *n* is piecewise linear the energy density is constant in each triangle), see Figure 2. Then, we sum the densities multiplied by the area of the faces to get the approximated total energy: $E = \sum_{\Delta \in Faces} e(\Delta) \cdot area(\Delta)$ where Δ is traversing over all the triangles in the tooth surface.

Most readers and users of DNE do not find this description particularly helpful. The next major publication to employ DNE (Winchester et al. 2014) did not expand on this description, and outside of the members of our authorship, no other users of DNE have published further details of how the measurement works. In a 2016 paper (Pampush et al. 2016, American Journal of Physical Anthropology) we are the first describe the energy-density calculation as being based on osculating circles and in the supplemental materials provide more effective visual aids than those provided in either Bunn et al. 2011 or Winchester et al. 2014. By using the osculating circle approach and moving away from the matrix algebra description (like above), we are able to show exactly how the measurement works using a simple hemisphere giving readers and users of DNE access to the internal construction of the measure in ways not previously offered (see Spradley et al. 2017 American Journal of Physical Anthropology, and Pampush et al. 2019 American Journal of Physical Anthropology). In this manuscript, we expand on our more thorough description of the DNE calculation, and directly connect the osculating circle measurement approach with successful correlation of knife stabbing depth (i.e., a performance metric, see Hainsworth et al. 2006 cited in text). This is *not* a review of the literature—it is a coherent, approachable deduction of how

the measurement works including a previously undescribed link with function that together advocate for why our proposed alteration is necessary. We have opted to place this in the methods, since Bunn et al. 2011 describe the 'mathematical background' for DNE in their methods. This deduction is not only one of the explicit goals of our paper, it is a useful contribution for the larger dental topography research community to better understand be fully informed as to how the DNE measurement operates.

R2 makes an about face from their prior critique with the following comment:

L144-153: the corollary of this section is that DNE is merely an 'abstraction of the morphology' as no studies have 'correlated [DNE] with performance outcomes' during mastication. Later in the manuscript the authors expound on the theoretical basis of DNE likely measuring some aspects of sharpness that will affect force to fracture food, but this has not been directly demonstrated for DNE.

The section of text (L144-153) the reviewer is referring to states:

In contrast to standard dental measures, the landmark-free approach which advantages the dental topography measurements also has the effect of disassociating them from models of tooth function and performance. Topography measurements are abstract expressions of surface-wide dental morphology that 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, these measurements are just abstractions of the morphology, and while they may still be useful for tracking broad changes or trends in tooth form, they cannot inform adaptive hypotheses or dietary reconstructions without clearer links to the known modes of masticatory function.

This section of our text follows the specific description of mastication which links homologous landmarks (i.e., tooth cusps) with leading models of tooth function, providing us the rationale for these assertions. Following this text, we deductively analyze DNE and do in fact explicitly link the method of the measurement with performance outcomes (the section R2 described as "unnecessary literature review," as noted above).

To better clarify our position, we have rewritten this section to read:

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 *Bauplanë* 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.

R2 later writes:

L188: do the authors seriously think that dental topographic measurements have been developed without any consideration of their likely functional consequences? The authors need to cite specific studies here to show which metrics they are referring to - which dental topographic measurements are a 'black box operation'? Which have been postulated

and then implemented without some degree of 'first principles' (the 'third method') being put forward? This is not to say that all of these methods are equally insightful about dental function and correlation with diet, but these are all strong words to be said in a manuscript that cannot push these issues forward beyond a minor improvement in one metric.

We think a clear link with function is at the core of the value of dental topography measurements, and that some of these approaches have been developed without any particular regard to the function of the teeth. Rather it seems, some of these measurements were developed because computing abilities have made them possible, and they have been justified post-hoc via re-sorting dental morphologies among known functional categories. There are several examples of this. In the paper we note that OPC does not appear to have a strong functional link for bunodont teeth, but at least the original authors have tried to articulate one using their original, more diverse dental sample. Other dental topography measurements such as Relief Index, Slope, Angularity, and Portion de Ciel Visible do not have clear functional rationales, or only very weak ones. We can offer specific deductive critiques of what we perceive to be 'black box operations' among the listed DT measurements if the editors require it.

We are trying to take a positive stance with our current paper and wish to only vaguely reference what we view as mis-steps by other researchers. There is too much to unpack regarding the production, justification, and use of many dental topography metrics (a criticism of each metric potentially representing a paper unto itself), and we would rather keep the focus on how to properly use this updated version of DNE, and to suggest the appearance of 'red flags' in other measurements. Dental topography as a subdiscipline is—in our opinion—in a very precarious moment of legitimacy. We want to use this paper to help push the use of these metrics in a certain direction and would prefer to leave discussion of the failures of other metrics or their applications to other publications after positioning Convex DNE appropriately. As noted above, R2 appears to differ in their opinion and/or interpretation of the field and its handling of methods. If this is so, then their perspective should be published in response to our manuscript so that a public dialog can emerge with the aim of strengthening and validating the field.

R2 takes issue with our description of OPC, but appears mistaken in their understanding of the metric:

L261: the formulation of OPC does not assume that 'the boundaries between differently-oriented patches represent cutting 'tools'': it is designed to correlate with the number of features on a tooth, but not that each 'patch' is a tool in itself. When the number of hemispherical cusps on a tooth increases from one (OPC~8) to two (OPC~16), we expect that the number of potential interactions between teeth and food doubles; it is not intended that the number of tools is 8 in the first, and 16 in the second tooth. Food can be fractured by both cusp and bladed tooth components - a tooth does not have to have blades to fracture food (see fundamental studies on dental function, as set out by Lucas 2004).

Evans et al. 2007 (Nature) created and defined OPC. In describing their new method, they write (pg.78, emphasis added):

"…An effective way of increasing processing capability is to add features onto the teeth that allow more food to be divided in each occlusal stroke. If we view teeth as 'tools' for breaking down food,[11] this is like adding extra tools to the tooth that function in food breakdown. **This is similar in meaning to 'breakage sites'.**[10] 'Dental complexity' is then any measure of the number of features, tools or breakage sites on a tooth."

Clearly the authors are using the term 'breakage sites' as the feature OPC is expected to correlate with. They cite Lucas 2006 "Dental Functional Morphology" for this definition of breakage sites, but Lucas does not offer a direct definition in his book. He refers again to 'breakage sites' in the book, but then cites earlier works including Lucas et al. 1985 and Lucas et al. 1986, neither of which offer a clear definition. However, Lucas (2006) does cite van der Glas et al. 1992 (Journal of Theoretical Biology) in reference to breakage sites, and these authors define breakage sites as follows pg. 105:

"A breakage site is defined as part of the occlusal surface of the post-canine teeth which is suitable for breaking particles of a particular size."

Again, this is a pretty vague definition, but it seems to be a generalization of the features of a tooth used in breaking down food and most would read this as: breakage sites = cusps and crests. We see several problems with this definition but these also extend to the OPC measurement. First, cusps and crests are most effective at breaking down different types of materials (as extensively outlined in Lucas 2006 and elsewhere). Crests are useful for shredding work-limited (tough) materials, while cusps are better for mashing soft fruits and crushing hard-objects. Conflating these two types of features within a measurement will lead to confounding ecological signals within the data unless the study design accounts for these differences in some other way. Evans et al. 2007 seemed to have accounted for this in their study design by incorporating species ranging from very simple, sectorial teeth with a few cusps and crests to those with highly complex, lophodont dentitions. Thus, the trends in their data are driven by the relative number/length of shearing crests, which the authors seem aware of when interpreting their findings (emphasis added):

Pg. 79 "For carnivorans, OPC shows a relatively clear gradation in dental complexity from low values in hypercarnivores, intermediate in the omnivores, and highest in the herbivores (Fig. 2; P <0.001 for all tests) in both the upper and lower tooth rows… The rodents illustrate a similar trend of dental complexity with diet (Fig. 2)…We note that the better resolving power of OPC [other measures were not significant with dietary correlations] may be due to **its identifying distinct functional surfaces (such as wear facets), fitting with the concept of tooth crown consisting of individual 'tools' for breaking down food**."

Given that the number of cusps is not drastically different between hypercarnivores and herbivores, OPC is increasing with the number of cutting crests on the postcanine teeth, while the number of cusps is being swamped out by the crest count. This is confirmed in noting that this measure works well with lophodont dentitions as other authors have shown but not with more generalized dentitions involving the typical tribosphenic cusps (Pineda-Munoz et al. 2017). Indeed Evans uses this interpretation in a follow up paper on the evolution of horse molars to argue that they show an increasing shearing efficiency throughout their North American lineage because an increase in OPC counts through time is linked to the evolution of more complex and lophed molars (Evans and Janis 2014, Ann. Zool. Fennici). For clades with conservative occlusal features (such as primates), OPC reveals no clear trends among taxa even when contrasting frugivores and folivores, showing a weak correlation between the measurement and the functional demands of teeth (Winchester et al., 2014)

As evidenced above, framing this argument requires a lot of space and we were trying to keep it short in the actual manuscript since this is not a paper about OPC. We have significantly modified our discussion of OPC to reflect this more nuanced perspective but thought the editors could benefit from this discussion in evaluating our manuscript against R2's comments.

R2 has an additional compound comment regarding DNE, its utility, and the deductive analysis:

L199: given how much space the authors give to the first two 'methods', the third method is rather superficially treated, particularly as it relates to the interpretation of DNE. How do we expect DNE to correlate with diets? If DNE measures sharpness, and sharpness affects 'the ability of the interdigitating tooth surfaces to reduce the particle size of chewed food' then why would sharpness not be maximised for all diets? Why would it differ among diets?

We have superficially treated the third method here because we plan on using it to explicate what the DNE measurement is capturing when deployed. We feel this terse introduction to deductive logic prepares readers for the longer discussion of the DNE measurement this reviewer previously referred to as a 'literature review.'

In the deductive analysis of DNE we have 2 main goals: First to show that DNE is a surface-wide extension of the osculating circle approach to measuring sharpness. Second, to show that this measure seems to be effective when applied to knives, that is, when used in a functional context.

This third method is not dependent on diet or dental morphology as the other two are. It is purely an analysis of whether or not DNE is measuring a *useful* property of a surface irrespective of the type of surface or the role of that surface. It seems a safe extension that if DNE is indeed measuring surface sharpness as we attempt to show, that this is a useful property to measure on a surface expected to be used in breaking down other objects/materials.

The reviewer then asks a set of hyperbolic questions regarding the application of DNE in a dietary ecology framework. First, we (and all other authors employing DNE in a dietary framework, to our knowledge) expect the measure to correlate with the need to cut foods and therefore the amount of tough, work-limited, dietary fiber materials in a given diet. Thus primates (and other mammals) consuming larger quantities of tough foods are expected to have higher DNE values on their teeth compared to related taxa consuming less tough food items. DNE is not always maximized because not all dietary materials are best broken down with shearing actions. Some materials are considered stress-limited; these types of materials tend to catastrophically fail when enough stress is imparted into them, as exemplified with the breaking of hard candy. Mammals possessing diets full of stress-limited foods tend to have rounded bulbous cusps and teeth capable of imparting larger force-loads into dietary objects while also dissipating these loads within their own teeth by evenly distributing the strain throughout the enamel cap avoiding the production of failure points. The 'architecture' of sharpness encourages the buildup and concentration of stress, making high DNE teeth unsuitable for hard-object crushing. Other food

materials are better ‘mashed’ rather than cut, like most ripe fruits, and the morphology best suited for this breakdown also involves rounded bulbous cusps. Thus animals with hard-objects (nuts, seeds, bark, etc.) or lots of fruit in their diets are predicted to have lower DNE values (and this has so far proven to be the case), since cutting is not as important during their masticatory events. All of this has been argued extensively in other papers, including: Winchester et al. 2014, Pampush et al. 2016 & 2018 all cited in this paper. It is strange that R2 is apparently either unfamiliar with this literature given its central importance to their critique and our manuscript, or is opting to purposefully ignore it when fielding comments we must reply to.

