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

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ABSTRACT   Inferred dietary preference is a major component of paleoecologies of extinct primates. Molar occlusal shape correlates with diet in living mammals, so teeth are a potentially useful structure from which to reconstruct diet in extinct taxa. We assess the efficacy of Dirichlet normal energy (DNE) calculated for molar tooth surfaces for reflecting diet. We evaluate DNE, which uses changes in normal vectors to characterize curvature, by directly comparing this metric to metrics previously used in dietary inference. We also test whether combining methods improves diet reconstructions. The study sample consisted of 146 lower (mandibular) second molars belonging to 24 euarchontan taxa. Five shape quantification metrics were calculated on each molar: DNE, shearing quotient, shearing ratio, relief index, and orientation patch count rotated (OPCR). Statistical analyses were completed for each variable to assess effects of taxon and diet. Discriminant function analysis was used to assess ability of combinations of variables to predict diet. Values differ significantly by diets for all variables, although shearing ratios and OPCR do not distinguish statistically between insectivores and folivores or omnivores and frugivores. Combined analyses were much more effective at predicting diet than any metric alone. Alone, relief index and DNE were most effective at predicting diet. OPCR was the least effective alone but is still valuable as the only quantitative measure of surface complexity. Of all methods considered, DNE was the least methodologically sensitive, and its effectiveness suggests it will be a valuable tool for dietary reconstruction. Am J Phys Anthropol 145:247–261, 2011.   © 2011 Wiley-Liss, Inc.

Dietary preference is a fundamental and driving component of ecology. Therefore, dietary reconstruction is integral to the inference of primate paleoecologies or the evolution of ecologies among extant species. It is intuitively logical that tooth form should correlate with dietary preference, as teeth are one of the first organs to encounter food. Through chewing, they play an important role in mechanically breaking down food and permitting release of nutrients stored within (Lucas, 2004). Enamel is the densest, hardest component in the mammal body (Cuy et al., 2002), and as such teeth are very well represented in fossil assemblages. Further, dental morphology is generally considered to be under tight genetic control, and so observed correlations between dental form and dietary function are often inferred as selective adaptations for overcoming food structural properties (Lucas, 2004). In primates, there is a strong correlation between diet and molar tooth shape (Kay, 1975; M'Kirera and Ungar, 2003; Boyer, 2008). Insectivores and folivores are generally recognized to have steeply sloped cusps for puncturing hard insect chitin and shearing tough cellulose. Frugivores and bamboo specialists tend to have blunter, flatter cusps for crushing and grinding fruits, hard objects, and fibrous bamboo

(Kay and Hiiemae, 1974; Rosenberger and Kinzey, 1976, 1978; Seligsohn and Szalay, 1978; Lucas, 1979). A chief goal of dietary reconstruction has been to attempt to quantify these shape differences in a replicable statistically comparable fashion.

Dietary reconstruction has been attempted with a number of different techniques. Historically, quantification of shearing crest lengths has been most successful (Kay, 1975; Kay and Hylander, 1978; Kay and Covert, 1984; Covert, 1986; Strait 1993a,b; Kirk and Simons, 2001). Kay (1975) determined that insectivorous and folivorous primates could be partitioned from frugivorous primates by the relative lengths of the cristid obliqua and the phase I traverse. Kay (1978, 1984; Kay and Hylander, 1978; Kay and Covert, 1984) developed this idea further to devise the "shearing quotient" (SQ), a quantitative measure for inferring diet from unworn primate molars. SQs are calculated by summing the length of mesiodistal shearing crests on a molar tooth. The SQ is the deviation of this summed crest length from a regression line of summed crest lengths of frugivorous extant primates and associated molar lengths. Folivorous and insectivorous primates tend to have higher SQ values while frugivorous primates tend to have lower SQ values (Kay and Covert, 1984; Anthony and Kay, 1993; Meldrum and Kay, 1997; Ungar, 1998). Even among frugivores, species that consume more hard objects have relatively low SQ values (Anthony and Kay, 1993; Meldrum and Kay, 1997). SQ analyses have been applied to all major groups of living primates, and these distinctions hold within each group. SQ analyses have also been performed on many fossil species, including Paleogene anthropoids from the Fayum of Egypt (Kay and Simons, 1980; Kirk and Simons, 2001); Miocene catarrhines of Europe and Africa (Kay, 1977; Ungar and Kay, 1995); platyrrhines (Anthony and Kay, 1993; Fleagle et al., 1996; Meldrum and Kay, 1997); and Miocene apes (Kay and Ungar, 1997).

Covert (1986) analyzed relative shearing potential in the molars of small-bodied primates (i.e., under 500 g) with a ratio of summed crest length over molar length, distinguishing faunivores from frugivores. Strait (1993a,b) compared shearing ratios (SRs) in a larger sample of small bodied primates with three different denominators: body mass, molar length, and molar area. Body mass most accurately distinguished faunivores from frugivores. Molar length and area were also effective, although less so than body mass. Strait suggested this was caused by frugivores having relatively smaller molars. Thus, SRs based on length or area tended to overestimate frugivore shearing potential while underestimating faunivore shearing potential. SRs have been used to infer diet in fossil omomyoids (Strait, 2001).

SQs and ratios are unfortunately not without disadvantages. Both rely on carefully selected shearing crest landmarks. Measuring the lengths of these shearing crests can be time-intensive, sensitive to observer error, and sensitive to particular forms or absence of anatomical landmarks used in measurements. These methods are also troubled by worn teeth, as the shearing crest landmarks required for measurement are obfuscated very soon in the primate lifespan. While some have attempted to develop solutions to this problem (Delson, 1973, 1975; Teaford, 1981, 1982, 1983a,b; Benefit, 1987), it has remained a challenge. Fossil assemblages are often comprised mostly of worn teeth, and so dietary inference using worn teeth is an important goal.

For these reasons, there has been recent momentum toward creating new methods of quantifying tooth shape (Reed, 1997; M'Kirera and Ungar, 2003; Evans et al., 2007; Boyer, 2008). This new generation of methods is often broadly termed "dental topographic analysis," and

these techniques generally claim to rely on fewer assumptions about the identification of anatomical features, more capability for characterizing worn teeth, and more sensitivity for inferring dietary preferences (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003; Evans et al., 2007; Boyer, 2008).

Ungar and Williamson (2000) introduced the "relief index" (RFI), a metric for quantifying overall tooth shape. The RFI of a tooth is the three-dimensional surface area of a tooth divided by the two-dimensional footprint of that tooth, multiplied by 100. This metric has been called analogous to SQs because it quantifies the relative shearing potential of a tooth. RFI values have been shown to distinguish folivores with high values from frugivores with low values in extant hominoids (M'Kirera and Ungar, 2003) and cercopithecoids (Ulhaas et al., 2004; Ungar and Bunn, 2008; Bunn and Ungar, 2009). Boyer (2008) demonstrated that RFI (calculated slightly differently) distinguished insectivores and folivores from frugivores in a broad sample composed of euarchontans. RFI values have been used to investigate molar macrowear and dental senescence (Dennis et al., 2004; King et al., 2005). RFI has also been used to assess diets of extinct taxa in fossil hominins (Ungar, 2004, 2007), hominoids (Merceron et al., 2006), and plesiadapids (Boyer et al., 2010).

While RFI is at least somewhat analogous to SQ, other metrics attempt to characterize other aspects of tooth shape. "Orientation patch count" (OPC) is a metric that quantifies tooth surface complexity (Evans et al., 2007). Evans et al. (2007) explain complexity in the following way: if teeth are viewed as tools to break down foods, complexity measures the number of tools on a tooth surface. RFI and other measures could on the other hand be considered measures of the shape of tools. OPC is calculated by determining the orientations of grid points on a topographic map in one of eight compass directions. Groups of contiguous points with the same compass direction are grouped into patches, and the number of patches is counted. Evans et al. (2007) calculated OPC of tooth rows belonging to carnivorans and rodents of five dietary categories ranging from hypercarnivores to herbivores. They found that despite the large phylogenetic and morphological gaps between these two orders, carnivorans and rodents belonging to the same dietary category had similar OPC values. Species belonging to differing dietary categories tended to have different OPC values regardless of order, with species belonging to more herbivorous categories having more complex tooth surfaces and relatively higher OPC values. To reduce the sensitivity of this metric to tooth orientation, Evans and Jernvall (2009) introduced a modification of OPC known as orientation patch count rotated (OPCR). OPCR has also been used to examine the complexity of individual teeth instead of full cheek tooth rows (Evans and Jernvall, 2009).

