

Dental Topography of Platyrrhines and Prosimians: Convergence and Contrasts

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ABSTRACT Dental topographic analysis is the quantitative assessment of shape of three-dimensional models of tooth crowns and component features. Molar topographic curvature, relief, and complexity correlate with aspects of feeding behavior in certain living primates, and have been employed to investigate dietary ecology in extant and extinct primate species. This study investigates whether dental topography correlates with diet among a diverse sample of living platyrrhines, and compares platyrrhine topography with that of prosimians. We sampled 111 lower second molars of 11 platyrrhine genera and 121 of 20 prosimian genera. For each tooth we calculated Dirichlet normal energy (DNE), relief index (RFI), and orientation patch count (OPCR), quantifying surface curvature, relief, and complexity respectively. Shearing ratios and quotients were also measured. Statistical analyses partitioned effects of diet and taxon on topography

in platyrrhines alone and relative to prosimians. Discriminant function analyses assessed predictive diet models. Results indicate that platyrrhine dental topography correlates to dietary preference, and platyrrhine-only predictive models yield high rates of accuracy. The same is true for prosimians. Topographic variance is broadly similar among platyrrhines and prosimians. One exception is that platyrrhines display higher average relief and lower relief variance, possibly related to lower relative molar size and functional links between relief and tooth longevity distinct from curvature or complexity. Explicitly incorporating phylogenetic distance matrices into statistical analyses of the combined platyrrhine-prosimian sample results in loss of significance of dietary effects for OPCR and SQ, while greatly increasing dietary significance of RFI. *Am J Phys Anthropol* 153:29–44, 2014. © 2013 Wiley Periodicals, Inc.

In living primates, gross molar shape and the number and form of specific molar features correlate strongly with feeding behavior (e.g., Gregory, 1922; Kay, 1975; Rosenberger and Kinzey, 1976; Covert, 1986; Anapol and Lee, 1994; Zuccotti et al., 1998; M'Kirera and Ungar, 2003; Evans et al., 2007; Boyer, 2008; Bunn et al., 2011; Cooke, 2011). Species that consume tough and/or stiff insect chitin or tough yet pliant cellulose-rich leaves tend to possess molars with high, sharp cusps and longer shearing crests for puncturing and shearing these materials. In contrast, species consuming relatively hard seeds or fruits tend to possess molars with low, bulbous (strongly convex) cusps and open basins for gripping and crushing these foods (Kay and Hiiemae, 1974; Rosenberger and Kinzey, 1976; Seligsohn and Szalay, 1978; Lucas, 1979; Strait, 1997; Lucas, 2004). Bulbous cusps allow minimal contact area with flat or convex potential food items, resulting in concentration of force and stress on the food item, thereby presenting good potential for initiating cracks that propagate well in hard, but more brittle objects (Lucas, 2004). In terms of size, species that eat large quantities of tough foods with nutrients limited relative to their metabolic needs (folivores and small insectivores) tend to have relatively larger teeth for their body mass (e.g., Kay, 1975; Gingerich et al.,

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1982; Gingerich and Smith, 1984; Strait, 1993). These presumably adaptive relationships between the forms of molar teeth and their functions in overcoming mechanical and structural defenses of foods have been instructive in understanding the ecology of living and extinct primate species (e.g., Kay, 1975, 1977; M'Kirera and Ungar, 2003; Ungar, 2007; Boyer, 2008; Boyer et al., 2010; Bunn et al., 2011; Cooke, 2011; Godfrey et al., 2012; Wilson et al., 2012). One of the more recent and promising approaches in this area has been coined "dental topographic analysis" (Ungar and Williamson, 2000).