Reviewer 2:

L213: given the strongly worded statements about how morphologists and ecologist should be 'skeptical of the biological relevance of any surprising or incongruous dental topography findings', why is this skepticism not applied to the typical interpretation of DNE in this manuscript?

Pardon our grumpiness, but to fully explain our position, please consider this theoretical example. Suppose the dietary ecology of a group of organisms is quite well known and established. Now imagine that a new type of measurement is invented. This measurement seems to present an objectivity and attention to detail that was previously unattainable. But the measurement is quite complex to the point that even mathematically and statistically savvy people need to do a fair amount of work to understand its calculation. When applied to the known group of organisms, this new measurement seems to indicate something very surprising and maybe even a reversal in thinking regarding the dietary ecology of our organism.
Are you ready to rewrite the ecology of the organism? Or would you prefer to better understand and investigate the measurement?

It is our very skepticism about DNE, and our deductive work over the last few years in studying it and related measurements which have lead us to write this paper. Given that the motivation for this paper is skepticism of the typical interpretation of DNE, leading us to propose a modification, we find R2’s question baseless. Such a question can only logically arise from either an extraordinarily cursory or incomplete reading of the manuscript, or a deliberate attempt to generate additional comments that imply an inconsistency not present in our work.

Reviewer	Reviewer Comment	Current Location in Manuscript (if applicable)	**Adjustment/Response**

R1.2	The authors have expanded the introduction, explained goals in more detail, and combined some figures. Most of my concerns have been considered or reasons have been given if not. To me the authors answers make sense. I'm looking forward to see the article published.		Thank you, we certainly put a lot of hard work into this paper.
R1.2	I have only one minor suggestion for improving the figures: the authors tried to combine figures, but more needs to be done: figure 2 and 4 can be combined, and figure 5 and 6 as well. In addition table 1 has a lot of empty space: I recommend to move it to the supplement and combine it with SOM Table S1.2.		We made all these changes. Moved table 1 to supplemental, combined figures 2 and 4, as well as 5 and 6.
R2.2	With the focus on defending the functional interpretation of DNE, additional effort should be put into critical evaluation of DNE - it has not been empirically tested, it is a metric of sharpness that cannot be immediately translated to a true size (e.g. radius of curvature in millimeters) that will have different consequences in the mouth of a real-sized animal. Showing both the strengths and weaknesses of all methods is essential for progress in methodological development.		In this paper, we have presented the most thorough analysis of the DNE calculation yet to appear in the literature as mentioned in the comment immediately above from the earlier review. We deductively analyzed the measure, and then discussed the implications for the way it is calculated. We specifically addressed the size issue, and would like to remind the reviewer that the measurement is unitless, and independent of size (facts repeated in every study utilizing DNE). We and many others have noted the advantages and pitfalls of this feature of the measure. I do not think there is anything else to address regarding this comment. The reviewer is correct to say that the measurement has not been 'empirically tested.' We would argue that the closet example of this type of testing has occurred in a paper published by our research group (Spradley et al. 2017, American Journal of Physical Anthropology) wherein we predict based on the underlying math what the DNE of a hemisphere should be. We then scanned a rubber ball, processed it, and measured its DNE, and found it to indeed be very close to the mathematical prediction.
R2.2	L58: shearing, cutting and shredding of food can also occur during Phase II and puncture-crushing.		We agree. We have altered this sentence to read "during Phases I and II…" We opted to leave out the comment that shearing is also going on during Puncture-Crushing, since most dental morphologists would agree that the shape of molars is likely most attuned to the functional needs

			during interdigitating occlusion, as noted later in the manuscript.
R2.2	L83-124: I do not think this level of detail on chewing is relevant to this study.		We disagree. In our view, most dental topography studies have focused far too little attention on how teeth actually work, as evidenced by the inclusion of Concave DNE signal in final DNE values in past studies. R1 both requested and appreciated this addition, and we think it is an important reminder. We also want our readership specifically thinking about this kind of stuff prior to reading our deductive analysis.
R2.2	L165: 'FPS, as a surrogate for swallowed food size' - do the authors mean surrogate for performance?		We mean both. But we are not sure that measuring chewed food particle size will result in clear answers since a simple solution is to take additional chew strokes if the teeth are dull. DNE on teeth of folivores may track chew-strokes. That would probably be the best way of confirming the performance aspect of this measurement in a biological setting. Regardless, the reviewer's comment is about our reporting of another paper. In this section of the text, we are describing what other researchers have done to try to 'ground-truth' dental topography to performance. We are accurately describing another research group's work without directly putting words in their mouth and are uncertain anything can be done to address this particular complaint.
R2.2	L177: 'where topography measurements are inferred to be functionally relevant if they successfully differentiate dental morphologies' - are these 'dental morphologies' being a priori distinguished by a human observer? Do you mean the topographic measurements are inferred to be relevant if they differentiate dentitions from animals with different diets or similar? This is what is more clearly stated in the next sentence.		The full quote from our paper reads: "A second approach employs the comparative method, where 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 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, these kinds of 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." We feel like this section is clear. Perhaps we do not entirely understand the complaint of the reviewer here, but we start with a topic sentence and then build from there and don't see a clear way of improving the language here.
R2.2	L191: I would argue that 'classic and simpler measurements like SQ' often have fundamental misunderstandings about their functional relevance: is it the length of the crest, its angle or its sharpness that is primarily being selected for? The foundational studies argue largely for an increase in length, but that is not the only aspect of shape that differs with SQ.		The way SQ works is predicated entirely on measuring the relative length of shearing crests. To measure SQ, a scholar would hand-measure the lengths of shearing crests, plot them against tooth length, and take the residual of that regression. It is blind to crest sharpness or orientation. In this way, when a correlation is found between SQ and an ecological variable(s), there is no confusion as to how to make a proper interpretation, since it is a measure of crest length. This clearly refutes this reviewer's speculation that the interpretation of SQ can be ambiguous. If we take the reviewers comments to mean that SQ is not always *effective* in testing ecological hypotheses, then they may have a point. Perhaps SQ is not useful in certain circumstances when the *sharpness* of crests, and not their relative lengths is the target of selection. This is a very good reason to turn to the DNE metric, which accounts for both the length of the convex sharp edge, and the sharpness of the edge. However, only Convex DNE would be similar (and therefore hold the same functional value) as SQ since only the outward facing sharp ridges are of any value.

R2.2	L194: this criticism of lack of quantitative correlation with feeding performance is directly relevant to DNE, and I am slightly mystified as to why the authors are so adamant to make this point several times in a manuscript that cannot answer the criticisms of the method they are employing. It is also largely a discussion point rather than being necessary for an Introduction to the topic.		As we point out in several places in the manuscript, the 'gold standard' for confirming the value of these dental topography metrics is a correlation between chewing efficiency and the measures. We agree with the reviewer that, like the other topography measurements, DNE has not been directly investigated for its relationship to performance *per se*. Acknowledging this about DNE and indeed all topography measurements is important because we may still learn important things about their value when this sort of work is completed. And, of course, this is a major short-coming in their current formulations and implementation by researchers. We must acknowledge this to better inform readers, and we think this belongs in the introduction. However, despite this lack of direct testing, there are several reasons to think that DNE is a better topography measure than most and we have tried hard to make that case here with lots of examples and thorough deductive analysis.
R2.2	L216: it seems the point trying to be made here is a specific criticism of a previous study that found that DNE did not strongly correlate with diet in great apes. It would be preferable that such criticism is more clearly stated rather than being obliquely referred to, so the reader is clear what point is being made. This is clearly a main motivation for the study but is hidden amongst many other superfluous points.		There has been some work published on great ape and hominin dental topography which we would prefer not to discuss in this paper. We want the focus of this work to be on the refinement and future application of DNE, and to discuss dental topography as a maturing discipline. Some mistakes have certainly been made, but this paper does not need to be about that.
R2.2	L224: no demonstrative link currently exists between DNE and 'chewing efficiency' - such tests have not been carried out, as was extensively discussed in the Introduction of this manuscript.		We agree and this was a sloppily written sentence on our part and certainly not our intention. We have rewritten the sentence to read: "…and is expected to produce a more coherent link between the DNE measurement and functional sharpness of occlusal surfaces."

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Sign-Oriented Dirichlet Normal Energy: Aligning Dental Topography and Dental Function in the R package `molaR`.

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DNE; crenulated enamel; occlusal sulci; enamel furrows; dental sharpness; curvature sign orientation

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.

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; Mills 1955; 1963; 1967; Butler 1973; 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 1967; Crompton and Hiiemae 1969; Kay and Hiiemae 1974c; Kay and Hiiemae 1974b; 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' crests 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 2014), 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; Kay and Sheine 1979; Sheine and Kay 1982). 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 *Bauplanë* 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 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. 2016b), 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). 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 break down (Strait 1997; Lucas 2006). That is, fibrous materials need to be cut with continuous application of force, whereas stress-limited materials which 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

[1] 'Breakage sites' are defined by van der Glas et al. (1992; pg. 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.

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:

$$DNE = \sum e(p) \times area(p) \quad \text{Eqn (1)}$$

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

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

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. 2016a).

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 and colleagues (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 stabbed, 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 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 (Eqn 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 Equation 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 sharp edge, since an osculating circle can be placed above or below the surface and simply has to trace the curve of the 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, in-folded 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 misinforming 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. 2016b). 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. 2016b), 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. 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 *MorphoSource.org* (Figure 1, Online Resource Table S1; 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 Table S1). In preparation for measuring DNE, all the surfaces were processed uniformly following protocols detailed elsewhere (e.g., Pampush et al. 2016a; 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 portion. Additional DNE parameters for outlier and boundary exclusion were left at their default values (Pampush et al. 2016b). 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 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 10k trees (Arnold et al. 2010) and reflects the modern cladistic systematic consensus that there are two basal clades of primates, Strepsirrhini 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 MCMCglmms, 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).

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 Figure 2A and B. All raw data, including the surface files used to perform these calculations are available in Online Resource 3.

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 Figure 3, and the differences between conventional (i.e. total) DNE and convex DNE are shown in the box plots of Figure 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 Figure 4A and 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 Figure 4C, and between scan resolution and concave DNE in Figure 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 the relationship appears to level-off (see Online Resource 3 for plots and Online Resource Table S2 for 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 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. 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.

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, 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, Figures 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 (Figures 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 (Figure 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; Selig et al. 2021). However, this new 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, Figure 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 Figures 2A, 2B 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 (Figure 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 (Figure 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 (Figure 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 fabricational 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 spandrelic 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 to consciously avoid the sharpshooter fallacy[2] (see Evers 2017). What function do the sulci serve

[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.

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 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 (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), the reverse of expectations under the stress-sink hypothesis.

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 fabricational) 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, Figures 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 point 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 a resolution 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, Figures 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 the 10 and 18 μm resolutions, there are no differences in the DNE-R or quantities of concave DNE (Table 5, Figure 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 was observed to decrease with coarser resolutions, but the concave DNE does so much more dramatically than does the convex DNE component (Online Resource 4).

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 Figure 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, Figure 4B). The analyses of species body mass averages against DNE-R (Figure 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.

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 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 and coherence.

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Figure Captions:

Figure 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.

Figure 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 illustrate convex and concave proportions of surface DNE. B illustrate 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). Prosimians and platyrrhines are sorted by dietary categories following Winchester et al. (2014), while apes are grouped by genus.

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

Figure 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 alone. 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.

Figure 5: M_2s models of representative M_2 specimens from each taxonomic grouping, all to the same scale 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_2s 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 (Figure 2B), but also generates high DNE values (Figure 6).

