On the Relationship Between Tooth Shape and Masticatory Efficiency: A Finite Element Study

MICHAEL A. BERTHAUME*
Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig, 04103, Germany

ABSTRACT

Dental topography has successfully linked disparate tooth shapes to distinct dietary categories, but not to masticatory efficiency. Here, the relationship between four dental topographic metrics and brittle food item breakdown efficiency during compressive biting was investigated using a parametric finite element model of a bunodont molar. Food item breakdown efficiency was chosen to represent masticatory efficiency as it isolated tooth–food item interactions, where most other categories of masticatory efficiency include several aspects of the masticatory process. As relative food item size may affect the presence/absence of any relationship, four isometrically scaled, hemispherical, proxy food items were considered. Topographic metrics were uncorrelated to food item breakdown efficiency irrespective of relative food item size, and dental topographic metrics were largely uncorrelated to one another. The lack of a correlation between topographic metrics and food item breakdown efficiency is not unexpected as not all food items break down in the same manner (e.g., nuts are crushed, leaves are sheared), and only one food item shape was considered. In addition, food item breakdown efficiency describes tooth–food item interactions and requires location and shape specific information, which are absent from dental topographic metrics. This makes it unlikely any one efficiency metric will be correlated to all topographic metrics. These results emphasize the need to take into account how food items break down during biting, ingestion, and mastication when investigating the mechanical relationship between food item shape, size, mechanical properties, and breakdown, and tooth shape. Anat Rec, 00:000–000, 2016. © 2016 Wiley Periodicals, Inc.

Key words: dental topography; finite element analysis; parametric finite element modeling; ambient occlusion (PCV); food item breakdown efficiency

Abbreviations used: DNE = dirichlet normal energy; EDJ = enamel dentin junction; FE = finite element; FEA = finite element analysis; GIS = geographic information systems; OPC = orientation patch count; OPCR = orientation patch count rotated; PCV = portion de ciel visible (portion visible sky); RFI = relief index.

*Correspondence to: Michael A. Berthaume; Deutscher Platz 6, 04103 Leipzig, Germany. Fax: +49 (0)341 3550 119. E-mail: michael_berthaume@eva.mpg.de

Received 8 October 2015; Revised 25 November 2015; Accepted 13 January 2016.

DOI 10.1002/ar.23328

Published online 00 Month 2016 in Wiley Online Library (wileyonlinelibrary.com).

INTRODUCTION

Dietary ecology has been hypothesized to play an important role in determining the morphology of the skull (e.g., Leakey et al., 2001; Rayfield et al., 2001; Dumont et al., 2014; Spoor et al., 2015). With advances in computer technologies, researchers now have the ability to test some of these hypotheses using previously unavailable methods: two such methods are dental topography and finite element analysis (FEA).

Dental topography is a method of quantifying and representing 2.5 or 3D whole tooth shape with a single metric. Originally developed using Geographic information systems (GIS) technology (Ungar and Williamson, 2000), it has since expanded to include non-GIS specific technologies and metrics. Three of the most common metrics used are Dirichlet normal energy (DNE; Bunn et al., 2011), a measure of curvature, relief index (RFI; M'Kirera and Ungar, 2003; Boyer, 2008), a measure of occlusal relief, and orientation patch count (OPC; Evans et al., 2007), a measure of the number of tools on the occlusal surface of a tooth. Teeth with higher DNE values are, on average, sharper, and it is hypothesized this makes them more efficient at fracturing food items. Teeth with higher RFI values have more tooth surface for the food item to come into contact with, and teeth with higher OPC values have more cusps and/or crests on the occlusal surface to breakdown food items.

In general, these dental topographic metrics have been successful at correlating mandibular tooth shape to dietary categories in extant mammals (e.g., Evans, 2013; Winchester et al., 2014). While there are some differences in methodologies used in choosing what tooth/teeth to use and in obtaining tooth shape (e.g., differences in scanning techniques and cropping methods), the following pattern emerges in many studies: taxa with more fibrous diets (e.g., folivores) tend to have higher dental topographic values than taxa with less fibrous diets (e.g., frugivores, hypercarnivores) and hard object feeders. This implies that species with higher fiber diets tend to have relatively sharper teeth with more tools and higher occlusal relief (M'Kirera and Ungar, 2003; Evans et al., 2007; Boyer, 2008; Bunn et al., 2011). Disregarding hypercarnivores, it is hypothesized that teeth with higher topographic scores are more efficient at cutting fibers, and selection has acted for these teeth in taxa with higher fiber diets. Conversely, it has been hypothesized that teeth with lower topographic scores are more efficient at breaking open fruits/hard food items and/or resisting fracture, and selection has acted for these teeth in taxa with frugivorous and/or hard diets (Berthaume et al., 2010; Godfrey et al., 2012).

It was previously hypothesized under the Pointed Cusp Hypothesis that teeth with sharper cusps would be more efficient at brittle food item fracture, because they would reduce the contact area between the tooth and the food item, increasing the stresses in the food item and promoting food item failure (Evans and Sanson, 2003; Berthaume et al., 2010, 2013). It was similarly hypothesized under the Blunt and Strong Cusp Hypotheses that blunt cusps would be more efficient at brittle food item fracture as they would reduce the energy necessary to fracture a brittle food item and reduce the stresses in the enamel, reducing the risk of enamel fracture (Kay, 1981; Luke and Lucas, 1983; Ungar, 2004; Lawn and Lee, 2009; Lee et al., 2009; Berthaume et al., 2010, 2013). While the Pointed and Strong Cusp Hypotheses are true for single cusped teeth (Evans and Sanson, 1998; Xie and Hawthorne, 2002; Crofts and Summers, 2014), they are not true for multicuspsed teeth (Berthaume et al., 2010, 2013). Instead, it was found that tooth asymmetry is more important in multicusped teeth, as symmetrical teeth distribute bite force equally between all cusps, creating an isostress condition in the food item. Conversely, asymmetrical teeth distribute the bite force unevenly between the cusps, which can produce the high stress concentrations in the food item while preventing high stresses from forming in the enamel, causing the food item to fail with less energy and a reduced risk of fracturing the enamel (Berthaume et al., 2014). Therefore, having a mix of sharp and dull cusps is more advantageous than having just sharp or just dull cusps when breaking down brittle food items.