Dental topographic analysis does not possess as many methodological weaknesses as SQ and SR analyses. It can be applied to worn molar teeth, and current techniques are much less reliant on manually selected landmarks. But there are still disadvantages that must be considered. Current methods employing laser scanners to capture shape data for dental topographic analysis are sensitive to manual orientation of the tooth during the initial scanning stage. Studies of RFI often section digital elevation models by only considering surface data above the lowest point on the talonid basin. This landmark is suitable for comparing species that are closely

TABLE 1. Taxa compromising the study sample, number of individuals in each taxon, assigned dietary category (if applicable), and references used to assign that category

Taxon (21 genera)	N	Dietary category	References
Arctocebus calabarensis	5	Insectivory	Charles-Dominique (1974)
Galago spp.	7		Charles-Dominique (1974); Harcourt and Nash (1986)
Loris tardigradus	4		Nekaris and Rasmussen (2002)
Tarsius spp.	9		Gursky (2000); Niemitz (1984); Davis (1962); Crompton (1989)
Tupaia spp.	12		Emmons (2000)
Avahi laniger	7	Folivory	Thalmann (2001); Albignac (1981); Ganzhorn et al. (1985); Harcourt (1991)
Cynocephalus spp.	5		Wischusen and Richmond (1998); Stafford and Szalay (2000)
Hapalemur spp.	7		Overdorff et al. (1999)
Indri indri	9		Powzyk and Mowry (2003)
Lepilemur spp.	5		Thalmann (2001); Russell (1977)
Propithecus spp.	7		Powzyk and Mowry (2003); Richards (1978); Simmen et al. (2003)
Eulemur fulvus fulvus & rufus	8	Omnivory	Sussman (1977); Overdorff (1993); Ganzhorn (1986); Rasmussen (1999); Simmen et al. (2003)
Galago alleni	3		Charles-Dominique (1974)
Lemur catta	6		Sussman (1977); Ganzhorn (1986); Gould (2006); Simmen et al. (2003)
Microcebus griseorufus	7		Hladik et al. (1980); Atsalis, (1999); Lahann, (2007); Génin (2008); Radespiel et al. (2006)
Mirza coquereli	3		Hladik et al. (1980); Pages, (1980); Petter et al. (1971)
Nycticebus spp.	6		Wiens et al. (2006); Streicher (2004)
Phaner furcifer	3		Hladik et al. (1980); Petter et al. (1971); Charles-Dominique and Petter (1980)
Tupaia minor	2		Emmons (1991)
Cheirogaleus spp.	8	Frugivory	Hladik et al. (1980); Lahann (2007)
Daubentonia madagascariensis	6		Sterling et al. (1994); Iwano and Iwakawa, (1988)
Perodicticus potto	6		Charles-Dominique (1974)
Varecia spp.	8		Moreland (1991); Vasey (2000)
Nycticebus javanicus	3	Unknown	

related phylogenetically but can create difficulty when comparing teeth with more disparate morphologies as discussed by Boyer (2008). An orientation-free metric for quantifying molar tooth shape without these issues would be a useful addition to the toolbox of dental topographic analysis.

In this study, we propose the Dirichlet normal energy (DNE) of the normal map of a tooth surface as such a metric. This technique for quantifying molar tooth shape is independent of position, orientation, scale, and landmarks. Surface "energy" is a concept from differential geometry. It measures some global property of the surface, usually quantifying its deviation from a stable minimal energy state. DNE measures the deviation of a surface from being planar. We hypothesize that the DNE of 3D tooth crown models will reflect diet. Specifically, we predict that DNE will differ between species with different dietary preferences, with higher DNE values in folivores and insectivores than in omnivores and frugivores. We also predict that DNE will correlate with other measures of shape quantification, as these quantifications are all driven by dietary signals.

In addition to introducing a new tool for inferring diet from molar morphology, this study also tests whether diet can be inferred more accurately by combining multiple metrics for quantifying tooth shape. Although all methods that correlate with diet are probably detecting somewhat similar selective adaptations to dietary preferences, it is likely that these methods are all capturing different elements of molar morphology. In the case of comparisons between metrics such as RFI and OPC, this is almost a certainty. Combining these techniques should allow us a more accurate window into the total adaptive system. We hypothesize that an analysis of molar shape morphology combining multiple shape-quantification

metrics will have more success predicting diet than individual methods. From this hypothesis, we predict that a statistical analysis combining SQs, SRs, relief indices, optimum patch counts, and DNE values will more accurately predict dietary preferences associated with unknown molar specimens together than any metric by itself or any combination of fewer numbers of metrics.

MATERIALS AND METHODS
Study sample and dietary categories

The study sample consisted of 146 lower second molars treated as belonging to 24 taxa (Table 1). Information on dietary preferences was used to characterize each taxon as a member of one of four diet preference groups: insectivore, folivore, omnivore, and frugivore. The taxa were codified into these groups using the first of two alternate diet-classification schemes from Boyer (2008), based on field studies reporting time spent foraging, gut contents, or fecal composition (Table 1). Taxa with diets consisting of >50% insects or leaves either as part of the regular diet or at least during 1–2 months out of the year were codified as insectivores or folivores, respectively. Taxa with diets consisting of more than 50% fruits and seeds with no substantial contribution of insects or leaves were codified as frugivores. Taxa with diets consisting of roughly equal proportions of fruits and either insects or leaves throughout the year were codified as omnivores. Additionally, taxa were codified as omnivores when different studies reported conflicting dietary preferences. *Eulemur spp.* and *Lemur catta* are classified as omnivores in this study due to conflicting reports from behavioral studies (e.g., Sussman, 1977; Simmen et al., 2003), although it should be noted that Boyer (2008) codified them as folivores.

Data preparation

High-resolution plastic replica casts were created from molds of lower second molars using gray-pigmented EPOTEK 301 epoxy, and scanned with a ScancoMedical brand μCT 40 machine (www.scanco.ch) at 10–18 μm resolution. The primary advantage of μCT-scanning is that it provides fully three-dimensional data instead of the "two-and-a-half dimensional" data provided by laser scanners (see a more detailed explanation in Boyer, 2008). The data captured by the μCT scanner was processed by the Scanco, ImageJ (NIH), and Amira (Visage Imaging) software packages to produce three-dimensional models of tooth surfaces. Using Amira these surface models were then cropped to include only the tooth crown using the approximate location of the root-crown junction. This differs from dental topographic analyses done by Ungar and colleagues who have used the bottom of the talonid basin as a reference point for cropping. The taxa compared here exhibit such morphological variation that such a reference point would be impractical. Aspects of the tooth crown relevant to chewing would be excluded in some taxa (in taxa with flat-basined talonids, nearly the entire talonid is excluded), while aspects irrelevant to such functional considerations (e.g., anterior roots) would be included in others.

Variables measured

Six variables were computed for each specimen: M_2 mesiodistal length, SQ, SR, OPCR, RFI, and DNE. M_2 length was measured using the length measurement tool in Amira and the natural log of each length was taken. For calculating SQs and SRs, Geomagic Studio 10 (Geomagic) was used to measure the lengths of six shearing crests: the paracristid, the protocristid, the postmetacristid, the preentocristid, the postentocristid, the posthypocristid, and the cristid obliqua (Fig. 1). Not all taxa measured possessed a clear hypoconulid. In those cases, the boundary between the postentocristid and the posthypocristid was placed at the point where the paraconid or termination of the paracristid on the M_3 contacts the M_2. This point was consistent with the position of the hypoconulid in the taxa examined which possessed clear hypoconulids and was easily reproduced in the taxa without a hypoconulid. The teeth in this sample were variably worn, which has traditionally been an issue with shearing crest measurement. In cases where wear facets had worn away the original shearing crest, the best approximation of the original shearing crest was used. In cases where cusps were worn flat, crest lengths were measured to or from the center of the flat cuspal region. Intraobserver variation with this protocol was relatively low, with less than 0.1 mm difference between highest and lowest measured total crest lengths. We also examined interobserver variation and the effects of downsampling and smoothing of models, finding interobserver variation to be low and a small effect of smoothing. Detailed methods and results of these tests are included as Supporting Information. All measurements for this study were taken on smoothed models by one observer.