Figure 6: Bar plots showing the relative contribution to total DNE from each face on the surface of the representative specimens illustrated in Figure 5. Face DNE values are ordered from most concave to most convex and colored consistently with the DNE plots in Figure 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.

Alba DM, Fortuny J, Moyà-Solà S. 2010. Enamel thickness in th eMiddle Miocene great apes *Anoiapithecus*, *Pierolapithecus*, and *Dryopithecus*. Proc Biol Sci 277:2237-2245.

Allen KL, Cooke SB, Gonzales LA, Kay RF. 2015. Dietary inference from upper and lower molar morphology in platyrrhine primates. PLoS ONE 10(3):e0118732. doi:0118710.0111371/journal.pone.0118732.

Anthony M, Kay RF. 1993. Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. Am J Sci 293A:356-382.

Arnold C, Matthews LJ, Nunn CL. 2010. The 10kTrees Website: A new online resource for primate phylogeny. Evol Anthropol 19:114-118.

Benazzi S, Nguyen HH, Kullmer O, Hublin JJ. 2013. Unravelling the functional biomechanics of dental features and tooth wear. PLoS ONE doi:DOI 10.1371/journal.pone.0069990.

Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol 55:1118-1137.

Boyer DM, Gunnell GF, Kaufman S, McGeary T. 2016. MorphoSource - Archiving and sharing 3D digitial specimen data. Paleont Soc P 22:157-181.

Brown JP. 1970. Rat molar morphology and dental caries. Caries Res 4:49-55.

Bunn JM, Boyer DM, Lipman Y, St. Clair EM, Jernvall J, Daubechies I. 2011. Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. Am J Phys Anthropol 145:247-261.

Butler PM. 1939. Studies of the mammalian dentition—Differentiation of the post-canine dentition. Proc Zool Soc Lond 109(1):1-36.

Butler PM. 1952. The milk-molars of Perissodactyla, with remarks on molar occlusion. Proc Zool Soc Lond 121(4):777-817.

Butler PM. 1956. The ontogeny of molar pattern. Biol Rev 31:30-70.

Butler PM. 1973. Molar wear facets of early Tertiary North American primates. In: Zingeser MR, editor. Craniofacial Biology of Primates: Symp Fourth Int Cong Primatology Vol 3: Karger, Basel. p 1-27.

Constantino PJ, Lee JJ-W, Morris D, Lucas PW, Hartstone-Rose A, Lee W-K, Dominy NJ, Cunningham A, Wagner M, Lawn BR. 2011. Adaptation to hard-object feeding in sea otters and hominins. J Hum Evol 61:89-96.

Crompton AW. 1971. The origin of the tribosphenic molar. In: Kermack DM, Kermack KA, editors. Early Mammals. p 65-87.

Crompton AW, Hiiemae K. 1969. Functional occlusion in tribosphenic molars. Nature 222:678-679.

Crompton AW, Hiiemae KM. 1967. Molar occlusion and mandibular movements during occlusion in the American opossum, Didelphis marsupialis L. Zool J Linn Soc 49:21-47.

Crompton RH, Hiiemae KM. 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. Zool J Lin Soc 49(1):21-47.

Damuth J, Janis CM. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. Biol Rev 86:733-758.

Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125(2):152-161.

Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N. 2002. Western lowland gorilla diet and resource availability: New evidence, cross-site comparisons, and reflections on indirect sampling methods. Am J Primatol 58(3):91-116.

Doran-Sheehy DM, Mongo P, Lodwick J, Conklin-Brittain NL. 2009. Male and female western gorilla diet: preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. Am J Phys Anthropol 140(4):727—738.

Evans AR, Hunter J, Fortelius M, Sanson GD. 2005. The scaling of tooth sharpness in mammals. Ann Zool Fenn 42:603-613.

Evans AR, Janis CM. 2014. The evolution of high dental complexity in the horse lineage. Ann Zool Fenn 51:73-79.

Evans AR, Wilson GP, Fortelius M, Jernvall J. 2007. High-level of similarity of dentitions in carnivorans and rodents. Nature 445:78-81.

Evers JLH. 2017. The Texas sharpshooter fallacy. Human Reproduction 32(7):1363.

Fossey D, Harcourt AH. 1977. Feeding ecology of free-ranging mountain gorillas (*Gorilla gorilla beringei*). In: Clutton-Brock TH, editor. Primate Ecology. New York: Academic Press. p 415-447.

Glowacka H, McFarlin SC, Catlett KK, Mudakikwa A, Bromage TG, Cranfield MR, Stoinski TS, Schwartz GT. 2016. Age-related changes in molar topography and shearing crest length in a wild population of montain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol 160(1):3-15.

Grafen A. 1989. The phylogenetic regression. Phil Trans R Soc Lond B 326(1233):119-157.

Grine FE, Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, editor. Evolutionary History of the "Robust" Australopithecines. New York: Aldine de Gruyter.

Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. J Statistical Software 33(2):1-22.

Hainsworth SV, Delaney RJ, Rutty GN. 2008. How sharp is sharp? Towards quantification of the sharpness and penetration ability of kitchen knives used in stabbings. Int J Legal Med 122(4):289-291.

Harper T, Parras A, Rougier GW. 2019. *Reigitherium* (Meridiolestida, Mesungulatoidea) an enigmatic Late Cretaceous mammal from Patagonia, Argentina: morphology, affinities, and dental evolution. J Mamm Evol 26:447-478.

Hiiemae KM. 1978. Mammalian mastication: a review of the activity of the jaw muscles and movements they produce in chewing. In: Butler PM, Joysey KA, editors. Development, Function and Evolution of Teeth. London: Academic Press. p 359-398.

Hiiemae KM. 1984. Functional aspects of primate jaw morphology. In: Chivers DJ, Hladik CH, editors. Food Acquisition and Processing in Nonhuman Primates. London: Acadmeic Press. p 257-281.

Hiiemae KM, Kay RF. 1972. Tends in the evolution of primate mastication. Nature 240:486-487.

Kanamori T, Kuze N, Bernard H, Malim TP, Kohshima S. 2010. Feeding ecology of Bornean orangutans (*Pongo pygmaeus morio*) in Danum Valley, Sabah, Malasia: A 3-year record including two mast fruitings. Am J Primatol 71:1-21.

Kay RF. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol 43:195-216.

Kay RF. 1977. The evolution of molar occlusion in Cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327-352.
Kay RF. 1981. The nut-crackers – a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55(2):141-151.
Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, editors. Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys, and Apes. New York: Columbia University Press. p 21-53.
Kay RF, Covert HH. 1984. Anatomy and behavior of extinct primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food Acquisition and Processing in Primates. New York: Springer US. p 467-508.
Kay RF, Hiiemae KM. 1974a. Jaw movement and tooth use in recent and fossil primates. Am J Phys Anthropol 40:227-256.
Kay RF, Hiiemae KM. 1974b. Jaw movement and tooth use in recent and fossil primates. American Journal of Physical Anthropology 40:227-256.
Kay RF, Hiiemae KM. 1974c. Mastication in Galago crassicaudatus, a cinefluorographic and occlusal study. In: Martin RD, Doyle GA, Walker AC, editors. Prosimian Biology. London: Duckworth. p 501-530.
Kay RF, Sheine WS. 1979. On the relationship between chitin particle size and digestibility in the primate Galago senegalensis. Am J Phys Anthropol 43:195-216.
Kay RF, Simons EL. 1980. The ecology of Oligocene African Anthropoidea. Int J Primatol 1:21-37.
Kirk EC, Simons EL. 2000. Diet of fossil primates from the Fayum depression of Egypt: A quantitative analysis of molar shearing. J Hum Evol 40:203-229.
Lanyon JM, Sanson GD. 1986. Koala (*Phascolarctos cinereus*) dentition and nutrition. II. Implications of tooth wear in nutrition. J Zool 209:169-181.
Ledogar JA, Winchester JM, St. Clair EM, Boyer DM. 2013. Diet and dental topography in pitheciine seed predators. Am J Phys Anthropol 150(1):107-121.
López-Torres S, Selig KR, Prufrock KA, Lin D, Silcox MT. 2018. Dental topographic analysis of paromomyid (Plesiadapiformes, Primates) cheek teeth: more than 15 million years of changing surfaces and shifting ecologies. Hist Biol 30(1-2):76-88.
Lucas PW. 2006. Dental Functional Morphology: How Teeth Work. Cambridge: Cambridge University Press. 355 p.
Lucas PW, Constantino PJ, Wood B, Lawn BR. 2008. Dental enamel as a dietary indicator in mammals. BioEssays 30:374-385.
McCarthy CT, Ní Annaidh A, Gilchrist MD. 2010. On the sharpness of straight edge blades in cutting soft solids: Part II—Analysis of blade geometry. Eng Fract Mech 77(3):437-451.
McHenry K, Bajcsy P. 2008. An overview of 3D data content, file formats and viewers. Urbana, IL: National Center for Supercomputing Applications. 1-21 p.
McLeod MN, Minson DJ. 1969. Sources of variation in the *in vitro* digestibility of tropical grasses. Grass and Forage Science 24(3):244-249.
Mills JRE. 1955. Ideal dental occlusion in the primates. Dental Practnr and Dent Rec 6:47-61.
Mills JRE. 1963. Occlusion and Malocclusion of the Teeth of Primates. In: Brothwell DR, editor. Dental Anthropology. Oxford: Pergamon Press. p 29-52.

Mills JRE. 1967. A comparison of lateral jaw movements in some mammals from wear facets on the teeth. Archs Oral Biol 12:645-661.
Mills JRE. 1973. Evolution of Mastication in Primates. In: Montagna W, Zingeser MR, editors. Symposia of the Fourth International Congress of Primatology. Basel: S. Karger. p 65-81.
Molnar S, Gantt DG. 1977. Functional implications of primate enamel thickness. Am J Phys Anthropol 46:447-454.
Nishihara T. 1995. Feeding ecology of Western Lowland gorillas in the Nouabalè-Ndoki National Park, Congo. Primates 36(2):151–168.
Pampush JD, Duque AC, Burrows BR, Daegling DJ, Kenney WF, McGraw WS. 2013. Homoplasy and thick enamel in primates. J Hum Evol 64(3):216-224.
Pampush JD, Spradley JP, Morse PE, Griffith D, Gladman JT, Gonzales LA, Kay RF. 2018. Adaptive wear-based changes in dental topography associated with atelid (Mammalia: Primates) diets. Biol J Linn Soc 124(4):584-606.
Pampush JD, Spradley JP, Morse PE, Harrington AR, Allen KL, Boyer DM, Kay RF. 2016a. Wear and its effects on dental topography measures in howling monkeys (*Alouatta palliata*). Am J Phys Anthropol 161(4):705-721.
Pampush JD, Winchester JM, Morse PE, Vining AQ, Boyer DM, Kay RF. 2016b. Introducing molaR: a new R package for quantitative topographic analyses of teeth (and other topographic surfaces). J Mamm Evol 23(4):397-412.
Parker GA, Maynard Smith J. 1990. Optimality theory in evolutionary biology. Nature 348:27-33.
Pineda-Munoz S, Lazagabaster IA, Alroy J, Evans AR. 2017. Inferring diet from dental morphology in terrestrial mammals. Method Ecol Evol 8:481-491.
Plummer M, Best N, Cowles K, Vines K. 2006. CODA: Convergence Diagnosis and Output Analysis for MCMC. R News 6:7-11.
Popowicz TE, Fortelius M. 1997. On the cutting edge: tooth blade sharpness in herbivorous and faunivorous mammals. Ann Zool Fenn 34:73-88.
Pruetz JD. 2006. Feeding ecology of savanna chimpanzees at Fongoli, Senegal. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding Ecology in Apes and Other Primates. Cambridge: Cambridge University Press. p 161—182.
R Core Team. 2017. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
Reilly GA, McCormack BAO, Taylor D. 2004. Cutting sharpness measurement: a critical review. Journal of Materials Processing Technology 153-154:261-267.
Renaud S, Ledevin R. 2017. Impact of wear and diet on molar row geometry and topography in the house mouse. Arch Oral Biol 81:31-40.
Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Method Ecol Evol 3:217-223.
Ross CF, Iriarte-Diaz J. 2014. What does feeding system morphology tell us about feeding? Evol Anthropol 23(3):105-120.
Ross CF, Iriarte-Diaz J. 2014. What does feeding system morphology tell us about feeding? Evolutionary Anthropology: Issues, News, and Reviews 23(3):105-120.
Schaller GB. 1963. The Mountain Gorilla. Chicago: University of Chicago Press.
Schwartz GT. 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. Am J Phys Anthropol 111:221-224.