Excluding the confounding effects of hypsodonty, DNE and RFI are measures of sharpness, while orientation patch count rotated (OPCR, a form of OPC) is a measure of the number of tools on the surface of the tooth. Given the lack of correlation between cusp sharpness in brittle food item breakdown efficiency, dental topographic measures of sharpness, such as DNE and RFI, may not be correlated to brittle food item breakdown efficiency. In addition, complex teeth with many tools on their surface, which would have high OPCR values (Evans et al., 2007; Santana et al., 2011), may not be efficient at brittle food item fracture, as the bite force is likely to be distributed between the many tools. Conversely, teeth with low OPCR values may be more efficient at brittle food item fracture as the bite force will be focused over a fewer number of tools, and create high stress concentrations in the food item. However, these relationships between dental topography and brittle food item breakdown efficiency have not yet been investigated.

Masticatory efficiency can be measured in terms of chewing or food item breakdown efficiency. Chewing efficiency is defined as "the ability to grind a certain portion of a test food during a given time (Helkimo et al., 1978)," is measured in terms of food item particle size reduction, and is frequently measured *in vivo*. In nonhuman subjects, it is measured by feeding individuals, collecting the masticated food particles either from the stomach or the feces, and sieving the masticated foods. Animals with higher chewing efficiencies will have a larger percentage of smaller food particles (Sheine and Kay, 1977; Kay and Sheine, 1979; Clauss et al., 2002; Fritz et al., 2009; Venkataraman et al., 2014). This makes chewing efficiency a measure of overall masticatory efficiency representative of an entire feeding bout, which does not separate tooth performance from other masticatory and/or digestive variables (e.g., jaw kinematics, muscle forces, digestive enzymes). Food item breakdown efficiency is the proficiency with which a tooth or teeth cause a food item to fail. It is tooth, food item, and bite specific: that is to say, efficiency can change from bite to bite during a feeding bout. Unlike chewing efficiency, there are several ways to mechanically measure food item breakdown efficiency, such as reaction force, energy, stresses in the food, and stresses in the tooth (e.g., Abler, 1992; Evans and Sanson, 1998; Anderson, 2009; Berthaume et al., 2010, 2013; Berthaume, 2013). This is because different food items break down in different manners (e.g., nuts are fractured, leaves are sheared, and fruits are crushed/juiced; Luke and Lucas, 1983; Lucas, 2004), making different performance metrics important when breaking down different food items. Unlike chewing efficiency, food item breakdown efficiency isolates the interaction between the tooth and the food item. This makes tooth shape more likely to be correlated with food item breakdown efficiency than chewing efficiency. Therefore, masticatory efficiency is being defined as food item breakdown efficiency in this study.

A limiting factor in relating dental topography to food item breakdown efficiency is the difficulty of measuring breakdown efficiency *in vivo*. In lieu of *in vivo* data, *in situ*, *in vitro*, or *in silico* data can be used. One method that has become increasingly popular for gathering biomechanical data *in silico* is finite element analysis (FEA).

FEA is an advanced engineering tool that is particularly useful in determining the performance of abstract shapes, such as teeth, under prescribed loading conditions. In terms of skeletal material, FEA has been applied largely to the crania (Rayfield, 2007), although significant strides have been made in understanding the relationship between tooth shape, microstructure, and biomechanical performance (Shimizu et al., 2005; Berthaume et al., 2010; Anderson et al., 2011; Benazzi et al., 2011; Anderson and Rayfield, 2012; Barani et al., 2012; Berthaume et al., 2013, 2014). Using FEA to compare several individuals can be difficult, as model construction can be time consuming and/or costly, requiring several sets of high resolution computed tomography (CT) scans that need to be extensively processed (Rayfield, 2007; Bright, 2014). Parametric finite element (FE) models offer a solution to this problem, giving the user the ability to easily alter the geometry of the model and quantify any changes in mechanical performance that may occur. This allows food item breakdown efficiency to be calculated for several disparate tooth morphologies in a relatively short period of time. Parametric FE models also allow for the construction of theoretical morphological landscapes, which provides a powerful tool in investigating how evolutionary forces may have acted on shape (McGhee, 2007; Stayton, 2009; Tseng, 2013; Dumont et al., 2014). Where parametric FE models fall short is in the ability to model complex, biological structures with simple geometries.

Here, the relationship between tooth shape, quantified through dental topography, and brittle food item breakdown efficiency are investigated using a parametric, FE model of a bunodont molar. Four efficiency metrics hypothesized to be important during brittle food item breakdown are considered: energy absorbed by the food item (energy exerted by the individual), tensile stresses in the food item (food item failure), tensile stresses in the enamel (tooth failure), and optimality (the ratio of maximum tensile stresses in the food item to maximum tensile stresses in the enamel) (Berthaume et al., 2013). Three metrics of dental topography correlated with diet were used to quantify tooth shape: DNE (Bunn et al., 2011; Winchester et al., 2014), RFI (M'Kirera and Ungar, 2003; Boyer, 2008), and complexity, measured through OPCR (Evans et al., 2007; Evans and Jernvall, 2009). In addition, one metric that has not yet been formally correlated to diet, a form of ambient occlusion (portion de ciel visible or "portion of visible sky," PCV), was also investigated (Fig. 1).