Dental topographic analysis is the quantitative assessment of the shape of a tooth surface and its features (M'Kirera and Ungar, 2003; Evans et al., 2007; Bunn et al., 2011). Techniques of dental topographic analysis require imaging equipment such as laser or μ CT scanners to create high-resolution digital three-dimensional models of physical dental specimens. Various geometric algorithms are then used to quantify aspects of dental form, such as curvature, relief, and complexity of molar occlusal surfaces. Variation in dental topography has been shown to closely reflect variation in the types of foods consumed by living primates—topographic relief, curvature, and complexity all tend to increase in species with sharper, higher cusps and longer shearing crests, and correspondingly tend to differentiate primates that primarily rely on insects, leaves, or fruits (M'Kirera and Ungar, 2003; Merceron et al., 2006; Boyer, 2008; Bunn and Ungar, 2009; Bunn et al., 2011). The aspects of shape quantified by each dental topographic variable are metrically independent, although they often correlate with each other (Boyer et al., 2010; Bunn et al., 2011). For example, measures of complexity appear primarily related to the "number of tools" (e.g., cusps, styles, and cones) present on a tooth surface, while shapes quantified by curvature and relief reflect the "shape of tools" (e.g., whether a cusp is tall or short and sports a strong crest) (Evans et al., 2007; Bunn et al., 2011). Although curvature and relief have been strongly correlated in a prosimian sample (Bunn et al., 2011), this may not be the case for all taxonomic samples. That is, increasing hypsodonty should theoretically result in increased relief, but most likely lower average curvature. Additionally, the most complex teeth in living primates tend to be those of species that consume extremely fibrous vegetation, such as bamboo-eating lemurs (Zohdy et al., 2008; Bunn et al., 2011).

Dental topographic analyses have been applied to many living primate groups and non-primate mammals (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003; Dennis et al., 2004; Ulhaas et al., 2004; King et al., 2005; Evans et al., 2007; Boyer, 2008; Ungar and Bunn, 2008; Bunn and Ungar, 2009; Evans and Jernvall, 2009; Bunn et al., 2011; Godfrey et al., 2012). In addition to probing the molar form-function relationship, this work has enhanced our knowledge of the ecology of living primate populations. King et al. (2005) examined dental relief and wear in a population of *Propithecus edwardsi* and were able to show evidence for an environmentally mediated effect of dental senescence on reproductive success in this population. Boyer (2008) and subsequently Godfrey et al. (2012) observed that *Eulemur fulvus* and *Lemur catta* molars exhibit greater relief, curvature, and complexity than predicted by typically observed diets (most frequently in wet eastern forests), and suggested that this supports the hypothesis that certain lemurs may be experiencing ecological disequilibrium between

dental morphology and diet, possibly as a result of human settlement of Madagascar and resulting environmental changes, including loss of megafauna. More recently these inferences for recent diet change from dental morphology were corroborated by comparisons of isotope values between modern and subfossil remains of *Lemur catta*, as well as *Microcebus*. Based on isotope analyses, both taxa were inferred to now feed in significantly wetter, less seasonally variable environments than they did previously (Crowley et al., 2012). In dry western forests Sussman (1977) observed much larger degrees of folivory for both *Lemur catta* and *Eulemur* than is typically observed in eastern forests (see Boyer, 2008 for a review). Thus these studies appear to substantiate a strong adaptive basis for dental topography in deep time. In other words, if microwear and isotopes reveal effects of the "last supper" and "recent (relative to mortality events) diet preferences," respectively, dental topography seems to show which food items were "critical suppers" on a scale that influences individual fitness. Interestingly, Godfrey et al. (2012) also provided the first evidence for a link between relative metabolic demands and tooth morphology, showing that complexity measured as OPCR (Orientation patch count rotated, see Methods) had a highly significant relationship to metabolic demands, which was unrelated to mechanical properties of consumed food.

Work on living populations is critical: in addition to enriching our knowledge of current ecology, it provides the comparative baseline for the inference of dietary preferences in fossil taxa. However, numerous living taxa remain to be assayed using topographic methods to quantify dental morphology. Of the radiations considered in previous dental topographic analyses, platyrrhines are one of the least-sampled to date. Dennis et al. (2004) examined dental topography of molar wear in repeatedly wild-caught *Alouatta palliata*, but their analyses were not comparative. Cooke (2011) employed three-dimensional geometric morphometric techniques (rather than dental topographic analysis) as a proxy for relief to examine the relationship between diet and dentition in a large sample of extinct and extant platyrrhine primates. Ledogar et al. (2013) did consider platyrrhine diet and dental topography in a comparative fashion, investigating molar topography of four seed-eating pitheciine genera along with two frugivorous taxa, *Aotus* and *Callicebus*. Their focus was heavily on the functional morphology of seed predation, finding that this behavior in pitheciines is reflected in the high complexity and low relief, shear, and curvature of molar occlusal surfaces in these species.