Seilacher A. 1973. Fabricational noise in adaptive morphology. Syst Zool 22(4):451-465.
Selig KR, Khalid W, Silcox MT. 2021. Mammalian molar complexity follows simple, predictable patterns. . P Natl Acad Sci USA 118(1):e2008850118.
Selig KR, López-Torres S, Sargis EJ, Silcox MT. 2019. First 3D dental topographic analysis of the enamel-dentine junction in non-primate Euarchontans: contribution of the enamel-dentine junciton to molar morphology. J Mamm Evol 26:587-598.
Sheine WS, Kay RF. 1977. An analysis of chewed food particle size and its relationship to molar structure in the primates *Cheirogaleus medius* and *Galago senegalensis* and insectivoran *Tupaia glis*. Am J Phys Anthropol 47:15-20.
Sheine WS, Kay RF. 1982. A model for comparison of masticatory effectiveness in primates. J Morph 172:139-149.
Shellis RP, Beynon AD, Reid DJ, Hiiemae KM. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:507-522.
Skinner MM, Evans AR, Smith T, Jernvall J, Tafforeau P, Kupczik K, Olejniczak AJ, Rosas A, Radovčić J, Thackeray JF, Toussaint M, Hublin JJ. 2010. Brief communication: Contributions of the enamel-dentin junction shape and enamel deposition to primate molar crown complexity. Am J Phys Anthropol 142(1):157-163.
Spradley JP, Pampush JD, Morse PE, Kay RF. 2017. Smooth operator: Observations on the effects of different mesh retriangulation protocols on the computation of Dirichlet normal energy. Am J Phys Anthropol 163(3):94-109.
Strait S. 1993. Molar morphology and food texture among small-bodied insectivorous mammals. J Mammal 74:391-402.
Strait SG. 1997. Tooth use and the physical properties of food. Evol Anthropol 5(6):199-211.
Taylor AB. 2006. Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. J Hum Evol 50:377-393.
Thiery G, Guy F, Lazzari V. 2017. Investigating the dental toolkit of primates based on food mechanical properties: Feeding action does matter. Am J Primatol 79:e22640.
Ungar PS. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J Hum Evol 46(5):605-622.
Ungar PS, Kay RF. 1995. The dietary adaptations of European Miocene cattarhines. P Natl Acad Sci USA 92:5479-5481.
Ungar PS, M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. P Natl Acad Sci USA 100(7):3874-3877.
Ungar PS, Williamson M. 2000. Exploring the effects of tooth wear on functional morphology: A preliminary study using dental topographic analysis. Palaeontol Electron 3(1):1-18.
Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). Am J Phys Anthropol 155:17-32.
Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J Hum Evol 55:60-74.
Wall CE, Vinyard CJ, Johnson KR, Williams SH, Hylander WL. 2006. Phase II jaw movements and masseter muscle activity during chewing in *Papio anubis*. Am J Phys Anthropol 129:215-224.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. Am J Primatol 7:323-356.

Williams SH, Kay RF. 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. J Mamm Evol 8(3):207-229.

Winchester JM, Boyer DM, St. Clair EM, Gosselin-Ildari AD, Cooke SB, Ledogar JA. 2014. Dental topography of platyrrhines and prosimians: Convergence and contrasts. Am J Phys Anthropol 153:29-44.

Zuccotti LF, Williamson MD, Limp WF, Ungar PS. 1998. Technical Note: Modeling primate occlusal topography using geographic information systems technology. Am J Phys Anthropol 107:137-142.

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Sign-Oriented Dirichlet Normal Energy: Aligning Dental Topography and Dental Function in the R package `molaR`.

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Key Words:
DNE; crenulated enamel; occlusal sulci; enamel furrows; dental sharpness; curvature sign orientation

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. ~~However, initial applications~~As initially implemented, ~~of~~ 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 Phase~~s~~ 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.

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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 ~~to~~ aimed at studying the morphological, functional, and adaptive properties of mammalian teeth. Using scanned and digitized dental surfaces, ~~dental topography~~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)~~,~~ ~~that is the focus of this work~~. DNE and ~~these~~ 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 ~~variably~~ 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 ~~permits~~ 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 ~~of these topography~~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). ~~That is~~Put differently, dental landmarks provide the essential vocabulary in characterizing exactly which and how ~~and what~~ parts of teeth are brought together to reduce food. Initial~~ly~~ 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; Mills 1955; 1963; 1967; Butler 1973; 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 1967; Crompton and Hiiemae 1969; Kay and Hiiemae 1974c; Kay and Hiiemae 1974b; 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 ~~while~~ in preparation~~ing it~~ 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, ~~informally called 'chewing,'~~ 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' crests come into occlusion during the initial upward and mediolingually-directed ~~first~~ 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 2014), 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 ~~independently~~ 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~~y~~ 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; Kay and Sheine 1979; Sheine and Kay 1982). Since it is well established that the digestibility (extractable energy), especially of high-fiber plant ~~foods~~ materials is

~~materially~~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 ~~dental topography~~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 ~~morphology~~ 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 ~~just~~ abstractions of the morphology, wherein two dramatically different dental *Bauplanë* 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.~~and w~~

~~hile they may still be useful for tracking broad changes or trends in tooth form, they cannot inform adaptive hypotheses or dietary reconstructions without clearer links to the known modes of masticatory function.~~

In practice, there may be three ways of showing or inferring that a ~~topography~~ DT measurement is capturing functionally relevant information about dental morphology to prove

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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 ~~to address this central issue~~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~~food~~ 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 ~~topography~~ 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, ~~these kinds of~~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~~at~~ 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 insightful. In contrast, classic and simpler measurements like SQ have already provided the core ecological insights and analogical frameworks these new ~~topography~~ 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 ~~captured~~ 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 ~~what these various~~the value of these measurements ~~values mean~~in functional terms (if at all), researchers employing ~~these kinds of~~DT measurements should remain skeptical of the biological ~~relevance~~ interpretations arising from~~of~~ any surprising or incongruous dental topography findings. ~~Put differently~~In other words, if the ~~topography~~ DT measurement values~~es~~ 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. 2016b), and is expected to produce a more ~~functionally~~ coherent link between the DNE measurement and ~~and chewing efficiency~~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 ~~dental topography~~ DT ~~measures~~measurements, not all aspects of its final summation can be deductively linked to masticatory performance. In particular, the ~~concave oriented~~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). 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 break down (Strait 1997; Lucas 2006). That is, fibrous materials need to be cut with continuous application of force, whereas stress-limited materials which 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 ~~This measurement assumes that the boundaries between differently oriented patches represent cutting 'tools,' and therefore the OPC value is presumed to corelate with the number of cutting components thus estimating the tooth's ability to process fiber. OPC may be effective when employed comparing the highly disparate teeth of certain mammalian orders, but issues of precision and coherence emerge when considering an object like a hemisphere, which possess no cutting ridges yet will produce an OPC measure of eight (Pampush et al. 2016a). These problems, as well as the general performance of the measurement, have led some researchers~~

[1] 'Breakage sites' are defined by van der Glas et al. (1992; pg. 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.

~~to conclude that OPC cannot be used for finer comparisons of dietary ecology or that it loses efficacy when applied to groups with conservative dental morphologies~~ (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 ~~a functionally~~ relevant ~~measurement~~properties of a dental surface.

The DNE of a surface is estimated with the formula:

$$DNE = \sum e(p) \times area(p) \quad \text{Eqn (1)}$$

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

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

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. 2016a).

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 and colleagues (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 stabbed, Hainsworth et al. (2008) measured the osculating circle radii of~~f~~ 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 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 (Eqn 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 Equation 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 sharp edge, since ~~the~~ an osculating circle can be placed above or below the surface and simply has to trace the curve of the 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 ~~positive~~ 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 ~~these~~ those results to draw ecological or adaptive inferences.

From the perspective of tooth shearing ability, a major flaw in the ~~current~~ 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, in-folded 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 ~~run the risk of~~may misinforming 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 ~~a function of~~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), ~~and~~ allowing researchers ~~can~~ to disregard the concave aspect of DNE and focus their functional ~~examinations and~~ 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 ~~context~~ 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. 2016b). 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. 2016b), PLY ~~surface~~ faces with a vertex on the boundary, and those faces with Dirichlet energy densities ~~in~~ 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 ~~quantified~~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. 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) ~~data set~~, downloaded from *MorphoSource.org* (Figure 1, Online Resource Table S1; 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 Table S1). ~~-~~In preparation for measuring DNE, all the surfaces were processed uniformly following protocols detailed elsewhere (e.g., Pampush et al. 2016a; Spradley et al. 2017), whereby the M_2 tooth crown was digitally segmented away from adjacent teeth as well as ~~the specimen's~~its roots using *Avizo 9.5* (FEI Houston, Hillsboro, OR). O~~A~~any ~~o~~cclusal surface damage ~~such as pits, cracks, and spalled enamel~~ was~~ere~~ 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. S~~First, sign-oriented~~ign 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 portion. Additional DNE parameters for outlier and boundary exclusion were left at their default values (Pampush et al. 2016b). 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 ~~quality~~ 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 ~~other~~ additional MCMCglmms were performed to investigate scaling allometry of concave DNE and the DNE-R ~~ratio~~. Logit-transformed DNE-R ~~ratios~~ was~~ere~~ compared with 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 ~~moniker~~ nomen and compare these taxa with platyrrhines and hominoids. The phylogenetic tree used for these analyses was downloaded from 10k trees (Arnold et al. 2010) and reflects the modern cladistic systematic consensus that there are two basal clades of primates, Strepsirrhini 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 MCMCglmms, non-phylogenetically controlled ANOVAs were performed examining logit-transformed DNE-R and ~~surface area ratios~~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 ~~surface area ratios~~SA-R were compared with diet in phylogenetically controlled ANOVAs within prosimians and platyrrhines using the R package `phytools` (Revell 2012).

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~~2~~. The DNE ratio (DNE-R) and surface ~~and~~ area ratio~~s~~ (SA-R)—both ~~(~~defined as concave/convex—~~)~~ are presented in heat-map style in Table 2~~3~~, illustrating that while the hominoids have much higher DNE-R ~~ratio~~ values, they possess relatively low ~~concave to convex surface area ratios~~SA-R values. Pie charts organized by taxonomic group and diet visually present these ratios in Figure 2A and B. All raw data, including the surface files used to perform these calculations are available in Online Resource 3.

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~~4~~). These trends are visualized in the colored histogram in Figure 3~~3~~, and the differences between conventional (i.e. total) DNE and convex DNE are shown in the box plots of Figure 2C~~4~~.