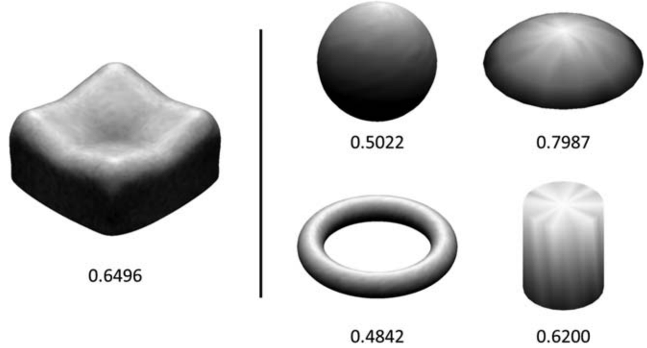

Fig. 1. Left: PCV distribution and value for one of the theoretical teeth (T1). Lighter areas indicate points with higher PCV and lower areas represent areas with lower PCV. **Right**: PVC on four simple shapes, a sphere, dish without a bottom, torus, and a cylinder. Note: the spottiness in the tooth and the "stripes" seen in the dish and cylinder are artifacts in the program, due to the fact that these are discontinuous surfaces. The top of the cylinder should be a solid color.

Ambient occlusion is a computer graphics rendering technique used to determine how exposed each point on a surface is to ambient lighting. When measured from the occlusal direction, a point on a tooth with higher PCV will be more likely to come into contact with a food item during a chewing cycle than a point with lower PCV. Final PCV values are determined by averaging all PCV values over the surface of the tooth. In the order Primates, molars with tall cusps (e.g., folivores) have basins that are more hidden from ambient light than molars with short cusps (e.g., hard object feeders), giving them relatively lower PCV values. As folivores tend to have higher and hard object feeders tend to have lower DNE, RFI, and OPCR scores in Primates (Winchester et al., 2014), PCV is hypothesized to be negatively correlated with these variables.

MATERIALS AND METHODS

A previously constructed parametric FE model of a four cusp bunodont molar was used to create 18 theoretical molars by varying tooth cusp radius of curvature (RoC) (Fig. 2; Berthaume et al., 2013, 2014). Cusps could either be sharp (RoC = 3 mm), medium (RoC = 5 mm), or dull (RoC = 7 mm). Tooth cusp heights, heights of the valleys between the cusps, and enamel thickness were held constant at 5, 3, and 1 mm, respectively. Distances between the cusp tips were held constant at 15.4 and 15.7 mm in the buccolingual and mesiodistal directions, respectively (Gingerich et al., 1982).

The shapes of the 18 theoretical teeth were determined using the Taguchi method (Fig. 3). The Taguchi method is a sampling method that dictates the minimum number of simulations that need to be run in order to construct a multivariate morphospace by unbiasedly sampling the variables being tested (Taguchi, 1987; Lee and Zhang, 2005; Lin et al., 2007). This subsequently provides a wide range of tooth shapes on which dental topography can be performed.

Simulations were run in ANSYS 14.0. Four food items of identical shape but different sizes were modeled per

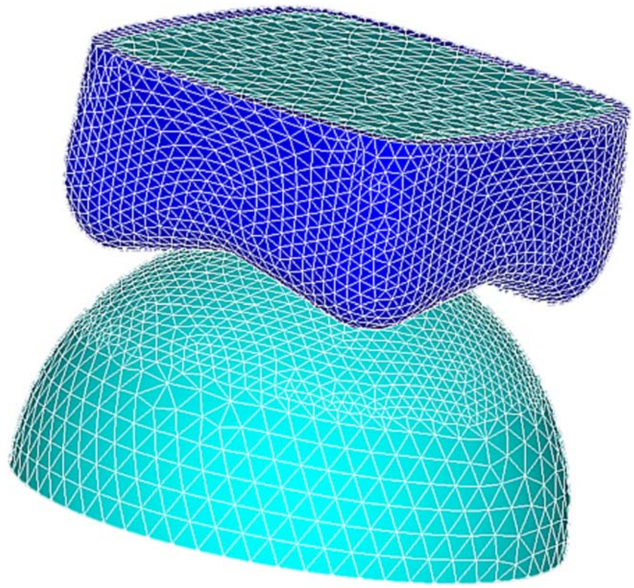

Fig. 2. Picture of one of the FE models (T1). The enamel of the tooth is depicted in *dark blue*, and is filled with dentin. The hemispherical food item is below the occlusal surface of the tooth.

tooth (small, medium, large, and x-large) to investigate the possible effects of relative food item size on the relationship between dental topography and food item breakdown efficiency. Details concerning model construction, simulations, and use of the Taguchi method can be found in (Berthaume et al., 2013) and (Berthaume et al., 2014), and are summarized in the electronic supplementary material (ESM1).

Four metrics for brittle food item breakdown efficiency were calculated at a 2 kN bite force. A 2 kN bite force was chosen as it is the approximate bite force needed for an orangutan to fracture a macadamia nut with its molars (Lucas et al., 1994). Energy absorbed by the food item was the sum of elemental strain energies across the food item, stresses in the food item were the maximum tensile stresses along the inner surface of the food item (Berthaume et al., 2010), stresses in the enamel were the maximum tensile stresses along the enamel dentin junction (EDJ), and optimality was the ratio of maximum tensile stresses in the food item to maximum tensile stresses in the enamel (Berthaume et al., 2013, 2014). This was done for four food items of identical shape and varying size to investigate whether any potential relationships between tooth shape and function were size dependent.