An analysis of platyrrhines with broader scope and a larger sample—incorporating species with diets that include alternate mechanically-challenging foods such as leaves or insects—is a clear next step. Such an analysis would be beneficial both for fleshing out our understanding of the molar form-function relationship in living platyrrhines and constructing baselines from which to infer the diets of fossil platyrrhines. Additionally, a broad platyrrhine sample would allow comparison with Bunn et al.'s (2011) prosimian sample, the largest topographic data set published to date (the term prosimian is used here solely as a term of convenience, with full appreciation for its likely paraphyletic nature). Currently it is not clear whether independent primate radiations (e.g., platyrrhines vs. strepsirrhines) show the same patterns of association between dental topography and dietary

TABLE 1. Dietary categorization of platyrrhine sample

Diet	Genus	References
Insectivory/ omnivory	<i>Saimiri</i>	Lima and Ferrari (2003); Stone (2007)
Folivory	<i>Alouatta</i>	Julliot and Sabatier (1993); Teaford and Glander (1996); Cristobal-Azkarate and Arroyo-Rodriguez (2007)
Frugivory	<i>Aotus</i>	Wright (1989)
	<i>Ateles</i>	Nunes (1998); Dew (2005); Suarez (2006)
	<i>Callicebus</i>	Kinzey (1977)
	<i>Lagothrix</i>	Peres (1994); Defler and Defler (1996); Di Fiore (2004); Dew (2005)
Hard-Object Feeding	<i>Cacajao</i>	Ayres (1989)
	<i>Cebus</i>	Izawa and Mizuno (1977); Lambert et al. (2004); Wright (2005); Taylor and Vinyard (2009)
	<i>Chiropotes</i>	van Roosmalen et al. (1981); Kinzey and Norconk (1993); Norconk (1996)
	<i>Pithecia</i>	Kinzey and Norconk (1993); Norconk (1996)

preferences. Addressing this could supplement our knowledge of dental-dietary relationships in these groups, and have implications for the analysis of diet in fossil species with uncertain phylogenetic relationships to extant taxa. Additionally, concerns remain regarding the phylogenetic independence of topographic metrics.

This study explores these issues by surveying the dental topography of molar teeth belonging to a wide sample of living platyrrhine species and by assessing the patterns that emerge when the new platyrrhine sample is combined with previously published data on prosimians (Bunn et al., 2011). Research questions and goals for this study include the following:

1. Does dental topography of platyrrhine lower second molars reflect dietary preferences? We expect a trend where insectivores and folivores exhibit the highest degree of molar curvature, relief, and complexity.
2. How does platyrrhine dental topography compare with that of strepsirrhines and tarsiers? How similar are the adaptive landscapes in terms of molar curvature, relief, and complexity—can they be analyzed jointly? Is it possible to predict the diets of platyrrhines from a known dataset of prosimians, and vice versa? If there are differences, do they result from phylogenetic constraints or differential selective pressures?

MATERIALS AND METHODS

Study sample

The study sample consisted of 111 high-resolution plastic replica casts of lower molar rows and isolated second molars (M_2 s) belonging to 11 platyrrhine genera, spanning three platyrrhine families and representing a variety of feeding preferences. This includes genera that consume large proportions of fruits, leaves, or insects, although genera characterized by consuming large amounts of fruit predominate (Table 1). The comparative prosimian sample consisted of 112 M_2 s belonging to 19 strepsirrhine genera and 9 M_2 s representing species of

the genus *Tarsius*. This dataset was previously published by Bunn et al. (2011), in which some relief index values were taken from Boyer (2008): details of collection, dietary categorization, and analysis of prosimian samples may be found in these two prior references. Supporting Information Table S1 includes details of dietary categorization of prosimian genera, and is taken from Table 1 of Boyer (2008) and Table 1 of Bunn et al. (2011). Relative to the platyrrhines surveyed here, our prosimian sample contains more specialized faunal predators (e.g., *Arctocebus*, *Tarsius*, *Galago senegalensis*) and leaf consumers (e.g., *Avahi*, *Indri*, *Lepilemur*). Meanwhile, our platyrrhine sample includes a greater proportion of fruit specialists, especially those that habitually consume very hard and/or tough seeds (e.g., *Cacajao*, *Chiropotes*, *Pithecia*).

All platyrrhine genera were assigned to one of the following four dietary categories based on previously published observational studies of feeding preferences: insectivory/omnivory, folivory, frugivory, and hard-object feeding (Table 1). This dietary classification schema is similar to that applied to the prosimian sample, and allows comparison with that sample. It should be noted, though, that compared to extant strepsirrhines and tarsiers the diet of *Saimiri* is more akin to that of omnivores like *Microcebus* and *Mirza* than specialist faunivores such as those listed above. Therefore, in comparisons with the prosimian sample this genus was coded as an omnivore in the manner of Bunn et al. (2011). Representative M_2 s of platyrrhines and prosimians of each dietary category are presented as Figure 1.