Multiple MCMCglmm results are presented in Table 45, describing the statistical relationships between DNE-R ~~ratio~~ 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 ~~ratio~~ in Figure 4A and B~~5~~. Three of these models returned significant correlations: DNE-R ~~ratio~~ is significantly correlated with tooth length across all specimens, and DNE-R ~~ratio~~ is also significantly correlated with tooth length within great apes, but not within the other groups. Finally, DNE-R ~~ratio~~ 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 ~~ratio~~ 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~~6~~ presents the results of MCMCglmm analyses comparing scanning resolution with two measures: DNE-R ~~ratio~~ 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 ~~ratio~~ is plotted in Figure 4C~~6A~~, and between scan resolution and concave DNE in Figure 4D~~6B~~. 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 ~~and~~ against concave DNE and ~~/~~DNE ~~ratio~~ 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. ~~The~~ DNE~~-ratio~~-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~~-ratio~~-R of 0.514 at the 18 µm scale. The 36 µm scan has a DNE~~-ratio~~-R of 0.431 as the relationship appears to level-off (see Online Resource 3 for plots and Online Resource Table S2 for 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 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~~7~~). 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 ~~surface area ratios~~SA-R within the prosimian and platyrrhine groupings show only one significant relationship to diet, among prosimians and DNE-R~~-ratio~~. These additional ANOVAs further suggest that the increase in DNE-R and ~~surface area ratios~~SA-R is not a product of diet, but rather suggests historical contingency in the *Bb~~a~~aupläne* of these primate molars.

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 ~~aspects~~ components of the occlusal surface ~~sometimes culminate in~~can consist of very sharp and deep crevices~~;~~. ~~however,~~such ~~the sharp edge of these~~ concave features ~~is~~ are oriented towards the enamel dentine junction and would not be expected to directly interact with a food bolus. Obviously, 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 ~~concave~~ both crevices and ~~convex components~~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~~4, Figures 2C and ~~3~~4). 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 (Figures 2C~~3~~ and 3~~4~~). 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 (Figure 5~~7~~), 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 ~~ratios ((~~DNE-R Table 2~~3~~). 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; Selig et al. 2021). However, this new 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~~3~~, Figure 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 Figures 2A, 2B and 5~~7~~). ~~That is, as compared to the~~

~~prosimians and platyrrhines analyzed in this work, these great apes tend to have much lower percentages of their total occlusal surface area in concave orientation (Table 3).~~ 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 (Figure 6) ~~Figure 8) since~~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 ~~materials~~. When the outsized concave contribution to total DNE is included during dietary interpretation of great apes, they cluster with ~~folivorous~~ primate folivores ~~(or insectivorous) primates~~ (Figure 2C4). 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, ~~meat, and~~ 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 ~~specimens~~ species Winchester et al. (2014) labeled as omnivores (Figure 2C~~5~~). 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 fabricational noise (Seilacher 1973). In keeping with Butler's (1956) model, for the comparatively thick-enameled primates like ~~hominins~~ *Homo, Australopithecus, Paranthropus* or *Pongo* (Grine and Martin 1988; Shellis et al. 1998) the deep occlusal sulci are possibly the spandrelic 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~~out~~ 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 ~~conflated~~ viewed as ~~with~~ 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 to consciously avoid the sharpshooter fallacy[2] (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 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 (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

[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.

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 ~~countering~~ 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), ~~producing an incoherent functional complex~~the reverse of expectations under the ~~is hypothesi~~stress-sink hypothesis.

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 fabricational) 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 ~~have no idea~~cannot discern whether they are measuring outward or inward oriented sharpness ~~(Figure 8)~~. 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 ~~ratios~~ than their prosimian and platyrrhine relatives (Table 2~~3~~, Figures 2 and 6~~8~~)? 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 point 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 a resolution of 10 and 18 μm, but the apes were scanned at lower 23-65 μm resolutions. There are detectable trends between DNE ~~ratio~~ R and concave DNE with scan resolution across the entire sample (Table 5~~6~~, Figures 4~~6~~), 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 ~~ratio~~ R values (concave to convex, Table 2~~3~~). Within only the prosimians and platyrrhines, both of which have specimens scanned at the 10 and 18 μm resolutions, there are no differences in the DNE ~~ratio~~ R or quantities of concave DNE (Table 5~~6~~, Figure 4~~6~~). The findings within ~~prosimians and platyrrhines~~the non-ape sample in~~, of~~ which some specimens have been scanned at roughly half the resolution of others ~~in the sample~~, suggest that the inflated concave DNE measures characteristic of great apes are not the result of scanning differences. ~~This interpretation is further supported by the theoretical premise~~Moreover, a ~~that~~ 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 ~~chimp~~ molar of a chimpanzee scanned at three different resolutions, both convex and concave DNE was observed to decrease with coarser resolutions, but the concave DNE does so much more dramatically than does the convex DNE component (Online Resource 4).

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~~5~~, and Figure 4~~5~~ support this suggestion. In a pattern very similar to the resolution analyses, when compared with tooth length, DNE-R ~~ratio~~ 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~~5~~, Figure 4~~5~~B). The analyses of species body mass averages against DNE-R ~~ratio~~ (Figure 4~~5~~A) 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 ~~surface area ratios~~SA-R among the three groups confirm that apes stand apart from the other primates analyzed here (Table 6~~7~~). In concert, these findings suggest that ~~the~~ DNE-R ~~ratio~~ results are not the product of scaling problems associated with producing the measurement nor the result of some sort of primate-wide scaling ~~mechanism~~phenomenon; rather they ~~are a phenomenon exclusive~~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.

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 ~~can be drawn~~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 ~~as has been practiced in prior studies~~. 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, ~~pigs~~bunodont artiodactyls, sea otters etc.), sharply grooved and inwardly oriented sulci or furrows contribute 'sharpness' components ~~that are not~~whose function~~ally~~ 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 ~~ascriptions~~ inferences about the~~of~~ 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, ~~L~~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 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 and coherence.

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Figure Captions:

Figure 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.

Figure 2: A and B s~~S~~ummary 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. ~~Upper plots~~A illustrate convex and concave proportions of surface DNE. ~~Lower plots~~B illustrate 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). Prosimians and platyrrhines are sorted by dietary categories following Winchester et al. (2014), while apes are grouped by genus.

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

~~**Figure 4:** 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). Prosimians and platyrrhines are sorted by dietary categories following Winchester et al. (2014), while apes are grouped by genus.~~

Figure ~~4~~5: Scatter plots comparing logit-transformed DNE-R ~~ratio~~ (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~~(A)~~ Logit-transformed DNE ratio (concave/convex) with scanning resolution; D~~(B)~~ concave DNE alone. 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.

~~**Figure 6:** Scatter plots comparing decompositions of the DNE measurement with scan resolution. (A) Logit-transformed DNE ratio (concave/convex) with scanning resolution; (B) concave DNE alone. 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.~~

Figure ~~5~~7: M_2s models of representative M_2 specimens from each taxonomic grouping, all to the same scale 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_2s 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 (Figure 2B), but also generates high DNE values (Figure ~~6~~8).

Figure ~~6~~8: Bar plots showing the relative contribution to total DNE from each face on the surface of the representative specimens illustrated in Figure ~~5~~7. Face DNE values are ordered from most concave to most convex and colored consistently with the DNE plots in Figure ~~5~~7. 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.

Alba DM, Fortuny J, Moyà-Solà S. 2010. Enamel thickness in th eMiddle Miocene great apes *Anoiapithecus*, *Pierolapithecus*, and *Dryopithecus*. Proc Biol Sci 277:2237-2245.

Allen KL, Cooke SB, Gonzales LA, Kay RF. 2015. Dietary inference from upper and lower molar morphology in platyrrhine primates. PLoS ONE 10(3):e0118732. doi:0118710.0111371/journal.pone.0118732.

Anthony M, Kay RF. 1993. Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. Am J Sci 293A:356-382.

Arnold C, Matthews LJ, Nunn CL. 2010. The 10kTrees Website: A new online resource for primate phylogeny. Evol Anthropol 19:114-118.

Benazzi S, Nguyen HH, Kullmer O, Hublin JJ. 2013. Unravelling the functional biomechanics of dental features and tooth wear. PLoS ONE doi:DOI 10.1371/journal.pone.0069990.

Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol 55:1118-1137.

Boyer DM, Gunnell GF, Kaufman S, McGeary T. 2016. MorphoSource - Archiving and sharing 3D digitial specimen data. Paleont Soc P 22:157-181.

Brown JP. 1970. Rat molar morphology and dental caries. Caries Res 4:49-55.

Bunn JM, Boyer DM, Lipman Y, St. Clair EM, Jernvall J, Daubechies I. 2011. Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. Am J Phys Anthropol 145:247-261.

Butler PM. 1939. Studies of the mammalian dentition—Differentiation of the post-canine dentition. Proc Zool Soc Lond 109(1):1-36.

Butler PM. 1952. The milk-molars of Perissodactyla, with remarks on molar occlusion. Proc Zool Soc Lond 121(4):777-817.

Butler PM. 1956. The ontogeny of molar pattern. Biol Rev 31:30-70.

Butler PM. 1973. Molar wear facets of early Tertiary North American primates. In: Zingeser MR, editor. Craniofacial Biology of Primates: Symp Fourth Int Cong Primatology Vol 3: Karger, Basel. p 1-27.

Constantino PJ, Lee JJ-W, Morris D, Lucas PW, Hartstone-Rose A, Lee W-K, Dominy NJ, Cunningham A, Wagner M, Lawn BR. 2011. Adaptation to hard-object feeding in sea otters and hominins. J Hum Evol 61:89-96.

Crompton AW. 1971. The origin of the tribosphenic molar. In: Kermack DM, Kermack KA, editors. Early Mammals. p 65-87.

Crompton AW, Hiiemae K. 1969. Functional occlusion in tribosphenic molars. Nature 222:678-679.

Crompton AW, Hiiemae KM. 1967. Molar occlusion and mandibular movements during occlusion in the American opossum, Didelphis marsupialis L. Zool J Linn Soc 49:21-47.

Crompton RH, Hiiemae KM. 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. Zool J Lin Soc 49(1):21-47.

Damuth J, Janis CM. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. Biol Rev 86:733-758.

Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125(2):152-161.

Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N. 2002. Western lowland gorilla diet and resource availability: New evidence, cross-site comparisons, and reflections on indirect sampling methods. Am J Primatol 58(3):91-116.

Doran-Sheehy DM, Mongo P, Lodwick J, Conklin-Brittain NL. 2009. Male and female western gorilla diet: preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. Am J Phys Anthropol 140(4):727—738.

Evans AR, Hunter J, Fortelius M, Sanson GD. 2005. The scaling of tooth sharpness in mammals. Ann Zool Fenn 42:603-613.

Evans AR, Janis CM. 2014. The evolution of high dental complexity in the horse lineage. Ann Zool Fenn 51:73-79.

Evans AR, Wilson GP, Fortelius M, Jernvall J. 2007. High-level of similarity of dentitions in carnivorans and rodents. Nature 445:78-81.

Evers JLH. 2017. The Texas sharpshooter fallacy. Human Reproduction 32(7):1363.

Fossey D, Harcourt AH. 1977. Feeding ecology of free-ranging mountain gorillas (*Gorilla gorilla beringei*). In: Clutton-Brock TH, editor. Primate Ecology. New York: Academic Press. p 415-447.

Glowacka H, McFarlin SC, Catlett KK, Mudakikwa A, Bromage TG, Cranfield MR, Stoinski TS, Schwartz GT. 2016. Age-related changes in molar topography and shearing crest length in a wild population of montain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol 160(1):3-15.

Grafen A. 1989. The phylogenetic regression. Phil Trans R Soc Lond B 326(1233):119-157.

Grine FE, Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, editor. Evolutionary History of the "Robust" Australopithecines. New York: Aldine de Gruyter.

Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. J Statistical Software 33(2):1-22.

Hainsworth SV, Delaney RJ, Rutty GN. 2008. How sharp is sharp? Towards quantification of the sharpness and penetration ability of kitchen knives used in stabbings. Int J Legal Med 122(4):289-291.

Harper T, Parras A, Rougier GW. 2019. *Reigitherium* (Meridiolestida, Mesungulatoidea) an enigmatic Late Cretaceous mammal from Patagonia, Argentina: morphology, affinities, and dental evolution. J Mamm Evol 26:447-478.