These shearing crest lengths were summed for each specimen to provide a measure of total shearing potential. A regression line was created for the frugivorous taxa of the sample with shearing potential as the dependent variable and M_2 length as the independent

variable. SQs were then measured as the deviation of each shearing potential sum from the expected regression line of frugivores. SRs were calculated by dividing each shearing potential sum by the associated M_2 length.

For the calculation of RFI, the three-dimensional surface area of the enamel crown was measured in Amira. The two-dimensional planimetric area of the crown was measured using ImageJ. The RFI is calculated here as the natural log of the square root of surface area divided by the square root of projection area. For specimens this study shares in common with Boyer (2008) the RFI values are exactly the same, as they were taken from this study.

OPCR was calculated using the Surfer software package (Golden Software) and the SurferManipulator tool (Evans et al., 2007). OPC was initially calculated by the method of Evans et al. (2007) on each individual tooth specimen using a minimum patch size of 3 and 8 orientations, with each successive OPC quantification rotating the orientation boundaries by $5.625°$. The eight OPC values were averaged to provide an OPCR value.

Mathematical background for DNE

Our quantification of tooth shape begins with computer-generated surface meshes representing tooth surfaces, comprised of many triangular polygons. To quantify the "curveness" of a surface mesh we examine, as is customary in differential geometry, the normal map. The normal map assigns to each point on the tooth surface a normal direction. In a sense, we want to quantify to what extent this normal map changes as we move around the surface. There are many possible ways to accomplish this. We choose a natural definition based on the Dirichlet energy of the normal map. Dirichlet energy is a commonly used concept in mathematics (Eells and Samson, 1964; Pinkall and Polthier, 1993; Hélein, 2002), but our application of it to the normal map of the surface is novel. In the continuous case (i.e., as the triangles of our tooth mesh are getting arbitrarily small), it is equivalent to measuring the sum of squares of the principle curvatures over the surface: this is a measure of how much a surface bends; if (and only if) both the principle curvatures are identically zero then the shape is planar.

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 $\|\blacksquare\|$ 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: $E = \int_M e(p) d\mathrm{vol}(p)$, where we integrate with respect to the surface area $d\mathrm{vol}(p)$. In case the directions u and v are not orthonormal, the energy density is calculated by $e(p) = tr(G^{-1}H)$, where $G = \begin{pmatrix} \langle u,u \rangle & \langle u,v \rangle \\ \langle u,v \rangle & \langle v,v \rangle \end{pmatrix}, H = \begin{pmatrix} \langle n_u,n_u \rangle & \langle n_u,n_v \rangle \\ \langle n_u,n_v \rangle & \langle n_v,n_v \rangle \end{pmatrix}$ 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
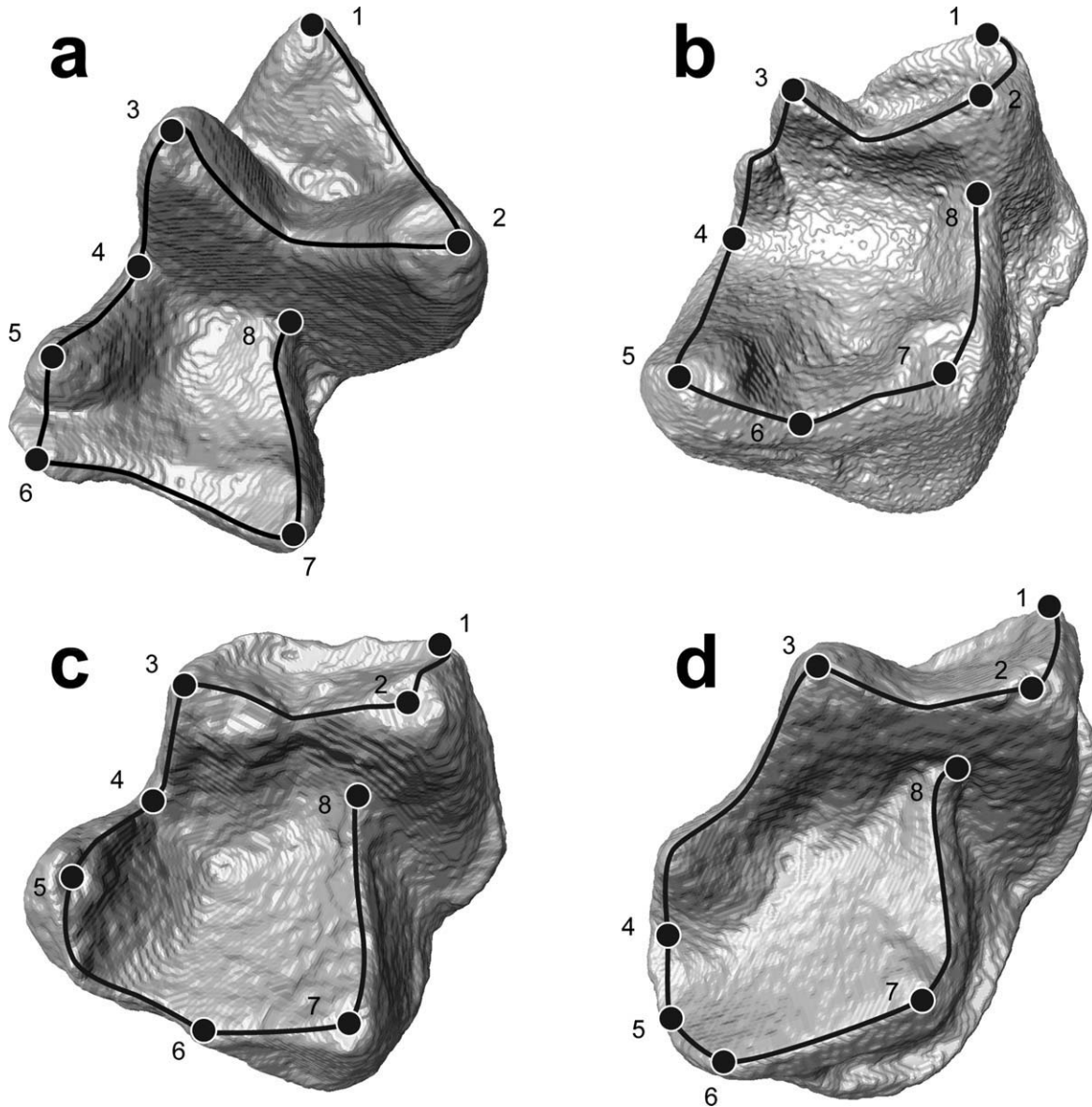
Fig. 1. Diagram of shearing crest measurements for the calculation of SQs and ratios. (**a**) *Tupaia*, (**b**) *Hapalemur*, (**c**) *Microcebus*, and (**d**) *Lepilemur*. Each numbered point indicates the beginning or ending point of a crest. The crests measured are as follows: 1–2, paracristid; 2–3, protocristid; 3–4, postmetacristid; 4–5, preentocristid; 5–6, postentocristid; 6–7, posthypocristid; and 7–8, cristid obliqua.

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: $E = \sum_{\Delta \in \text{Faces}} e(\Delta) \cdot \text{area}(\Delta)$, where Δ is traversing over all the triangles in the tooth surface.