Our dietary schema is also roughly similar to the schema employed by Cooke (2011) in a recent geometric morphometric analysis of platyrrhine M_2 s, with one exception. We have coded our *Cebus* sample, consisting of six M_2 s of *Cebus apella* and four M_2 s of *Cebus capucinus*, as hard-object feeders, whereas Cooke (2011) included only *C. capucinus* and classified them as frugivore/omnivores, due to dietary differences between the two species. We treat these specimens as hard-object feeders due to *C. apella*'s habitual ingestion of highly mechanically challenging materials including large seeds and a suite of nondental morphological features related to the production and dissipation of large bite forces (Izawa and Mizuno, 1977; Lambert et al., 2004; Wright, 2005; Taylor and Vinyard, 2009). It is beneficial to keep in mind, however, that given tool use and manual processing by these primates, consumption of these objects may not necessarily impose constraints on the occlusal molar apparatus, and that selective pressures on the molars of *C. apella* may differ for this reason.

Sample preparation, scanning, and surface mesh creation

The sample was collected from museum specimens in the American Museum of Natural History, the Smithsonian Institution National Museum of Natural History, the Harvard University Museum of Comparative Zoology, and the Stony Brook University Museum of Anatomy. Each tooth row was cleaned with acetone if necessary to remove debris and was molded using President Jet Microsystem poly-vinylsiloxane medium or light body (Coltène/Whaledent). High-resolution plastic replica casts were created from molds with EPOTEK 301 epoxy mixed with gray pigment. Prior to μ CT scanning casts were trimmed using Dremel tools and Exacto

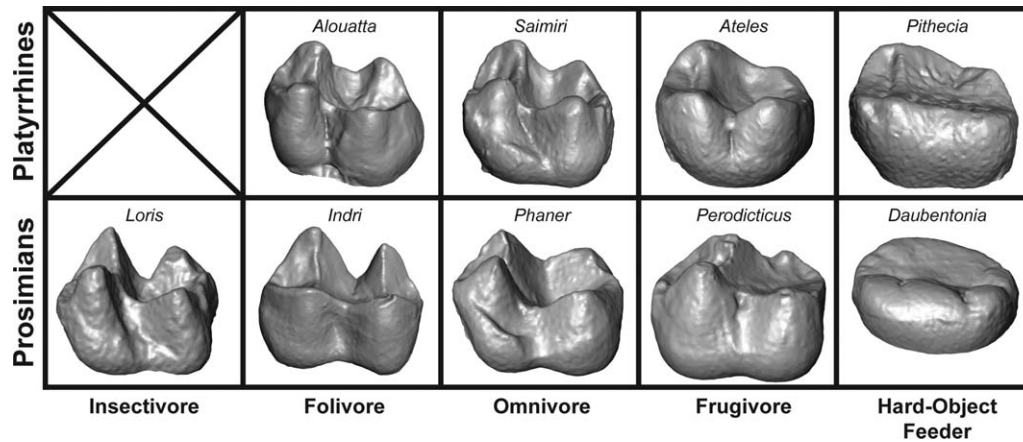


Fig. 1. A comparison of randomly chosen representatives of each diet group sampled. Surface models are shown from an oblique buccal angle, anterior to the left. Platyrrhines exhibit a similar but muted trend of shape variation relative to prosimians.

knives to the M_2 for more efficient use of scan time. Replica casts glued to plastic discs were scanned by a Scanco Medical brand μ CT 40 scanner at resolutions between 10 and 18 μ m (depending on absolute tooth size). Resultant cross-section image stacks of multiple teeth were cropped down to single teeth using ImageJ (NIH) and segmented in Avizo v. 6-7 (Visage Imaging) to create volumetric renderings of tooth surfaces, which were then interpolated as triangular surface meshes. Again using Avizo, these surface models were cropped to include only the tooth crown using the approximate location of the root-crown junction. All surface mesh files and original μ CT scans for this study can be downloaded directly from the site <https://www.morphosource.org>. Specimens can be found by searching by catalogue number or browsing by taxon.