In order to perform dental topography, models of the molars were exported from ANSYS into Strand7 as *.cdb files, and then exported as 3D *.stl models. Outer occlusal surfaces of the molars were isolated using CloudCompare, and a copy of the surfaces were imported into AVIZO 6.0 as *.ply ASCII files. Occlusal surfaces were then simplified down to 9,995–10,000 triangles, a necessity for DNE (Bunn et al., 2011) and smoothed with the Smooth Surface command (iterations = 100, lambda = 0.6. Boyer, 2008). The simplified surfaces were imported into MorphoTester (beta version, http://morphotester.apotropa.com/), where DNE was calculated with 0.1%

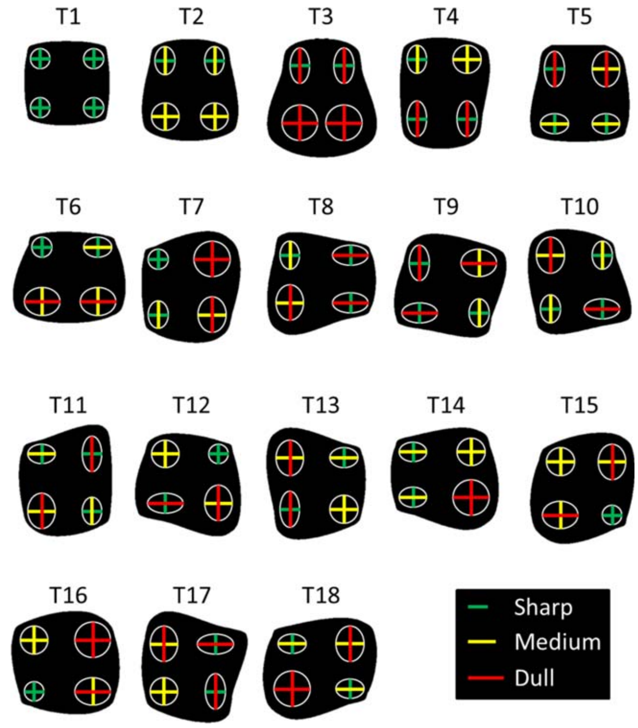

Fig. 3. Occlusal views of the 18 theoretical molars used in this study. *Short*, *green lines* indicate sharp cusps (RoC = 3 mm), *medium*, *yellow line* indicate cusps that are neither sharp nor dull (RoC = 5 mm) and *long*, *red lines* indicate dull cusps (RoC = 7 mm).

TABLE 1. *P*-values and Pearson's correlation coefficients for linear regressions between dental topographic metrics

P-value	DNE	RFI	OPCR	PCV
DNE	–	–	–	–
RFI	0.00067[a]	–	–	–
OPCR	0.08787	0.01052	–	–
PCV	0.01799	5.78E-10[a]	0.01631	–
R				
DNE	–	–	–	–
RFI	0.725	–	–	–
OPCR	0.414	0.587	–	–
PCV	−0.572	−0.956	−0.557	–

[a]Significant using a Bonferroni adjusted *P*-value for multiple comparisons of $P = 0.0083$.

outlier removal. The original, unsimplified version of the tooth was then imported into MorphoTester, where surface and outline area were measured, and used to calculate RFI (Boyer, 2008). OPCR was calculated using the unsimplified versions of the teeth and SurferManipulatorExe20110921 following the protocol from Wilson et al., 2012. While postcanine tooth rows are frequently used to calculate OPC and OPCR, isolated lower second molars provide reasonable estimations of diet (Evans and Jernvall, 2009). PCV was calculated by importing the surface file into Cloudcompare v2.6.0 (http://www.danielgm.net/cc/) and clicking the "PCV" button on the main screen. The average PCV value for the surface of the tooth was calculated by clicking the "Fits a