An important property of this energy is its independence of the surface's initial position, orientation, and scale. First, to see why it is invariant to position and orientation note that all the components of our energy formula are independent of the initial position and orientation of the surface. In particular, the inner product of the normal differences stays the same if the surface is rotated and/or reflected and/or translated. This is true also to the faces' areas, and the inner product of the direction vectors u and v (these are the mesh edges). Second, its invariance to scale is a direct outcome of the integration with regard to the surface area. For example, if we blow-up the surface by a scale of two, G^{-1} will be scale by one quarter and the area of each face by four, so the total energy stays the same.

DNE has a number of methodological advantages over current techniques. This metric does not rely on landmarks and is applicable to any 3D object. No methodological changes must be made for disparate morphologies. This method is also completely independent of manual orientation and scale. Orienting 3D tooth models in a featureless virtual space to approximate how that tooth would fit in a jaw is not a trivial task, and so this is a significant advantage.
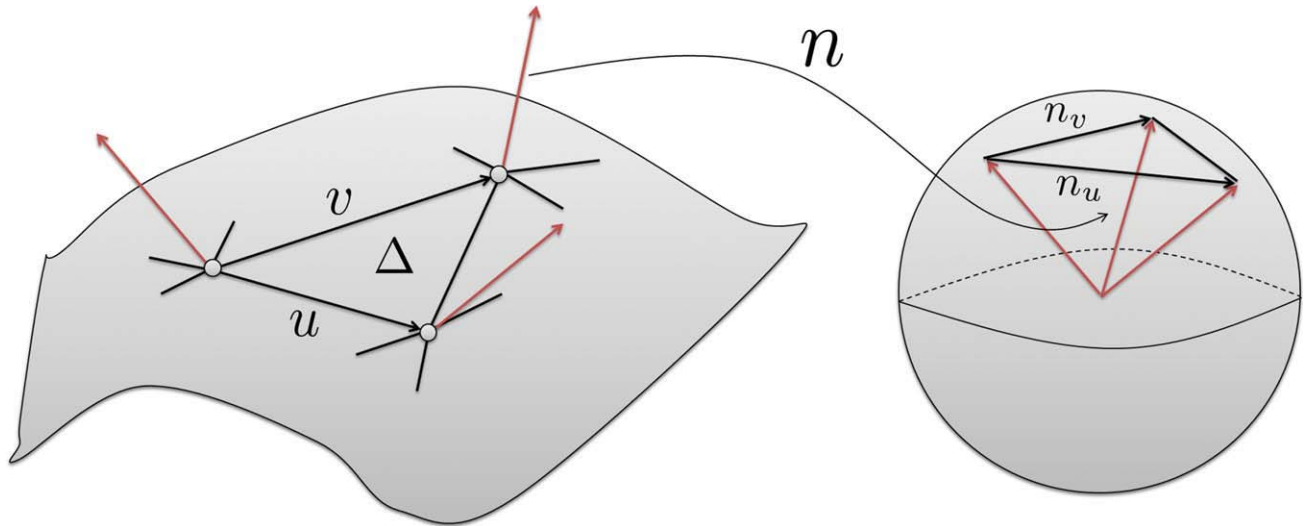
Fig. 2. Diagram demonstrating approximated normals of vertices used to calculate the Dirichlet normal surface energy for a single triangular face. Faces on more curved surfaces will produce larger outlined polygons from translated nearby vertex normals. Example translated normals and resultant outlined polygon are seen on the right.

Fig. 3. Tooth crown models indicating $e(p)$, variation in energy across a tooth surface. This indicates levels of relatively high and low curvature across the tooth surface. Warmer colors indicate higher curvature, whereas cooler curvatures indicate lower curvature. (**a**) *Tupaia*, (**b**) *Hapalemur*, (**c**) *Microcebus*, and (**d**) *Lepilemur*.

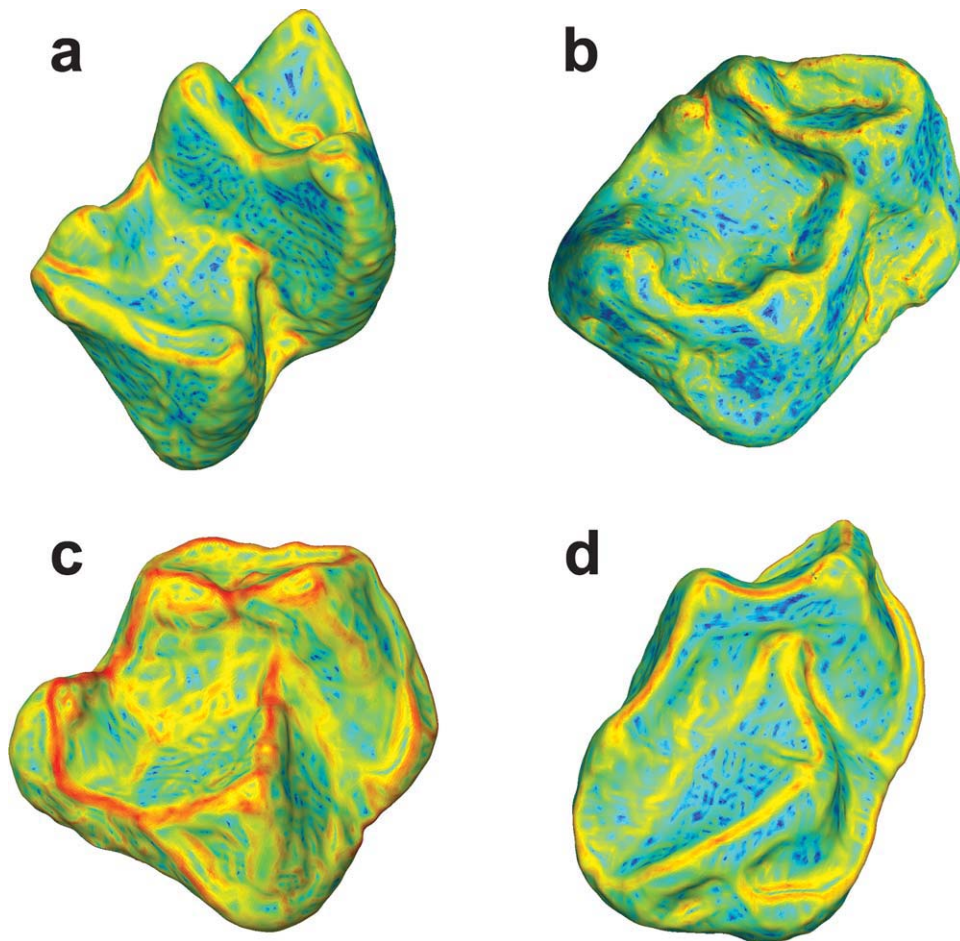For computing DNE, models were first examined in Amira for defects produced by the casting process, such as bubbles. If defects were present, they were removed using the surface editor module of Amira. The Simplifier module was then used to downsample surface meshes to 10,000 triangle faces. This resulted in meshes with between 9,990 and 10,000 faces. The models were then smoothed 100 iterations with the SmoothSurface module. The actual calculation of DNE was completed using Teether, a MATLAB application written by YL, using the normal calculation and formulae described above. Figure 3 depicts $e(p)$, that is the variation in energy across the surface, for four different tooth surfaces. Each triangle is colored proportional to its energy, and as indicated above, the total DNE is the sum of all these local energies multiplied with the triangles' area.

Sensitivity to cropping

To evaluate the sensitivity of DNE to variable methods of cropping a tooth model (i.e., varying how much of the tooth surface is used in quantifying aspects of dental topography) a single tooth model was taken from each of *Arctocebus calabarensis, Propithecus spp., Microcebus griseorufus*, and *Varecia spp.* and cropped using seven different methods. These methods included 1) cropping to include only crown enamel (the standard method for other comparisons in this study); 2) cropping to include only crown enamel but done so as to leave sharp jagged edges bounding the model's lower border; 3) cropping to include crown enamel but done so as to leave rounded edges bounding the model's lower border; 4) cropping to exclude all surface below the lowest point on the talonid basin (e.g., Ungar and M'Kirera, 2003); 5) cropping to exclude all surface below the lowest point on the trigonid basin but done so as to leave sharp jagged edges bounding the model's lower border; 6) cropping to exclude all surface below the lowest point on the trigonid basin but done so as to leave rounded edges bounding the model's lower border; and 7) cropped to include only surface immediately visible from directly above the model (simulating a 2.5d model created by laser scanning). DNE was computed for each of these cropping methods. To compare with traditional metrics, RFI was also computed for each of these cropping variants. The coefficients of variation were calculated for both DNE and RFI for each specimen and then tested statistically for equality with Fligner–Killeen tests with an α-level of 0.05 (Fligner and Killeen, 1976; Donnelly and Kramer, 1999).