Variables measured

A total of five variables were measured on each M_2 : shearing ratio (SR), shearing quotient (SQ), and three topographic variables: Dirichlet normal energy (DNE), relief index (RFI), and orientation patch count-rotated (OPCR). SR and SQ are measures of the length of molar shearing crests relative to body size, and are not considered topographic variables here largely due to their landmark-based nature. To calculate both variables, shearing crest lengths were measured from each surface using the point distance tool of Geomagic Studio 10 (Geomagic, Inc.). For further details and repeatability tests for this method of measuring shearing crests, see Bunn et al. (2011). Two-dimensional occlusal area and total length of each molar were then measured using ImageJ. SR was calculated as the natural log of the ratio of shearing crest length to the square root of occlusal area (Boyer, 2008). SQ per specimen was calculated by the method of Anthony and Kay (1993), as percent difference between actual and “expected” shearing crest lengths. “Expected” shearing crest lengths were derived from a size-correction function of molar length by shearing crest length constructed solely from frugivores of the sample.

DNE is a measure of total curvature across a tooth surface, employing the change in the normal vector (relative to the surface) map over a tooth surface to quantify this curvature (Bunn et al., 2011; full definition and details can be found there). To prepare surface meshes

for DNE calculation, each model was down-sampled to 10,000 polygonal faces using the *Simplification* module of Amira (Visage Imaging). Surface noise was reduced using Amira’s *Smooth Surface* module with 100 iterations of smoothing with a lambda of 0.6. DNE was then calculated using the MATLAB application Teether.

RFI can be simply defined as the ratio of the three-dimensional true surface area of a tooth to the area occupied by the tooth surface’s projection into a two-dimensional occlusal plane (Boyer, 2008). Computing RFI was done in two steps. First, the true surface area of the occlusal surface was measured in Avizo. Next a screen shot was acquired of the occlusal outline of the tooth with a scale bar in Avizo. From this occlusal outline, a two-dimensional planimetric area of the occlusal surface was computed in ImageJ and/or Sigma Scan Pro 5.0. RFI was then calculated as the natural log of the ratio of the square root of true surface area to the square root of planimetric area.

OPCR is defined as the number of discrete contiguous areas of similar aspect (necessarily bordered on all sides by other contiguous areas of dissimilar aspect) across a tooth surface, averaged across eight distinct rotations of a surface mesh in XY space to normalize for differences in orientation between meshes (Evans et al., 2007; Evans and Jernvall, 2009). Aspect here is defined as the XY or compass direction. OPCR is a measure of complexity on an occlusal surface. OPCR was calculated using the applications Surfer (Golden Software) and Surfer Manipulator (Evans, 2008). First, OPC was calculated by the method of Evans et al. (2007) for each molar surface with a minimum patch size of 3. Eight total OPC values were collected for each tooth automatically and averaged by Surfer Manipulator. Each replicate represented the OPC value recalculated after rotating the orientation boundaries of the surface mesh 5.625 degrees. This rotation factor ensured that minor differences in XY orientation of individual meshes should not overly affect the resulting OPCR value.

Statistical analyses

Aside from phylogenetically informed analyses, all statistical tests were performed with an alpha level of 0.05 using the application SPSS 11.0 (SPSS, Inc.). To determine whether and how platyrrhine topography reflects diet in comparison with prosimians, a two-way ANOVA

was carried out with dietary preference and taxonomic factors for each variable measured. Due to significant interactions found between the effects of taxonomic group and dietary preference, phylogenetically informed statistical analyses were undertaken, and one-way ANOVAs were calculated for the platyrrhine sample alone by dietary group factor. Pairwise comparison tests were then completed using Tukey's Honestly Significant Difference (HSD) test in order to further partition and explore significant variation.

Phylogenetically informed analyses. Phylogenetically informed statistical analyses incorporate information on the potential interdependence and autocorrelation among taxonomic data points in order to account for differences and similarities between genera caused by phylogenetic distance. All phylogenetic comparative statistical analyses were performed using the R statistical programming language version 2.15 (R Core Team, 2012) using the Caper (Comparative Analyses of Phylogenetics and Evolution in R) package (Orme, 2012). Phylogenetic ANOVA in Caper allows taxon residuals from diet group means to be autocorrelated with branch lengths. The calculation of group means and their standard errors are therefore adjusted by this autocorrelation model. Phylogenetic tree data for all taxa were downloaded from the official website of the 10kTrees Project (Arnold et al., 2010) at www.10ktrees.fas.harvard.edu. These analyses were performed on species means. As phylogenetic ANOVA can currently *only* be executed using species means, we also performed a series of one-way standard ANOVAs on species means with DNE, RFI, OPCR, SR, and SQ response variables to serve as an equivalent baseline for comparison with similar statistical power.