Hiiemae KM. 1978. Mammalian mastication: a review of the activity of the jaw muscles and movements they produce in chewing. In: Butler PM, Joysey KA, editors. Development, Function and Evolution of Teeth. London: Academic Press. p 359-398.

Hiiemae KM. 1984. Functional aspects of primate jaw morphology. In: Chivers DJ, Hladik CH, editors. Food Acquisition and Processing in Nonhuman Primates. London: Acadmeic Press. p 257-281.

Hiiemae KM, Kay RF. 1972. Tends in the evolution of primate mastication. Nature 240:486-487.

Kanamori T, Kuze N, Bernard H, Malim TP, Kohshima S. 2010. Feeding ecology of Bornean orangutans (*Pongo pygmaeus morio*) in Danum Valley, Sabah, Malasia: A 3-year record including two mast fruitings. Am J Primatol 71:1-21.

Kay RF. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol 43:195-216.

Kay RF. 1977. The evolution of molar occlusion in Cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327-352.
Kay RF. 1981. The nut-crackers – a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55(2):141-151.
Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, editors. Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys, and Apes. New York: Columbia University Press. p 21-53.
Kay RF, Covert HH. 1984. Anatomy and behavior of extinct primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food Acquisition and Processing in Primates. New York: Springer US. p 467-508.
Kay RF, Hiiemae KM. 1974a. Jaw movement and tooth use in recent and fossil primates. Am J Phys Anthropol 40:227-256.
Kay RF, Hiiemae KM. 1974b. Jaw movement and tooth use in recent and fossil primates. American Journal of Physical Anthropology 40:227-256.
Kay RF, Hiiemae KM. 1974c. Mastication in Galago crassicaudatus, a cinefluorographic and occlusal study. In: Martin RD, Doyle GA, Walker AC, editors. Prosimian Biology. London: Duckworth. p 501-530.
Kay RF, Sheine WS. 1979. On the relationship between chitin particle size and digestibility in the primate Galago senegalensis. Am J Phys Anthropol 43:195-216.
Kay RF, Simons EL. 1980. The ecology of Oligocene African Anthropoidea. Int J Primatol 1:21-37.
Kirk EC, Simons EL. 2000. Diet of fossil primates from the Fayum depression of Egypt: A quantitative analysis of molar shearing. J Hum Evol 40:203-229.
Lanyon JM, Sanson GD. 1986. Koala (*Phascolarctos cinereus*) dentition and nutrition. II. Implications of tooth wear in nutrition. J Zool 209:169-181.
Ledogar JA, Winchester JM, St. Clair EM, Boyer DM. 2013. Diet and dental topography in pitheciine seed predators. Am J Phys Anthropol 150(1):107-121.
López-Torres S, Selig KR, Prufrock KA, Lin D, Silcox MT. 2018. Dental topographic analysis of paromomyid (Plesiadapiformes, Primates) cheek teeth: more than 15 million years of changing surfaces and shifting ecologies. Hist Biol 30(1-2):76-88.
Lucas PW. 2006. Dental Functional Morphology: How Teeth Work. Cambridge: Cambridge University Press. 355 p.
Lucas PW, Constantino PJ, Wood B, Lawn BR. 2008. Dental enamel as a dietary indicator in mammals. BioEssays 30:374-385.
McCarthy CT, Ní Annaidh A, Gilchrist MD. 2010. On the sharpness of straight edge blades in cutting soft solids: Part II—Analysis of blade geometry. Eng Fract Mech 77(3):437-451.
McHenry K, Bajcsy P. 2008. An overview of 3D data content, file formats and viewers. Urbana, IL: National Center for Supercomputing Applications. 1-21 p.
McLeod MN, Minson DJ. 1969. Sources of variation in the *in vitro* digestibility of tropical grasses. Grass and Forage Science 24(3):244-249.
Mills JRE. 1955. Ideal dental occlusion in the primates. Dental Practnr and Dent Rec 6:47-61.
Mills JRE. 1963. Occlusion and Malocclusion of the Teeth of Primates. In: Brothwell DR, editor. Dental Anthropology. Oxford: Pergamon Press. p 29-52.

Mills JRE. 1967. A comparison of lateral jaw movements in some mammals from wear facets on the teeth. Archs Oral Biol 12:645-661.
Mills JRE. 1973. Evolution of Mastication in Primates. In: Montagna W, Zingeser MR, editors. Symposia of the Fourth International Congress of Primatology. Basel: S. Karger. p 65-81.
Molnar S, Gantt DG. 1977. Functional implications of primate enamel thickness. Am J Phys Anthropol 46:447-454.
Nishihara T. 1995. Feeding ecology of Western Lowland gorillas in the Nouabalè-Ndoki National Park, Congo. Primates 36(2):151–168.
Pampush JD, Duque AC, Burrows BR, Daegling DJ, Kenney WF, McGraw WS. 2013. Homoplasy and thick enamel in primates. J Hum Evol 64(3):216-224.
Pampush JD, Spradley JP, Morse PE, Griffith D, Gladman JT, Gonzales LA, Kay RF. 2018. Adaptive wear-based changes in dental topography associated with atelid (Mammalia: Primates) diets. Biol J Linn Soc 124(4):584-606.
Pampush JD, Spradley JP, Morse PE, Harrington AR, Allen KL, Boyer DM, Kay RF. 2016a. Wear and its effects on dental topography measures in howling monkeys (*Alouatta palliata*). Am J Phys Anthropol 161(4):705-721.
Pampush JD, Winchester JM, Morse PE, Vining AQ, Boyer DM, Kay RF. 2016b. Introducing molaR: a new R package for quantitative topographic analyses of teeth (and other topographic surfaces). J Mamm Evol 23(4):397-412.
Parker GA, Maynard Smith J. 1990. Optimality theory in evolutionary biology. Nature 348:27-33.
Pineda-Munoz S, Lazagabaster IA, Alroy J, Evans AR. 2017. Inferring diet from dental morphology in terrestrial mammals. Method Ecol Evol 8:481-491.
Plummer M, Best N, Cowles K, Vines K. 2006. CODA: Convergence Diagnosis and Output Analysis for MCMC. R News 6:7-11.
Popowicz TE, Fortelius M. 1997. On the cutting edge: tooth blade sharpness in herbivorous and faunivorous mammals. Ann Zool Fenn 34:73-88.
Pruetz JD. 2006. Feeding ecology of savanna chimpanzees at Fongoli, Senegal. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding Ecology in Apes and Other Primates. Cambridge: Cambridge University Press. p 161—182.
R Core Team. 2017. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
Reilly GA, McCormack BAO, Taylor D. 2004. Cutting sharpness measurement: a critical review. Journal of Materials Processing Technology 153-154:261-267.
Renaud S, Ledevin R. 2017. Impact of wear and diet on molar row geometry and topography in the house mouse. Arch Oral Biol 81:31-40.
Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Method Ecol Evol 3:217-223.
Ross CF, Iriarte-Diaz J. 2014. What does feeding system morphology tell us about feeding? Evol Anthropol 23(3):105-120.
Ross CF, Iriarte-Diaz J. 2014. What does feeding system morphology tell us about feeding? Evolutionary Anthropology: Issues, News, and Reviews 23(3):105-120.
Schaller GB. 1963. The Mountain Gorilla. Chicago: University of Chicago Press.
Schwartz GT. 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. Am J Phys Anthropol 111:221-224.

Seilacher A. 1973. Fabricational noise in adaptive morphology. Syst Zool 22(4):451-465.
Selig KR, Khalid W, Silcox MT. 2021. Mammalian molar complexity follows simple, predictable patterns. . P Natl Acad Sci USA 118(1):e2008850118.
Selig KR, López-Torres S, Sargis EJ, Silcox MT. 2019. First 3D dental topographic analysis of the enamel-dentine junction in non-primate Euarchontans: contribution of the enamel-dentine junciton to molar morphology. J Mamm Evol 26:587-598.
Sheine WS, Kay RF. 1977. An analysis of chewed food particle size and its relationship to molar structure in the primates *Cheirogaleus medius* and *Galago senegalensis* and insectivoran *Tupaia glis*. Am J Phys Anthropol 47:15-20.
Sheine WS, Kay RF. 1982. A model for comparison of masticatory effectiveness in primates. J Morph 172:139-149.
Shellis RP, Beynon AD, Reid DJ, Hiiemae KM. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:507-522.
Skinner MM, Evans AR, Smith T, Jernvall J, Tafforeau P, Kupczik K, Olejniczak AJ, Rosas A, Radovčić J, Thackeray JF, Toussaint M, Hublin JJ. 2010. Brief communication: Contributions of the enamel-dentin junction shape and enamel deposition to primate molar crown complexity. Am J Phys Anthropol 142(1):157-163.
Spradley JP, Pampush JD, Morse PE, Kay RF. 2017. Smooth operator: Observations on the effects of different mesh retriangulation protocols on the computation of Dirichlet normal energy. Am J Phys Anthropol 163(3):94-109.
Strait S. 1993. Molar morphology and food texture among small-bodied insectivorous mammals. J Mammal 74:391-402.
Strait SG. 1997. Tooth use and the physical properties of food. Evol Anthropol 5(6):199-211.
Taylor AB. 2006. Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. J Hum Evol 50:377-393.
Thiery G, Guy F, Lazzari V. 2017. Investigating the dental toolkit of primates based on food mechanical properties: Feeding action does matter. Am J Primatol 79:e22640.
Ungar PS. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J Hum Evol 46(5):605-622.
Ungar PS, Kay RF. 1995. The dietary adaptations of European Miocene cattarhines. P Natl Acad Sci USA 92:5479-5481.
Ungar PS, M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. P Natl Acad Sci USA 100(7):3874-3877.
Ungar PS, Williamson M. 2000. Exploring the effects of tooth wear on functional morphology: A preliminary study using dental topographic analysis. Palaeontol Electron 3(1):1-18.
Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). Am J Phys Anthropol 155:17-32.
Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J Hum Evol 55:60-74.
Wall CE, Vinyard CJ, Johnson KR, Williams SH, Hylander WL. 2006. Phase II jaw movements and masseter muscle activity during chewing in *Papio anubis*. Am J Phys Anthropol 129:215-224.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. Am J Primatol 7:323-356.

Williams SH, Kay RF. 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. J Mamm Evol 8(3):207-229.

Winchester JM, Boyer DM, St. Clair EM, Gosselin-Ildari AD, Cooke SB, Ledogar JA. 2014. Dental topography of platyrrhines and prosimians: Convergence and contrasts. Am J Phys Anthropol 153:29-44.

Zuccotti LF, Williamson MD, Limp WF, Ungar PS. 1998. Technical Note: Modeling primate occlusal topography using geographic information systems technology. Am J Phys Anthropol 107:137-142.