Data analysis

All statistical tests were performed with an α-level of 0.05 using the SPSS 11.0 software package (SPSS). Shapiro–Wilks tests indicated all groupings of data were normal, but Levene's tests indicated the data exhibited heterogeneity of variances. Therefore, to assess the effects of diet and taxon on each variable separate one-way Welch analyses of variance (ANOVAs) were performed with dietary category and taxon as factors. Post-hoc Games–Howell pairwise comparison tests were run for each ANOVA. Correlations between variables were assessed with Pearson's r tests.

The capability of variables to predict diet in isolation or in combination was assessed using discriminant function analysis (DFA). The DFAs were run in SPSS entering all variables at once and with prior probabilities of

TABLE 2. Coefficients of variation for RFI and DNE of variably cropped models of specimens and associated taxa

Taxon	Single specimen CV		Taxon CV	
	RFI	DNE	RFI	DNE
Arctocebus	0.074	0.047	0.086	0.187
Propithecus	0.174[a]	0.012[a]	0.049	0.119
Microcebus	0.109	0.054	0.044	0.062
Varecia	0.163[a]	0.044[a]	0.043	0.129

[a] RFI and energy differ with $P < 0.05$, Fligner–Killeen test.

TABLE 3. Descriptive statistics for shearing quotients, shearing ratios, relief index, OPCR, and DNE by dietary category

Variable	Diet	N	Mean	Std. error
Shearing quotient	I	37	16.173	0.895
	F	40	9.709	1.267
	Om	38	3.289	1.057
	Fr	22	0.027	0.567
	Total	137	8.060	0.738
Shearing ratio	I	37	3.199	0.046
	F	40	3.127	0.097
	Om	38	2.481	0.042
	Fr	22	2.394	0.031
	Total	137	2.847	0.045
Relief index	I	37	0.600	0.007
	F	40	0.532	0.010
	Om	38	0.488	0.005
	Fr	28	0.401	0.010
	Total	143	0.512	0.007
OPCR	I	37	53.646	1.014
	F	40	51.698	1.530
	Om	38	44.396	0.807
	Fr	28	43.150	1.512
	Total	143	48.588	0.719
DNE	I	37	274.921	6.577
	F	40	221.771	8.084
	Om	38	181.625	4.676
	Fr	28	125.458	6.899
	Total	143	205.996	5.509

group membership determined from group sizes. This analysis created discriminant functions to maximize variance between the mean values of diet groups for variables in the sample. Ability for dietary prediction was evaluated using a jack-knife (or "leave one out") classification method. Overall success was assessed by calculating the percent of specimens accurately assigned to diet categories. For the most successful sets of variables, percentage of taxa wherein a mode of specimens was correctly predicted was also calculated. Successful modal classification for a taxon indicates that more specimens of that taxon were predicted to belong to the correct dietary category than any other category. A technique with high modal classification success could accurately infer diet in taxa of large sample sizes even if its overall accuracy on individual specimens were much lower. Many sets of variables were analyzed. Each variable was analyzed on its own, as was every possible combination of multiple variables. This totaled 63 different DFAs.

RESULTS
Sensitivity to cropping

RFI and DNE were computed for seven variably cropped models of one specimen each of *Arctocebus calabarensis, Propithecus verreauxi, Microcebus griseorufus,*
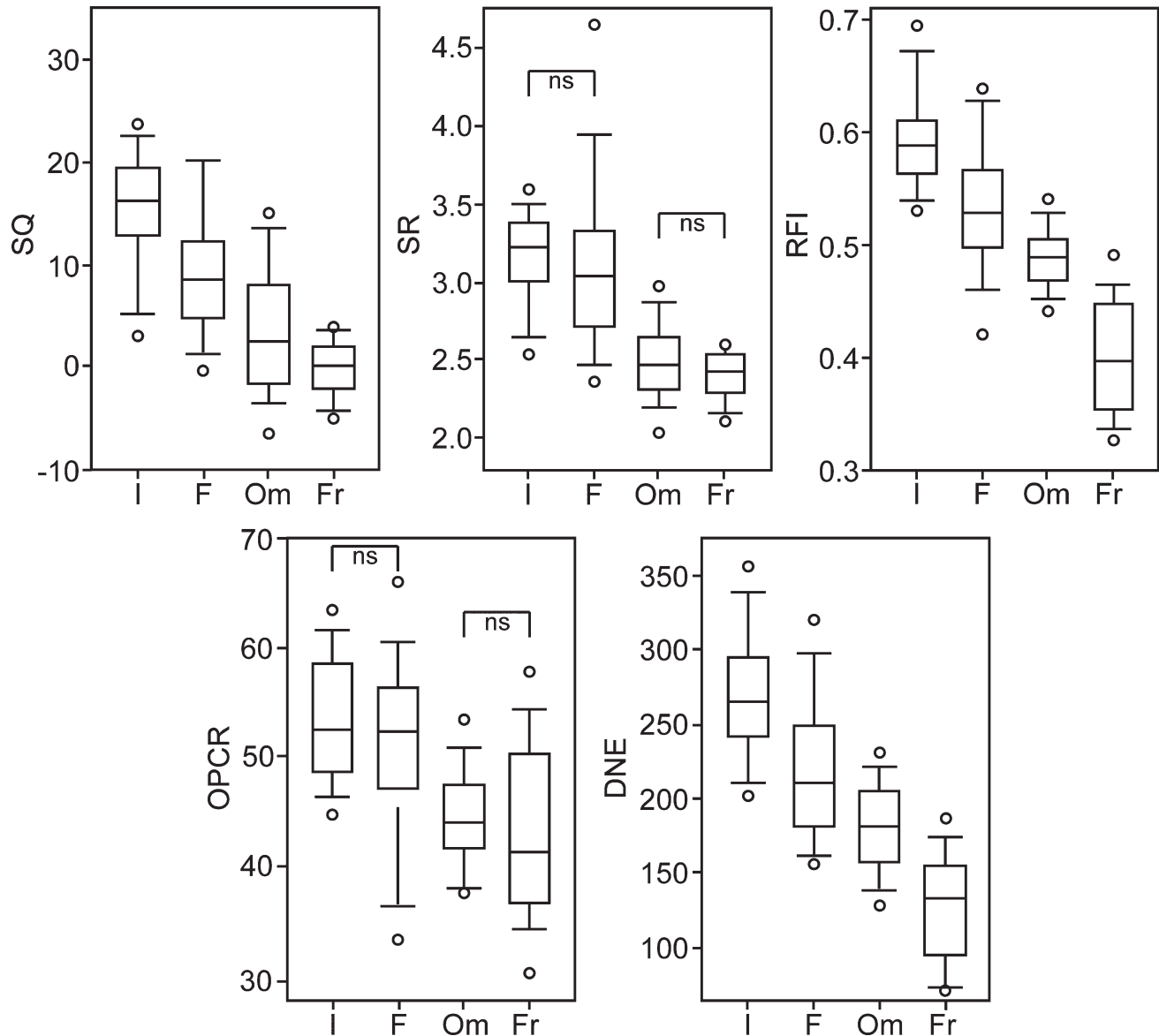
Fig. 4. Box-plots of SQs, SRs, RFI, OPCR, and DNE for all taxa of each dietary category. All pairwise comparisons are significant with $P < 0.05$ except for those indicated as not significant.

and *Varecia variegata* to assess sensitivity to varying types of cropping relative to variation within taxa (Table 2). In all four comparisons, the coefficient of variation (CV) of RFI is greater than that of DNE. The CV of DNE in *Propithecus* and *Varecia* is significantly lower than the CV of RFI according to Fligner–Killeen tests with $P < 0.05$. The CV of DNE for each differently cropped specimen is less than the associated CV of DNE for all specimens within that taxon. The opposite is mostly true for RFI, with CVs for three of four differently cropped specimens larger than intrataxon CVs.