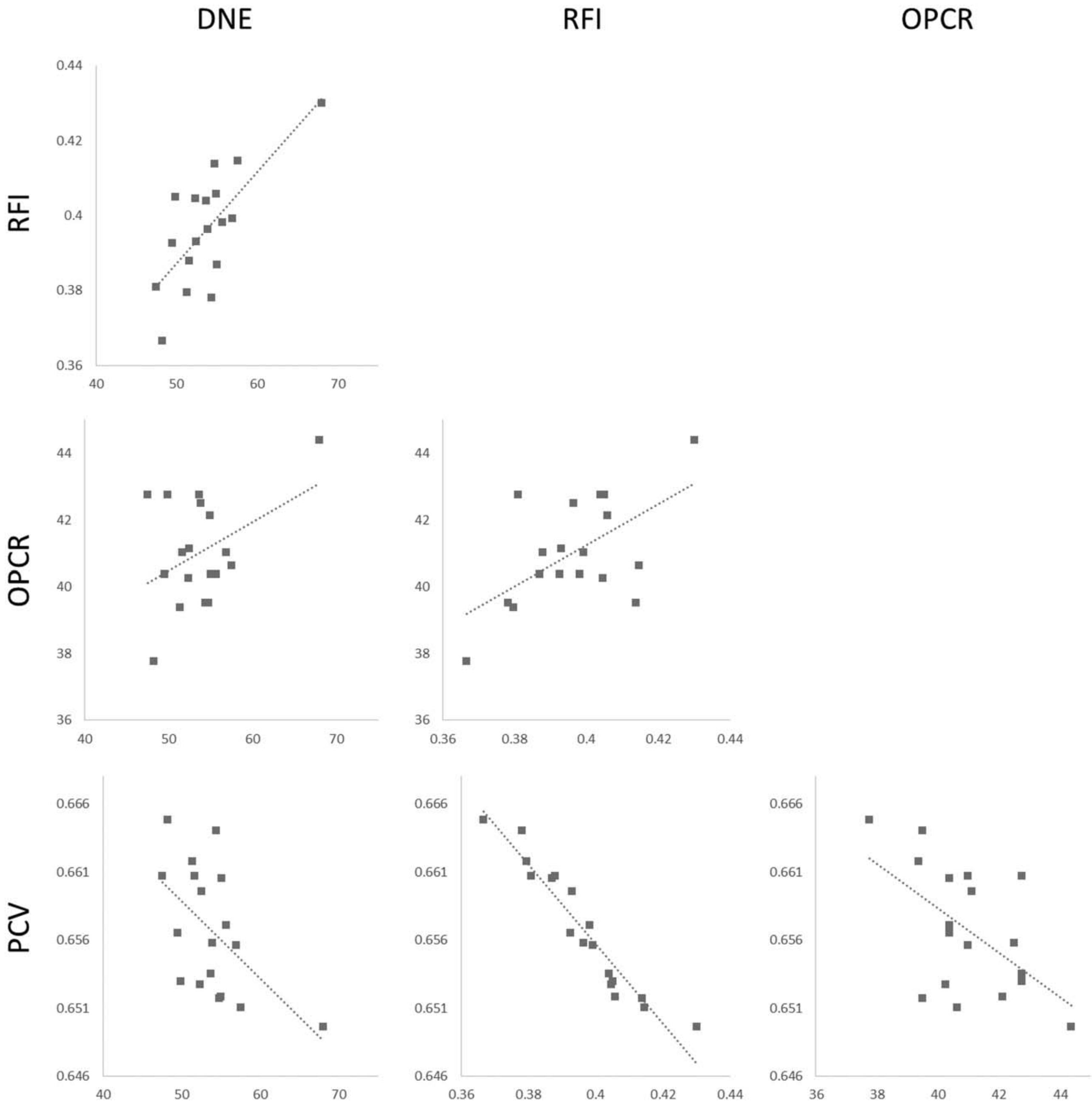

Fig. 4. Graphical representation of the correlations between dental topographic values. Tooth T1 had a higher DNE value than the rest of the teeth, but was kept in the analysis as it was constructed using an unbiased sampling method.

statistical model on the active scalar field" button, and recorded for analysis.

As lower DNE, RFI, and OPCR scores are correlated with hard food item consumption in Primates (Winchester et al., 2014), I hypothesize these topographic metrics will be positively correlated with stresses in the enamel and energy absorbed by the food item, and negatively correlated with stresses in the food item and optimality. These hypotheses are based on the predictions that selection may have acted to prevent enamel fracture during hard object feeding (minimizing stresses in the enamel), promote food item breakdown (minimizing energy, maximizing stresses in the food item) or for both (maximizing optimality). Given the hypothesized relationship between PCV and DNE, RFI, and OPCR, I expect the opposite relationships to exist between PCV and the aforementioned efficiency metrics. Relationships between topographic metrics and efficiency were tested using linear regressions and Pearson's correlation coefficients in R (R Development

TABLE 2. *P*-values and coefficients of determination for linear regressions between dental topographic and efficiency metrics

	R^2				*P*-value			
	Energy	Stress, food item	Stress, enamel	Optimality	Energy	Stress, food item	Stress, enamel	Optimality
18.2								
DNE	0.0470	0.0981	0.1163	0.0578	0.3876	0.2056	0.1661	0.3364
RFI	0.0002	0.0021	0.0014	0.0034	0.9549	0.8571	0.8845	0.8189
OPCR	0.0003	0.0000	0.0231	0.0035	0.9422	0.9830	0.5475	0.8158
AO	0.0075	0.0052	0.0123	0.0005	0.7331	0.7767	0.6620	0.9332
14.1								
DNE	0.0009	0.0406	0.1699	0.0052	0.9044	0.4230	0.08919	0.7761
RFI	0.0065	0.0005	0.0316	0.0175	0.7501	0.9293	0.4806	0.6006
OPCR	0.0000	0.0000	0.0081	0.0052	0.9939	0.9892	0.7228	0.7762
AO	0.0200	0.0162	0.0046	0.0526	0.5755	0.6148	0.7894	0.3601
10.0								
DNE	0.0078	0.0440	0.0309	0.0346	0.7283	0.4033	0.4851	0.4598
RFI	0.0204	0.0004	0.0004	0.0005	0.5723	0.9400	0.9384	0.9284
OPCR	0.0079	0.0183	0.0082	0.0206	0.7258	0.5928	0.7209	0.5698
AO	0.0296	0.0059	0.0055	0.0021	0.4945	0.7616	0.7709	0.8567
5.9								
DNE	0.0020	0.0173	0.0966	0.0355	0.8603	0.6024	0.2094	0.4541
RFI	0.0126	0.0087	0.0024	0.0031	0.6576	0.7126	0.8483	0.8263
OPCR	0.0363	0.0922	0.0920	0.0020	0.4486	0.2207	0.2211	0.8601
AO	0.0335	0.0129	0.0016	0.0092	0.4675	0.6531	0.8741	0.7048

[a]Significance occurs at a Bonferroni adjusted *P*-value for multiple comparisons of $P = 0.00078$.

Core Team, 2013), with a Bonferroni correction for multiple comparisons.

RESULTS

Linear regressions revealed a positive relationship between RFI and DNE and a negative relationship between RFI and PCV (Table 1, Fig. 4). No other statistically significant relationships existed between topographic measurements, or between any dental topographic and food item breakdown efficiency metrics, regardless of relative food item size (Table 2, Fig. 5, ESM2).