Figure 1

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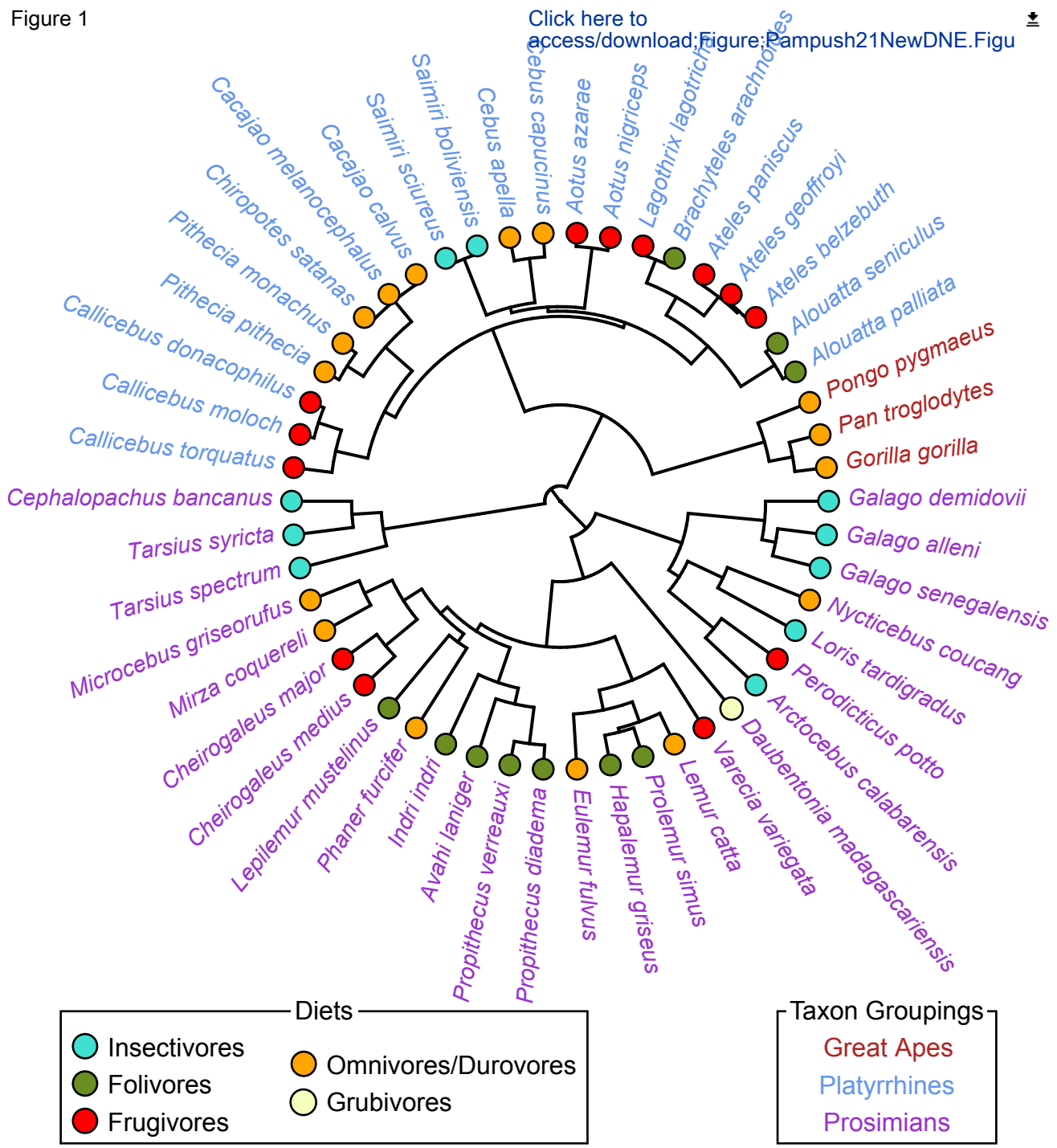


Figure 2

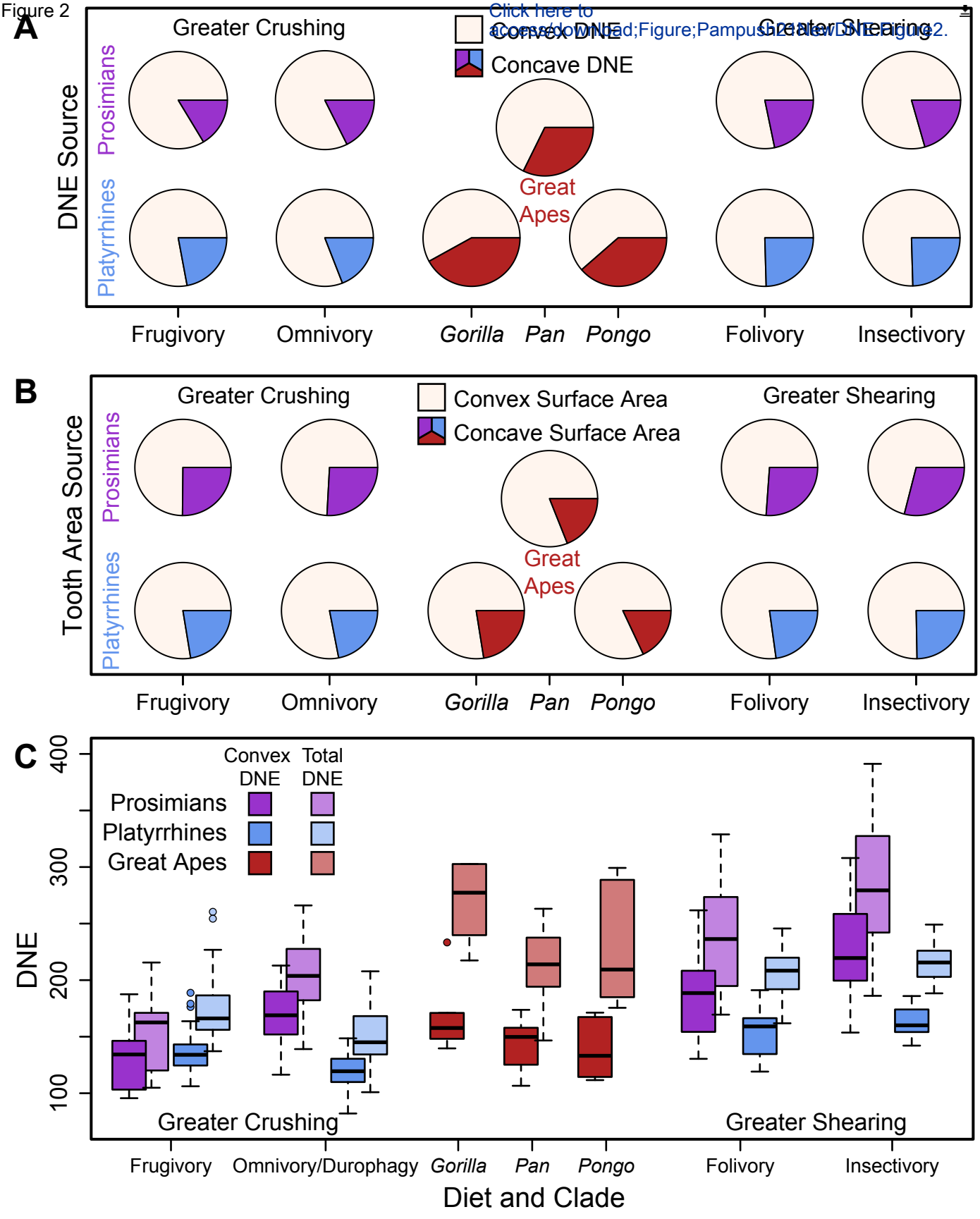

A
Greater Crushing
Convex DNE
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DNE Source
Prosimians
Platyrrhines
Great Apes
Frugivory
Omnivory
Gorilla
Pan
Pongo
Folivory
Insectivory
B
Greater Crushing
Convex Surface Area
Concave Surface Area
Greater Shearing
Tooth Area Source
Prosimians
Platyrrhines
Great Apes
Frugivory
Omnivory
Gorilla
Pan
Pongo
Folivory
Insectivory
C
Convex DNE
Total DNE
Prosimians
Platyrrhines
Great Apes
DNE
100
200
300
400
Greater Crushing
Greater Shearing
Frugivory
Omnivory/Durophagy
Gorilla
Pan
Pongo
Folivory
Insectivory
Diet and Clade

Figure 3

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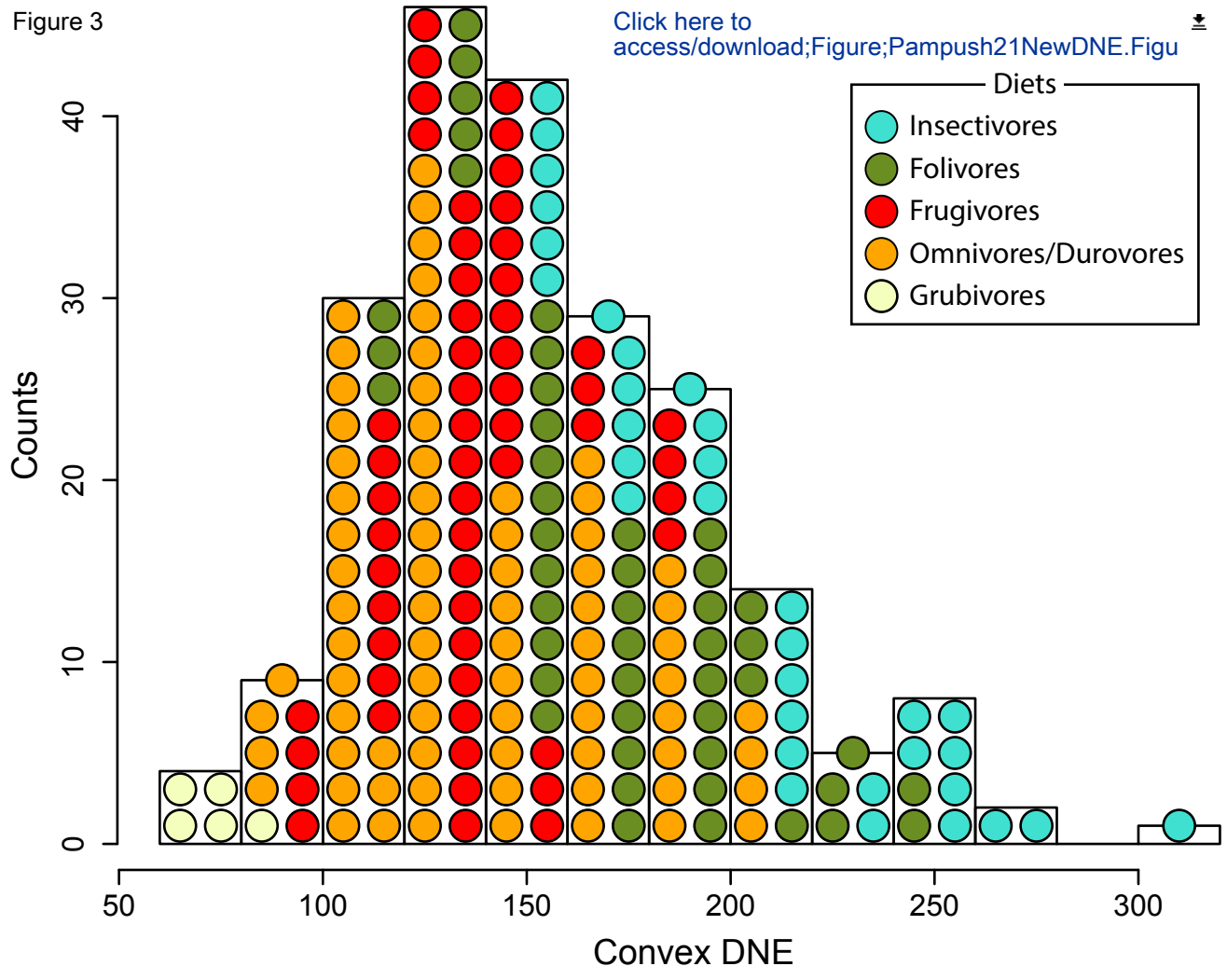