Effects of diet

Five variables representing teeth in the sample were partitioned according to four different dietary categories to assess the effect of diet on their variance (Table 3, Fig. 4). Values of all metrics are highest on average in insectivores and decrease in value from insectivores to folivores to omnivores to frugivores. Overall Welch ANOVAs indicate that dietary category significantly explains sample variance for every metric with $P < 0.001$ [SQ: $N = 139$, $F(3,71.293) = 69.743$; SR: $N = 139$, $F(3,74.349) = 71.578$; RFI: $N = 146$, $F(3,71.293) = 87.260$; OPC: $N = 146$, $F(3,72.659) = 23.131$; E: $N = 146$, $F(3,74.988) = 79.205$]. F-ratio values for Welch ANOVA results are provided, with degrees of freedom listed in parentheses. Pairwise comparisons were significant with $P < 0.05$ among all diet category for SQ, RFI, and DNE. SR and OPCR had significant differences among all dietary categories except insectivory and folivory, and omnivory and frugivory.

Effects of taxon

Five variables representing teeth in the sample were partitioned according to 24 different taxonomic categories to assess the effect of taxonomic identity on their variance

TABLE 4. Descriptive statistics for shearing quotients, shearing ratios, relief index, OPCR, and DNE by taxon

Taxon	N	SQ Mean	SQ Std. error	SR Mean	SR Std. error	RFI Mean	RFI Std. error	OPCR Mean	OPCR Std. error	DNE Mean	DNE Std. error
Arctocebus calabarensis	5	7.381	2.846	2.803	0.171	0.597	0.023	46.800	1.428	290.258	24.262
Galago spp.	7	18.101	1.300	3.117	0.046	0.585	0.005	49.057	0.777	259.752	11.573
Loris tardigradus	4	16.797	2.355	3.302	0.148	0.588	0.008	52.000	2.483	250.336	13.889
Tarsius spp.	9	19.592	1.364	3.317	0.072	0.566	0.005	59.889	1.645	279.018	7.833
Tupaia spp.	12	15.919	0.708	3.296	0.044	0.639	0.015	55.042	1.425	282.503	14.420
Avahi laniger	7	12.863	1.246	3.212	0.089	0.568	0.015	55.571	0.948	242.986	11.242
Cynocephalus spp.	5	26.656	2.827	4.411	0.244	0.632	0.005	51.525	2.760	318.516	15.091
Hapalemur griseus	5	3.573	0.753	2.607	0.046	0.488	0.008	51.000	2.839	208.719	10.302
Indri indri	9	9.722	0.456	3.256	0.042	0.473	0.017	55.556	1.859	172.673	4.697
Lepilemur spp.	5	0.382	0.690	2.404	0.041	0.522	0.008	34.660	0.832	239.798	12.527
Propithecus spp.	7	6.074	0.524	2.895	0.045	0.550	0.010	49.143	1.262	191.295	8.590
Prolemur simus	2	7.618	0.925	2.962	0.085	0.498	0.004	74.000	10.875	220.820	27.610
Eulemur spp.	8	−4.184	0.968	2.169	0.055	0.502	0.009	40.038	1.149	178.298	9.790
Galago alleni	3	7.673	1.174	2.741	0.058	0.520	0.008	45.667	1.667	175.501	12.515
Lemur catta	6	0.222	0.897	2.428	0.057	0.480	0.010	39.833	1.046	181.235	9.351
Microcebus griseorufus	7	10.704	1.532	2.637	0.047	0.478	0.008	46.000	1.024	214.708	5.016
Mirza coquereli	3	−0.043	2.065	2.348	0.094	0.471	0.014	43.667	0.667	188.901	6.475
Nycticebus spp.	6	1.744	0.524	2.467	0.027	0.478	0.008	48.000	1.414	144.438	6.043
Phaner furcifer	3	6.537	3.479	2.608	0.150	0.469	0.009	46.000	0.577	170.135	5.470
Tupaia minor	2	14.606	0.261	3.013	0.037	0.532	0.037	55.875	4.125	207.381	24.325
Cheirogaleus spp.	8	−0.416	0.947	2.336	0.042	0.345	0.005	41.375	2.095	121.322	11.351
Daubentonia sp.	6					0.364	0.004	46.667	3.263	75.890	2.272
Perodicticus potto	6	0.872	1.483	2.423	0.077	0.457	0.011	51.767	1.822	134.126	4.414
Varecia spp.	8	−0.163	0.685	2.429	0.047	0.443	0.007	35.825	1.266	160.270	7.327
Total	143	8.060	6.601	2.847	0.045	0.512	0.007	48.588	0.719	205.996	5.509

TABLE 5. Summary of pairwise comparisons between taxa

	Total pairs 1[a]	Significant pairs SQ	Significant pairs SR	Total pairs 2[a]	Significant pairs RFI	Significant pairs OPCR	Significant pairs DNE
Total	253	103	97	276	108	67	102
Within diet	61	20	17	64	10	7	8
Among diets	192	83	80	212	98	60	94
I-Fr	18	12	10	24	20	7	21
I-Om	48	18	18	48	21	19	19
F-Fr	18	11	12	24	20	6	20
Om-Fr	24	6	4	32	13	6	11
F-Om	48	20	23	48	12	15	12
I-F	36	16	11	36	12	7	9

Numbers of significant pairwise comparisons ($P < 0.05$) are separated first by whether they compared taxa within a dietary category or between two categories, and then by specific between-diet pairs.
[a] Total pairs 1 gives total possible comparisons between taxa excluding *Daubentonia*. Total pairs 2 gives total possible comparisons including *Daubentonia*.

(Table 4). Each metric differs significantly among taxa with $P < 0.001$ [SQ: $N = 139$, $F(22,32.207) = 56.561$; SR: $N = 139$, $F(22,30.680) = 33.782$; RFI: $N = 146$, $F(23,31.602) = 103.934$; OPC: $N = 146$, $F(23,32.869) = 25.943$; E: $N = 146$, $F(23,31.894) = 71.493$]. *F*-ratio values for Welch ANOVA results are provided, with degrees of freedom listed in parentheses. For each metric, a large majority of significant post-hoc pairwise comparisons are between taxa with different diets (Table 5). RFI has the highest number of overall significant comparisons, while OPCR has the lowest. DNE has the highest ratio of number of significantly different pairs of taxa with differing diets to significantly different pairs of taxa with similar diets.

RFI proved to be the most effective metric in significantly separating insectivores from omnivores, folivores from frugivores, and omnivores from frugivores. DNE was most effective for significantly separating insectivores from frugivores. SQs were most effective for significantly distinguishing insectivores from folivores. SRs were most effective at distinguishing folivores from omnivores.

TABLE 6. Correlations between pairs of variables as R^2 values

Variable pair	R^2
SQ/SR	0.863
SQ/RFI	0.451
SQ/OPCR	0.347
SQ/DNE	0.556
SR/RFI	0.424
SR/OPCR	0.339
SR/DNE	0.475
OPCR/RFI	0.118
DNE/RFI	0.736
DNE/OPCR	0.103

Correlations between metrics

All shape-quantification metrics were significantly positively correlated with each other at $P < 0.01$ (Table 6). SQs and SRs are correlated with an R^2-value of 0.86, making them the most highly correlated pair of variables. DNE and OPCR have the lowest amount of correlation,

having an R^2-value of 0.10. OPCR has the lowest average correlation with all other metrics with an average R^2 of 0.23. SQs have the highest average correlation with 0.55.

Dietary prediction

A total of 63 discriminant function analyses were run. Among these, we examined the results of a subset representing the overall and modal success rates for each metric alone, the three most successful combinations, and the combination of RFI/OPC/DNE/natural log of M_2 length (Table 7). The DFA combining RFI/OPC/DNE/natural log of M_2 was chosen to examine the accuracy of a technique including only metrics with little or no dependence on morphological homology and expertise. While overall success is highest for all variables combined except M_2 length, its modal success percentage is equal to that of all variables combined. Similarly, the combination of all variables except DNE has equal overall success to all variables, but its modal success is lower. The combination of RFI/OPC/DNE/natural log of M_2 length has both lower overall and modal success than the three most successful combined analyses.