DISCUSSION

Results indicate that dental topography is unrelated to brittle food breakdown efficiency, regardless of relative food item size. Given the strong relationship between dental topography and diet, this may be surprising, but is not unexpected from a solid mechanics perspective. Dental topographic measurements are "whole tooth" measurements which do not contain locationally specific information, and therefore no information concerning stress or energy production. It has been shown in Berthaume et al. (2013, 2014) that a multicusped tooth optimally shaped for brittle food item fracture will have a series of cusps, some of which are promoting food item failure and some of which are balancing and trapping the food item. Therefore, in order for a tooth to be efficient at brittle food item fracture, it requires an intermediate sharpness (i.e., an intermediate DNE/RFI score) where the cusps are patterned in a particular manner. This could explain why there was no correlation between DNE/RFI and food item breakdown efficiency. And as OPCR reflects the number of tools more than their arrangement, this could be why OPCR was not correlated to food item breakdown efficiency.

In addition, the role of the cusps during food item breakdown changes with food item size: for relatively small food items, the sides of the cusps play a more important role than the tips of the cusp during food item breakdown, while for relatively large food items, the reverse is true. Dental topographic metrics, however, are independent of relative food item size, and therefore cannot reflect this change. Finally, it is possible to change a tooth's dental topography but not its food item breakdown efficiency by increasing the tooth's size while keeping inter-cusp distances and basin shape constant. These reasons all make it impossible to create a relationship that mathematically correlates dental topography to food item breakdown efficiency across mammals.

Teeth have been hypothesized to be optimal for their function (Lucas, 2004); this implies that teeth should be shaped in a way that reflects diet and be maximally efficient at processing these foods. Given the correlation between dental topography and diet (Evans et al., 2007; Boyer, 2008; Evans, 2013; Winchester et al., 2014), one might expect dental topography to be highly correlated to efficiency. At least for brittle food item consumption and hypothetical teeth, this is not true, and is not likely to be true should real teeth be used. Tooth shape and efficiency represent local, and not global, optima (Alexander, 1996). This means the shape of a tooth will be highly affected by its ancestral state, and the tooth shape that will be selected for will be the one located on the closest adaptive peak. This iterates the importance of phylogeny in determining tooth function from shape, as the most efficient tooth for a given diet will have both different dental topographic and food item breakdown efficiency values for distantly related mammals, such as ungulates and primates. Furthermore, even more closely related groups within these clades, such as cercopithecines and hominoids, will produce differently shaped optimal teeth due to their differences in their initial

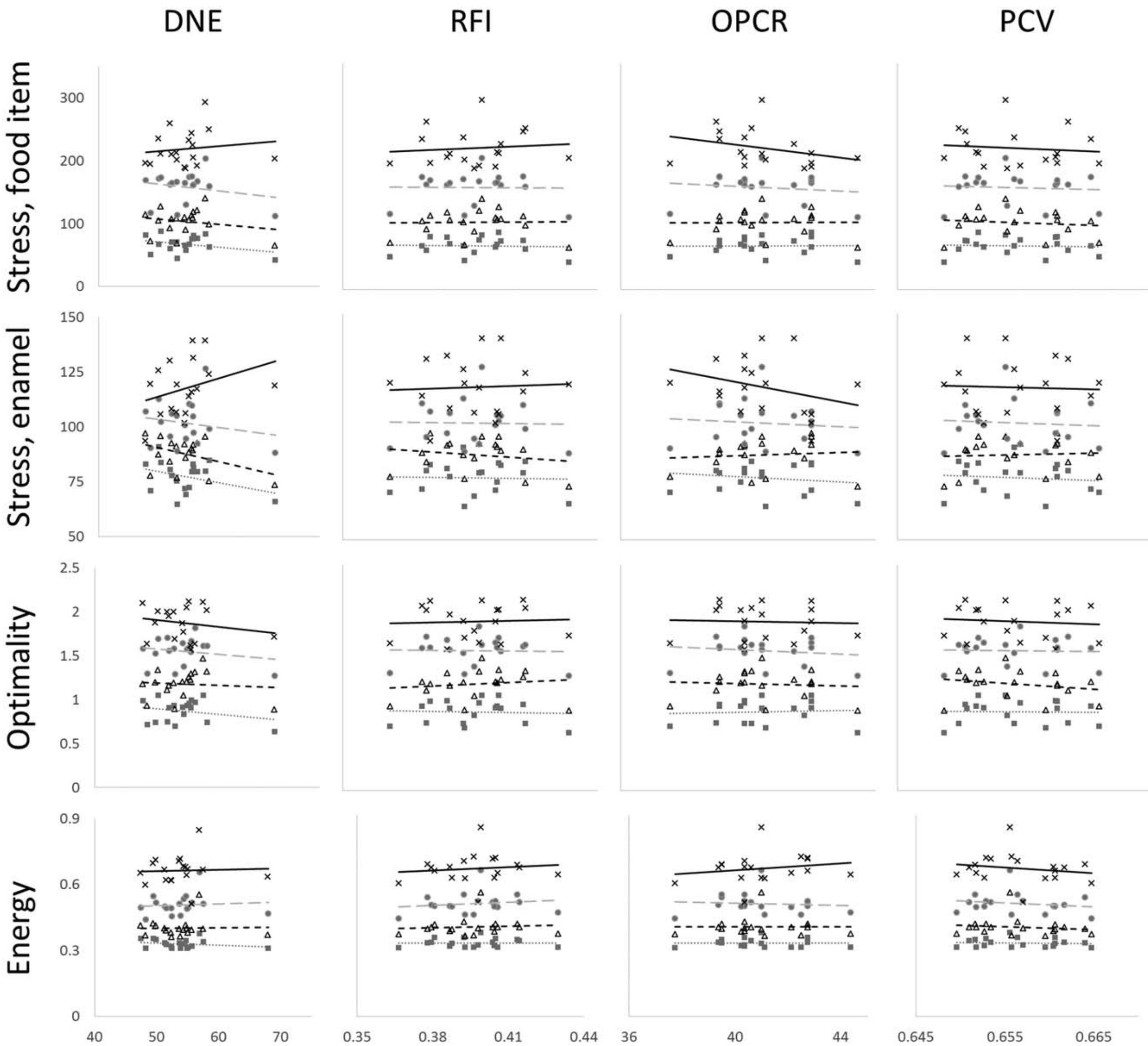

Fig. 5. Graphical representation of correlations between dental topographic scores and efficiency metrics. Each symbol represents a food item with a different size: *crosses* represent the small food item, *circles* the medium, *triangles* the large, and *squares* the x-large.

starting morphology (i.e., bilophodont vs. bunodont molars). While some morphological convergence will likely be reached across these clades in terms of general tooth morphology (e.g., lower cusps and thicker enamel), complete morphological and efficiency convergence is unlikely to be achieved.