Figure 4

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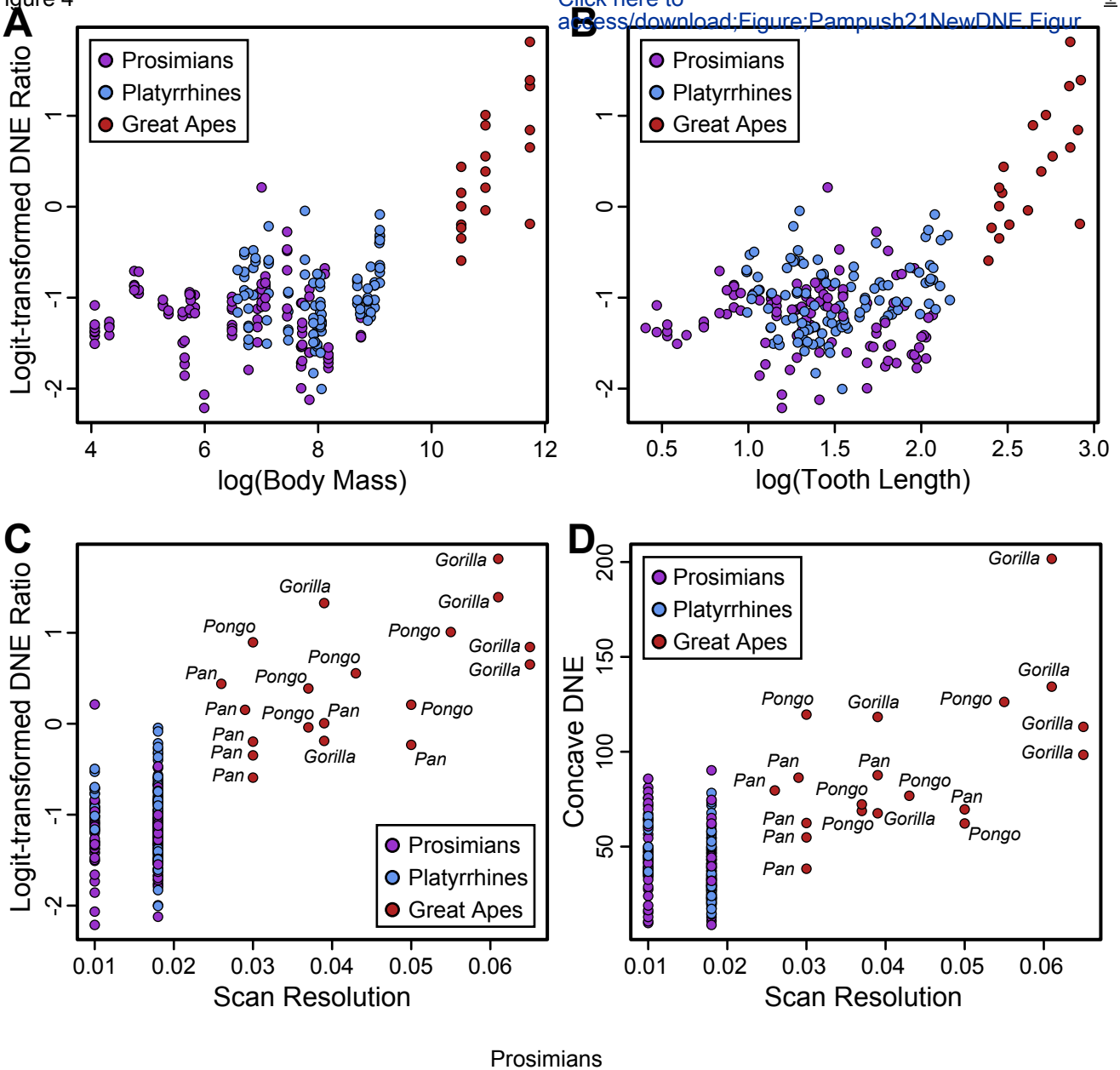
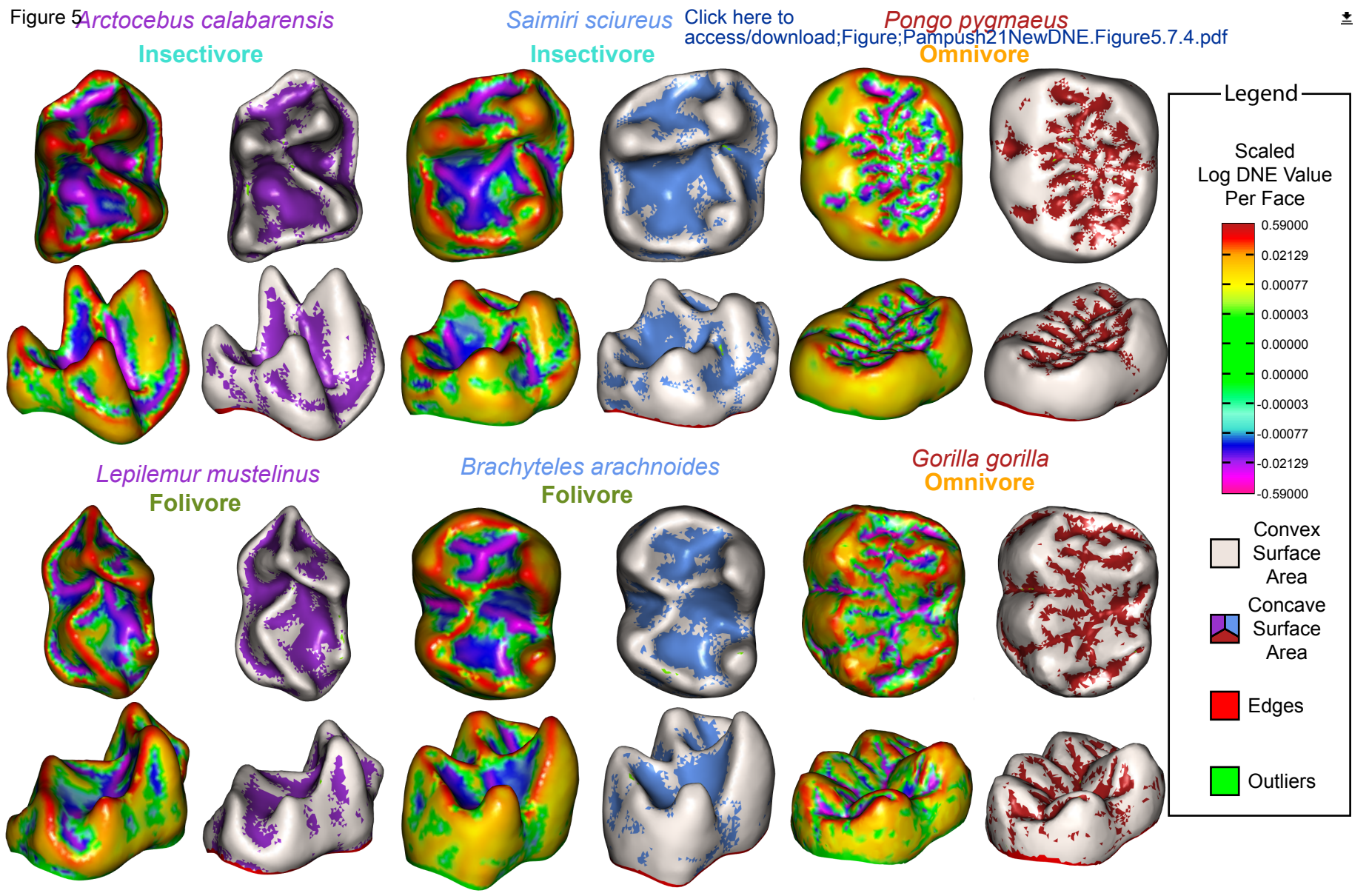


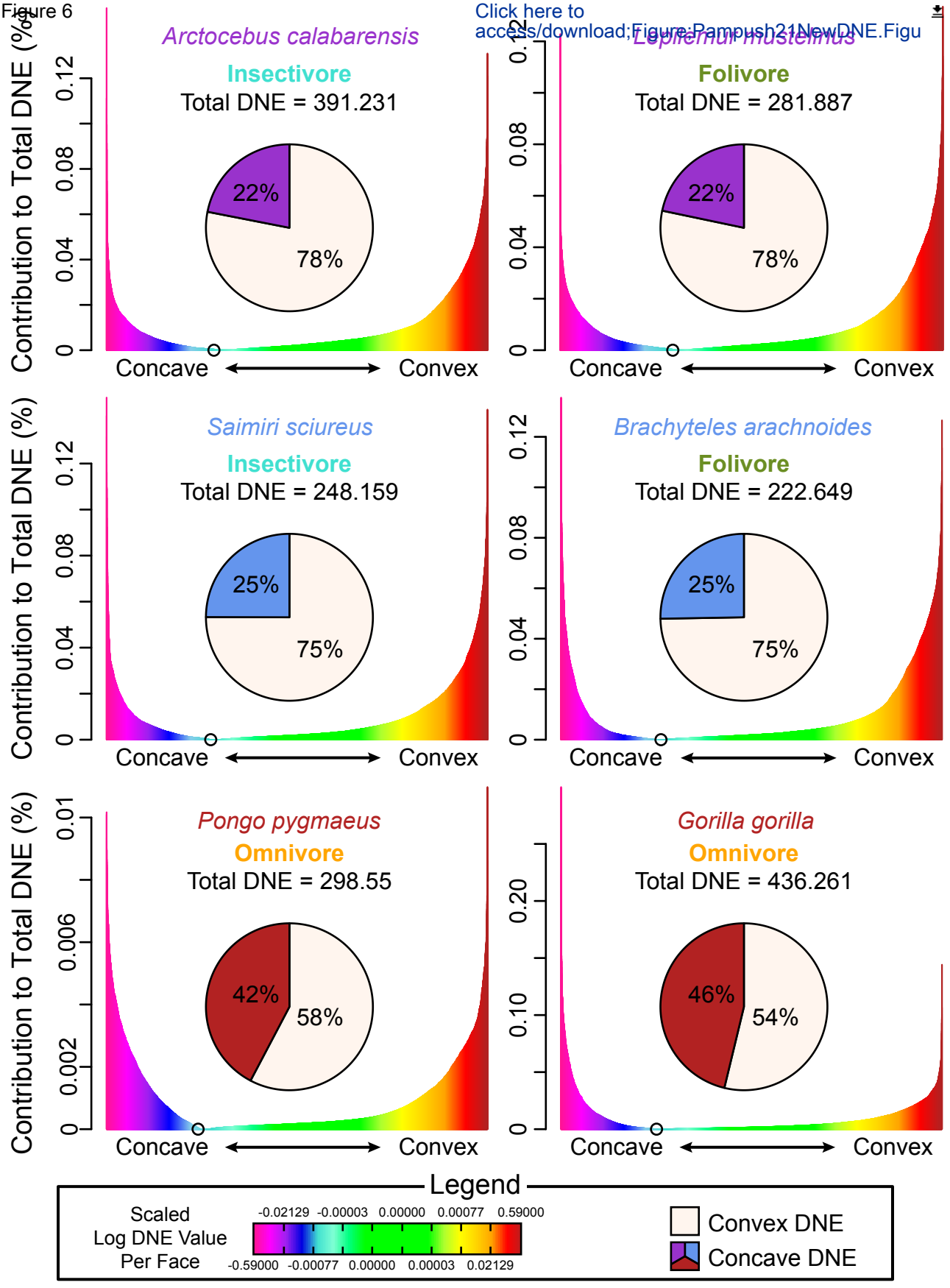
Figure 5



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Figure 6

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Table

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Table 1: Mean DNE values

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

Table 2: Ratio Values.

Group	Diet/Genus	Concave/Convex DNE Ratio (DNE-R)	Concave/Convex Surface Area Ratio (SA-R)
Prosimii	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	*Gorilla*	0.723	0.290
	Pan	0.476	0.233
	Pongo	0.628	0.219

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

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	*p*
(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

Notes: 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.

Table 4: MCMCglmm results of size analyses

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

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

Table 5: MCMCglmm results of resolution analyses

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

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

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

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

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Both Mykolas Imbrasas and Simon Chapple, graduate students at the University College London have requested to have their names moved to the acknowledgements. Upon reflect they did not feel their contributions rose to the level of authorship.

Thank you.