The structure matrices for the four listed combined analyses indicate correlations between variables and individual discriminant functions (Table 8). All analyses have a first function explaining between 71.6 and 81.3% of the sample, a second function explaining 18–26.9%, and a third function explaining 0.7–1.5%. The first function of each analysis is most strongly correlated with RFI and DNE. For the three analyses including SQs and SRs, the second function is most correlated with M_2 length and

SR. The third function is most strongly correlated with SQs. For the analysis not including SQs and SRs, the second function is dominated by the natural log of M_2 length, and the third by positive correlation with OPCR.

All combined analyses discussed here habitually misclassify *Lepilemur spp.* and *Perodicticus potto* specimens as omnivores. All of these combined analyses also misclassify one *Tupaia minor* specimen as an insectivore, causing all combinations to fail to correctly infer the diet of this species by mode.

DISCUSSION AND CONCLUSIONS
Dirichlet normal energy

The prediction that DNE would differ among species with different dietary preferences was strongly supported. In the specimens considered, DNE significantly differed among all four dietary categories. Some previous studies [e.g., Kay (1975), Boyer (2008)] have had difficulty quantitatively distinguishing between insectivores and folivores. In many of these cases, it is possible to use Kay's threshold to separate insectivores from folivores on the basis of body size independent of molar-shape quantification. However, this requires more analysis and requires the experimenter to select a proxy for body size, which is in itself not a trivial problem. DNE's capability to more consistently distinguish insectivores from folivores in one analysis is potentially an advantage over previous techniques. It should be noted, though, that RFI and SQ as calculated in this study also significantly differed among all dietary categories. This may be due to a peculiarity of this sample, or for SQs the slightly modified method of measuring shearing crest lengths. DNE's ability to infer diet is further supported by the effects of taxon on DNE and its ability to predict diet by itself in a DFA. Most of the significant differences in DNE values among taxa correspond to differences in dietary preferences. Of all metrics, DNE has the highest ratio of significantly different pairs of taxa with differing diets to significantly different pairs of taxa with similar diets. This suggests that compared to other metrics, differences in DNE between taxa are more due to shape variance presumably caused by diet-related selection than other factors. The DFA with DNE by itself also had the highest rate of modal dietary classification by taxon.

TABLE 7. Summary of success of discriminant function analyses in correctly predicting diet

Variables analyzed	Overall success (%)	Modal success (%)
SQ	51.5	47.8
SR	47.1	52.2
RFI	66.4	69.6
OPCR	42.7	47.8
DNE	59.4	73.9
SQ/SR/RFI/OPCR/M_2	83.1	81.8
SQ/SR/RFI/OPCR/DNE/M_2	83.1	86.3
SQ/SR/RFI/OPCR/DNE	83.8	86.3
RFI/OPCR/DNE/M_2	79.7	78.2

TABLE 8. Percentage of sample variation explained by first, second, and third discriminant functions of the four combined analyses listed in Table 7, and structure coefficients for each variable on each function

	Percentage variation	Structure Coefficients					
		SQ	SR	RFI	OPCR	DNE	M_2
SQ/SR/RFI/OPCR/M_2							
Function 1	71.6	0.573	0.485	0.819	0.373		−0.231
Function 2	26.9	0.212	0.531	0.158	0.298		0.648
Function 3	1.5	0.571	0.384	−0.360	0.224		−0.267
SQ/SR/RFI/OPCR/DNE/M_2							
Function 1	72.2	0.556	0.485	0.788	0.37	0.713	−0.196
Function 2	26.2	0.148	0.467	0.066	0.251	0.099	0.653
Function 3	1.5	0.495	0.300	−0.418	0.169	0.133	−0.283
SQ/SR/RFI/OPCR/DNE							
Function 1	74.6	0.556	0.475	0.793	0.366	0.716	
Function 2	24.2	0.196	0.532	0.139	0.294	0.161	
Function 3	1.2	0.669	0.51	−0.395	0.282	0.25	
RFI/OPCR/DNE/M_2							
Function 1	81.3			0.838	0.350	0.759	−0.149
Function 2	18.0			−0.109	0.222	−0.051	0.839
Function 3	0.7			−0.534	0.674	0.037	−0.513

These results suggest that one should be able to accurately infer diet in fossil specimens using DNE.

The prediction that DNE correlates significantly with other measures of shape quantification was also supported. DNE correlates significantly with all of the shape-quantification metrics considered. This is not surprising—if variability of all metrics is driven at least in part by "overall dietary preference," then one expects them to be correlated. DNE is most strongly correlated with RFI, and most weakly with OPCR. Evans et al. (2007) interpreted OPC as a measure of surface complexity, whereas measures such as RFI are unsurprisingly measures of topographic relief. These results suggest that DNE is capturing topographic relief more so than surface complexity. Essentially, DNE should reflect the shape of tools on the occlusal surface. High, steeply sloped cusps and sharp shearing crests produce increased DNE values, while low, bulbous cusps produce decreased values. This reflects inferred adaptations for masticating hard insect chitin or tough plant cellulose or for crushing and grinding potentially hard fruits. Based on the support of the two stated predictions, the first hypothesis was supported: DNE values reflect diet.

Methodologically, of all the metrics considered in this study DNE is the least dependent on manually chosen landmarks or morphological expertise on the part of the user. SQs and SRs require a large number of carefully chosen landmarks that can create difficulties when comparing disparate morphologies. Even the relatively more automated dental topographic techniques are dependent on manually orienting the tooth crown model to align with the occlusal plane. While this is not a landmark in the typical sense, properly aligning tooth crown models requires the analyzer to identify how a "disembodied" tooth-crown model in mostly featureless virtual space would fit into a jaw. This requires a nontrivial amount of morphological experience. Plyusnin et al. (2008) observed the concept of automated phenotype analysis offers a similar promise to the field of morphological research as automated genomics does to genetic research. Reducing the amount of morphological expertise required to implement tools for molar-shape quantification is an important step toward that goal.

These results also suggest that DNE has an advantage over the closely correlated RFI in that it is relatively unaffected by variable methods of cropping 3d tooth models. RFI values computed from differently cropped specimens were consistently more variable than RFI values computed from all specimens in associated taxa. DNE values for differently cropped specimens were consistently less variable than associated taxa and were also consistently less variable than the aforementioned RFI values. Given the diversity of equipment and methods for the collection of 3d surface data, DNE's insensitivity to the cropping of 3d models is potentially very useful. In general, the more automated nature of DNE and its capability for inferring diet suggest that it could be a valuable new tool for molar-shape quantification and paleontological diet inference. Simply put, when faced with a choice of whether to use two different methods that produce equivalent results, a researcher will choose that which is less sensitive to data quality and observer assumptions.

Combined analyses

The prediction that a combined analysis would be more accurate at predicting diet compared to any technique alone was supported. A combined analysis incorporating all metrics had the highest overall rate of success in predicting diet with 83.8% overall success and 86.3% modal success. This is much higher than the predictive success rate of any metric used in isolation. This is also higher than any other possible combined analysis of the six variables considered, although many of the differences in overall success are slight. The structure matrices indicate that most of the variation in each analysis was explained by RFI and DNE. SQs, SRs, and M_2 length each explain a lesser amount of variation. OPC explains the least amount of variation in the sample for each analysis.

Further, as the success rates of the combinations listed in Table 7 indicate, every combined analysis is much more effective at predicting diet than any individual metric. Therefore, the prediction that combined analyses would more accurately predict diet than single metrics in general is supported. These results support the hypothesis that combining multiple shape-quantification metrics will have more power to predict diet than individual techniques. If for some reason, a researcher were to be restricted to only one technique or simply wanted to pick the tool most effective for inferring diet by itself, these results suggest that RFI or DNE may be the best methods. OPCR seems to be the weakest method for inferring diet from primate lower second molars. This is considered further below.