The results of this study are limited as only brittle food items were considered here, and many food items consumed by mammals (e.g., ripe fruits, soft insects, raw meat) are ductile, not brittle. As ductile items break down in a different manner, they must be analyzed using different efficiency metrics (e.g., energy release rate, level of plastic deformation, von Mises stress and strain). In addition, these FE models take into account only the compressive, crushing forces (Phase I) that occur during mastication, and ignore the shear forces (Phase II). Although Phase I forces are more important during mastication of brittle food items that need to be crushed, such as nuts and seeds, Phase II forces may be more important when breaking down other food items that need to be sheared, such as leaves. Finally, only one food item shape, a sphere, was modeled in this study, and other common food item shapes (rods, flat plates; Lucas, 2004) were ignored.

The strong relationship between RFI and DNE is consistent with findings from previous studies (Bunn et al., 2011; Winchester et al., 2014). Interestingly, PCV has a strong relationship with RFI but not DNE. While this study did not investigate the relationship between PCV and dietary categories, the strong negative relationship between PCV and RFI implies PCV may be lower in insectivores and folivores, and higher in frugivores and hard object feeders (Winchester et al., 2014). Therefore, animals with more fibrous diets will have lower PCV values than animals with more fibrous diets and hard object feeders. This relationship is supported by preliminary analyses on primate teeth (Berthaume and Winchester, unpublished).

One metric that is addressed in many dental topographic studies but was ignored here was the shearing quotient (Kay, 1981; Bunn et al., 2011; Winchester et al., 2014). Shearing quotient is the residual of crest length regressed against tooth length, and provides a measurement for the Phase I shearing edges on a molar (Boyer et al., 2014). As it has been used in previous dental topographic studies (Bunn et al., 2011; Winchester et al., 2014), and been shown to be correlated with chewing efficiency in some primates (Sheine and Kay, 1982), it was of interest to investigate shearing quotient in this study. However, the theoretical teeth lacked defined shearing crests, making it impossible to measure (a problem sometimes encountered with real teeth, e.g., Daubentonia; Winchester et al., 2014).

As different types of food items break down in different manners (high stresses, strains, energy, force, etc.) and not all dental topographic metrics are correlated to one another (Table 1, Bunn et al., 2011; Winchester et al., 2014), it is unlikely one masticatory performance metric will be correlated to all dental topographic metrics. Therefore, in order to properly understand the relationship between dental topography and diet, factors other than tooth shape, such as food item breakdown and jaw kinematics, must be taken into account.

ACKNOWLEDGEMENTS

The author thanks Julia Winchester for supplying Morphotester, Alistair Evans for creating and supplying SurferManipulator, and Andrew Smith, Justin Ledogar, and Alistair Evans for their help with SurferManipulator, and Paul Constantino for comments on the manuscript.

LITERATURE CITED

Abler W. 1992. The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. Paleobiology 18:161–183.

Alexander RM. 1996. Optima for Animals. Princeton, NJ: Princeton University Press.

Anderson PSL. 2009. The effects of trapping and blade angle of notched dentitions on fracture of biological tissues. J Exp Biol 212:3627–3632.

Anderson PSL, Rayfield EJ. 2012. Virtual experiments, physical validation: dental morphology at the intersection of experiment and theory. J R Soc Interface 9:1846–1855.

Anderson PSL, Gill PG, Rayfield EJ. 2011. Modeling the effects of cingula structure on strain patterns and potential fracture in tooth enamel. J Morphol 272:50–65.

Barani A, Bush MB, Lawn BR. 2012. Effect of property gradients on enamel fracture in human molar teeth. J Mech Behav Biomed Mater 15:121–130.

Benazzi S, Kullmer O, Grosse IR, Weber GW. 2011. Using occlusal wear information and finite element analysis to investigate stress distributions in human molars. J Anat 219:259–272.

Berthaume MA. 2013. Tooth cusp radius of curvature as a dietary correlate in primates. Doctoral Dissertations Available from Proquest 1–184.

Berthaume M, Grosse IR, Patel ND, Strait DS, Wood S, Richmond BG. 2010. The effect of early hominin occlusal morphology on the fracturing of hard food items. Anat Rec 293:594–606.

Berthaume MA, Dumont ER, Godfrey LR, Grosse IR. 2013. How does tooth cusp radius of curvature affect brittle food item processing? J R Soc Interface 10:20130240.

Berthaume MA, Dumont ER, Godfrey LR, Grosse IR. 2014. The effects of relative food item size on optimal tooth cusps sharpness during brittle food item processing. J R Soc Interface 11: 20140965.

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

Boyer DM, Winchester J, Kay RF. 2014. The effect of differences in methodology among some recent applications of shearing quotients. Am J Phys Anthropol 156:166–178.

Bright JA. 2014. A review of paleontological finite element models and their validity. J Paleontol 88:760–769.

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.

Clauss M, Lechner-Doll M, Streich J. 2002. Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end. Oecologia 131:343–349.

Crofts SB, Summers AP. 2014. How to best smash a snail: the effect of tooth shape on crushing load. J R Soc Interface 11:20131053.

Dumont ER, Samadevam K, Grosse I, Warsi OM, Baird B, Davalos LM. 2014. Selection for mechanical advantage underlies multiple cranial optima in new world leaf-nosed bats. Evolution 68:1436–1449.

Evans AR. 2013. Shape descriptors as ecometrics in dental ecology. Hystrix, Ital J Mammal 24:133–140.

Evans AR, Jernvall J. 2009. Patterns and constraints in carnivoran and rodent dental complexity and tooth size. J Vertebr Paleontol 2009:92A.

Evans AR, Sanson GD. 1998. The effect of tooth shape on the breakdown of insects. J Zool 246:391–400.

Evans AR, Sanson GD. 2003. The tooth of perfection: functional and spatial constraints on mammalian tooth shape. Biol J Linn Soc 78:173–191.

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

Fritz J, Kienzle E, Hummel J, Arnold C, Nunn C, Clauss M. 2009. Comparative chewing efficiency in mammalian herbivores. Oikos 118:1623–1632.

Gingerich PD, Smith BH, Rosenberg K. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. Am J Phys Anthropol 58:81–100.

Godfrey LR, Winchester JM, King SJ, Boyer DM, Jernvall J. 2012. Dental topography indicates ecological contraction of lemur communities. Am J Phys Anthropol 148:215–227.

Helkimo E, Carlsson GE, Helkimo M. 1978. Chewing efficiency and state of dentition. Acta Odontol Scand 36:33–41.

Kay RF. 1981. The nut-crackers – a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141–151.

Kay RF, Sheine WS. 1979. On the relationship between chitin particle size and digestibility in the primate Galago senegalensis. Am J Phys Anthropol 50:301–308.

Lawn BR, Lee JJ-W. 2009. Analysis of fracture and deformation modes in teeth subjected to occlusal loading. Acta Biomater 5: 2213–2221.

Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, McDougall I. 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. Nature 410:433–440.

Lee WCC, Zhang M. 2005. Design of monolimb using finite element modelling and statistics-based Taguchi method. Clin Biomech 20: 759–766.

Lee JJ-W, Kwon J-Y, Chai H, Lucas PW, Thompson VP, Lawn BR. 2009. Fracture modes in human teeth. J Dent Res 88:224–228.

Lin C-L, Chang S-H, Chang W-J, Kuo Y-C. 2007. Factorial analysis of variables influencing mechanical characteristics of a single tooth implant placed in the maxilla using finite element analysis and the statistics-based Taguchi method. Eur J Oral Sci 115:408–416.

Lucas PW. 2004. Dental functional morphology: how teeth work. Cambridge: Cambridge University Press.

Lucas PW, Peters CR, Arrandale SR. 1994. Seed-breaking forces exerted by orang-utans with their teeth in captivity and a new technique for estimating forces produced in the wild. Am J Phys Anthropol 94:365–378.

Luke DA, Lucas PW. 1983. The significance of cusps. J Oral Rehabil 10:197–206.

M'Kirera F, Ungar PS. 2003. Occlusal relief changes with molar wear in Pan troglodytes troglodytes and Gorilla gorilla gorilla. Am J Primatol 60:31–41.

McGhee GR. 2007. The geometry of evolution: adaptive landscapes and theoretical Morphospaces. New York, NY: Cambridge University Press.

R Development Core Team. 2013. R: a language and environment for statistical computing. Vienna, Austria: R Found Stat Comput.

Rayfield EJ. 2007. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. Annu Rev Earth Planet Sci 35:541–576.

Rayfield EJ, Norman DB, Horner CC, Horner JR, Smith PM, Thomason JJ, Upchurch P. 2001. Cranial design and function in a large theropod dinosaur. Nature 409:1033–1037.

Santana SE, Strait S, Dumont ER. 2011. The better to eat you with: functional correlates of tooth structure in bats. Funct Ecol 25:839–847.

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 the insectivoran Tupaia glis. Am J Phys Anthropol 47:15–20.

Sheine WS, Kay RR. 1982. A model for comparison of masticatory effectiveness in primates. J Morphol 172:139–149.

Shimizu D, Macho GA, Spears IR. 2005. Effect of prism orientation and loading direction on contact stresses in prismatic enamel of primates: implications for interpreting wear patterns. Am J Phys Anthropol 126:427–434.

Spoor F, Gunz P, Neubauer S, Stelzer S, Scott N, Kwekason A, Dean MC. 2015. Reconstructed Homo habilis type OH 7 suggests deep-rooted species diversity in early Homo. Nature 519:83–86.

Stayton CT. 2009. Application of thin-plate spline transformations to finite element models, or, how to turn a bog turtle into a spotted turtle to analyze both. Evolution 63:1348–1355.

Taguchi G. 1987. System of experimental design: engineering methods to optimize quality and minimize costs. White Plains, New York: UNIPUB/Kraus International Publications.

Tseng ZJ. 2013. Testing adaptive hypotheses of convergence with functional landscapes: a case study of bone-cracking hypercarnivores. PLoS One 8:e65305.

Ungar P. 2004. Dental topography and diets of Australopithecus afarensis and early Homo. J Hum E 46:605–622.

Ungar PS, Williamson MD. 2000. Exploring the effects of tooth wear on functional morphology: a preliminary study using dental topographic analysis. Palaeontol Electron 3:1–18.

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.

Wilson GP, Evans AR, Corfe IJ, Smits PD, Fortelius M, Jernvall J. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483:457–460.

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.

Xie Y, Hawthorne H. 2002. Effect of contact geometry on the failure modes of thin coatings in the scratch adhesion test. Surf Coatings Technol 155:121–129.