A primary focus in the initial development of dental topographic analysis was the ability to solve the "worn tooth conundrum," the inability of previous methods to adequately account for worn teeth effectively closing the door on exploiting the majority of dental fossil assemblages (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003). This sample avoided extremely worn teeth, but still included a diverse array of varying stages of wear. The method used here for measuring shearing crest lengths for the calculation of SQs and ratios attempts to account for worn shearing crests and cusps by approximating where the shearing crest would lie in an unworn tooth. While this technique possibly introduces subjectivity and requires a degree of morphological expertise, it was effective in that SQs were capable of significantly differentiating between all dietary categories in the sample. However, SQs or SRs could not be measured from *Daubentonia* due to a lack of apparently homologous crests. These techniques therefore are limited in their application by morphological disparity. Some researchers may wish to avoid such methodological headaches by employing only methods able to easily quantify shape from worn teeth regardless of morphology—RFI, OPCR, and DNE. The analysis combining RFI, DNE, OPCR, and M_2 length had overall and modal success rates of 79.7 and 78.2%, respectively. Compared to the most successful analysis this is a small drop in success percentage overall and a more moderate drop for modal success. This suggests that RFI, DNE, and OPCR to the exclusion of SQs and SRs are still effective for predicting diet, especially for samples with high degrees of wear. However, diet may be most accurately inferred when SQs and/or SRs are incorporated into the analysis.

Two taxa are habitually misclassified by combined analyses. In all of the most successful combined analyses, 100% of *Lepilemur spp.* specimens are incorrectly classified as omnivorous despite strong and consistent behavioral evidence (Russell, 1977; Thalmann, 2001) and evidence from microwear (Godfrey et al., 2004) that *Lepi-*

lemur's diet consists largely of leaves. This prediction seems to be driven by OPCR, SQs and SRs, and M_2 length as all of these variables when analyzed individually predict 100% of *Lepilemur* as omnivorous. Analyses using DNE and RFI correctly predict *Lepilemur* as a folivore by modal success. This suggests that M_2s of *Lepilemur* have occlusal relief most similar to that of other folivores, even though they are less complex, have relatively shorter shearing crests, and are smaller than molars of typical folivores. It is possible that *Lepilemur* molars have been selectively adapted for folivory through increases in relief, rather than increases in complexity or shearing crests. Seligsohn and Szalay (1978) suggested that the occlusal morphology of *Lepilemur* is consistent with an emphasis on cutting edges. It makes sense that increasing relief would emphasize cutting edges. *Perodicticus* is the other taxon commonly misclassified: Only DNE by itself correctly predicts its diet. It is possible that the diet of *Perodicticus* is more reliant on insects than is commonly thought.

Boyer (2008) observed that *Nycticebus coucang javanicus* (*Nycticebus javanicus*) had higher RFI values than other *Nycticebus* species. From this, he suggested that *N. javanicus* consumes more insect matter than congeners. As no studies of its diet exist, this taxon was not included in predictive discriminant function analyses, and Boyer's (2008) suggestion cannot yet be tested. However, applying discriminant functions of the combined analyses to this taxon yields a prediction of omnivory for all three specimens in each analysis. On this basis, we argue that its diet will not largely differ from congeneric taxa. When dietary data are finally obtained, it will be interesting to see whether combined analyses give a more realistic signal, or whether *N. javanicus* is another case like *Lepilemur*.

Orientation patch count rotated

Using molar rows, Evans et al. (2007) was able to distinguish between carnivores and herbivores in both carnivorans and rodents using OPC. The broad taxonomic focus of Evans et al. (2007) used dietary groupings that reflected trophic level differences, and as such was not tested on the finer level dietary groupings used in this study. Consequently, OPCR was unable to distinguish between insectivores and folivores in our sample. Interestingly, a detailed examination of Evans et al.'s (2007) dataset shows that the only "insectivorous" carnivoran (*Otocyon*) has relatively high OPC values (162 vs. a mean of 68 for "hypercarnivores"). This high value is in the range of the plant dominated omnivore category of Evans et al. and may thus reflect difficulty in separating insectivores from folivores. In addition, a majority of the strictly herbivorous taxa examined by Evans et al. (2007) were fibrous vegetation feeders with complex folded enamel that is most likely a selective adaptation for increasing shear through wear (e.g., Rensberger, 1973). For the most part, herbivorous taxa in this study are folivores and do not possess complicated enamel folding, as seen in some carnivorans and herbivorous rodents. Instead, they possess the same general cusp-and-shearing-crest organizational pattern as insectivores. Only *Hapalemur simus*, a fibrous-food eating folivore, has complexly crenulated enamel that leads to it exhibiting the highest OPCR value in the sample ($n = 2$, range = 63–84).

Taken together, OPCR may not have the resolution to distinguish primate diet categories as used here. An obvious avenue of future study is to examine the effects of dietary groupings, from trophic level categories to mechanical properties of foods. The low rate of correlation and relatively lower ability to correctly infer diet in our sample may also indicate that, at least during primate evolution, selection has acted on occlusal relief more than complexity, or it has acted on complexity in way that has tended to homogenize it.

While OPCR could not elucidate dietary differences in our sample, it still has important utility for understanding the evolutionary history of primate diet preferences even when using nontrophic level diet categorization. Boyer et al. (2010) found different species of stem-primates *Plesiadapis* and *Platychoerops* to differ significantly in OPCR of their M_2s. In *Plesiadapis tricuspidens*, the species inferred to be the most dietarily generalized of those examined, OPCR values averaged 56 making it similar to *Hapalemur griseus* as well as some other primate folivores and frugi-folivores. However, both *Plesiadapis cookei* and *Platychoerops daubrei* had values overlapping and exceeding those of *Hapalemur simus*. This likely indicates that while *Plesiadapis tricuspidens* was similar to many modern prosimian primates in the toughness of its diet, the other two species had a diet matched only by *Hapalemur simus* among living prosimian primates. As OPCR is the only metric that captures the exceptional complexity associated with fibrous food diets, it is an essential tool for evaluating whether fossil primate taxa occupied a realm of dietary space defined by the extant radiation, or were outside of that space. There is already evidence that some fossil primate taxa fell outside the range of extant variation (e.g., Ungar and Kay, 1995). If OPCR ultimately reveals that a significant portion of the fossil primate radiation cannot be understood solely by functional analogy to extant primate species/communities, this would represent an important contribution to our knowledge of the evolutionary history of primate ecomorphology.

SUMMARY

This study introduced DNE as a quantitative measure of shape and tested its effectiveness in distinguishing between primates with differing dietary preferences. DNE differs between insectivores, folivores, omnivores, and frugivores with insectivores having the highest DNE followed by folivores and omnivores and then frugivores. Correlation with RFI suggests this metric is a measure of occlusal relief—that is, the shape of the tools on a tooth surface. Methodologically, this metric has advantages over all molar shape-quantification techniques commonly used due to its independence from landmarks and orientation, and to its insensitivity to variable cropping. DNE has the potential to become a valuable tool in the paleoprimatologist's arsenal of methods.

This study also gauged the effectiveness of combined dental topographic variables at predicting diet. The hypothesis that combined analyses would be much more capable of accurately predicting diet was overwhelmingly supported. If all available metrics can be applied to a given sample, a combined analysis using all of these will probably provide the most accurate inference of diet. However, some of the methods used here are not well-suited to certain types of specimens such as worn teeth. Results from this study suggest that using only those methods which can easily handle worn teeth—RFI, OPC, and DNE—will not infer diet as accurately as if all

metrics were included, but the loss of accuracy is not devastating and may well be desirable in the case of worn teeth or highly disparate morphologies.

Some more observations were also made from this data regarding individual shape-quantification techniques. OPC, which has shown much promise in carnivorans and rodents, is not as well-suited to separating the extant primate taxa in our sample as other variables considered. The low utility of OPCR in extant primates of this sample may have many possible explanations, which will be narrowed and clarified by future studies including more and a greater diversity of taxa.

ACKNOWLEDGMENTS

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