We also used a phylogenetic generalized least squares (PGLS) approach to check for existence of correlations between all pairs of topographic variables. Bunn et al. (2011) showed that correlations existed among different topographic variables; however, these could have been artifacts of phylogenetic non-independence.

Discriminant function analyses. In order to gauge the most efficient combination of variables for accurate dietary prediction within and among radiations, a series of discriminant function analyses were performed. Distinct DFAs were run on the platyrrhine sample, the prosimian sample, and a combined sample of the two groups. Combinations of variables tested included individual variables alone; individual variables and natural log of M_2 length; all three topographic variables only; and all three topographic variables with natural log of M_2 length, SR, and SQ individually and in combination. All DFAs were run entering all variables simultaneously and with prior probabilities of group membership determined from group sizes, and predictive success was evaluated using a jack-knife classification method. Additionally, the diets of platyrrhine specimens were predicted using the topographic-variable DFA computed from the prosimian sample, and likewise the diets of prosimian specimens were predicted from the topographic-variable DFA computed from the platyrrhine sample. This provided a test of the ability of topographic variables to predict diet in "unknown"

specimens despite large evolutionary distance from the extant baseline sample.

RESULTS

DNE, RFI, OPCR, SR, and SQ values of platyrrhine teeth digitized by μ CT scanning were partitioned by genus and dietary category to assess dental topographic variation (Fig. 2; Table 2, and Supporting Information Tables S2, S3). In DNE and RFI, there is an overall trend of folivorous *Alouatta* and *Brachyteles* and omnivorous/insectivorous *Saimiri* exhibiting the highest values, frugivorous genera with intermediate values, and hard-object feeding genera with the lowest values. SR is similar, except that *Saimiri* has more moderate shear, similar to that of the frugivores in the sample. For SQ, values are broadly similar across dietary groups, except for lower values in hard-object feeders. Patterns of OPCR are more complicated, with high complexity found in the pitheciines and frugivores *Callicebus* and *Lagothrix*.

Compared with prosimians, platyrrhines exhibit generally higher RFI and OPCR, similar DNE and SR, and markedly lower SQs. Prosimians, however, tend to occupy extremes of dental topography on both high and low ends of the scale, both within and across dietary categories. In fact, in almost all dental topographic variables the trend of platyrrhine variation can be seen as similar to that of prosimians, but with muted intergroup variance. OPCR is the one exception to this observation: platyrrhine hard-object feeders and frugivores show markedly higher complexity than prosimians of any dietary group. Average OPCR in pitheciines *Pithecia* (80.1) and *Chiropotes* (77.5) is higher than in *Prolemur simus* (74.0), the most complex prosimian. *P. simus*, with its diet of extremely fibrous bamboo pith, is in fact somewhat of an outlier among prosimians in complexity, with the next highest mean complexity found in *Tarsius* (59.8). Of the platyrrhines *Cacajao* (65.5), *Callicebus* (71.6), and *Lagothrix* (64.6) all boast greater complexity than is seen in tarsiers. At least in the pitheciines, this very high degree of complexity is likely related to high degrees of enamel crenulation in the molar occlusal surfaces of these species.

Two-way ANOVAs were performed on variables measured to determine whether dietary category and platyrrhine/prosimian grouping explained sample variance (Table 3). Significant interaction between diet and taxonomic factors is present in all variables analyzed, suggesting that dental topographic metrics vary by diet differentially in platyrrhines and prosimians, and preventing further univariate analyses of the effect of diet in these groups as a combined sample.

One-way ANOVAs testing for the effect of diet on platyrrhines are significant for every variable (DNE: $df = 3$, $F = 72.695$, $P < 0.001$; RFI: $df = 3$, $F = 75.139$, $P < 0.001$; OPCR: $df = 3$, $F = 13.662$; $P < 0.001$; SRA: $df = 3$, $F = 55.062$, $P < 0.001$; SQ: $df = 3$, $F = 14.199$, $P < 0.001$). Post hoc pairwise comparisons for this analysis indicate that across variables, most dietary groups are significantly different from other groups. Some exceptions do exist. Folivores *Alouatta* and *Brachyteles* and omnivorous/insectivorous *Saimiri* do not differ in DNE ($P = 0.454$), OPCR ($P = 0.928$), or SQ ($P = 0.967$). Additionally, *Saimiri* does not differ from frugivorous genera in RFI ($P = 0.069$), OPCR ($P = 0.273$), or SQ ($P = 0.964$). Finally, SQ does not significantly distinguish

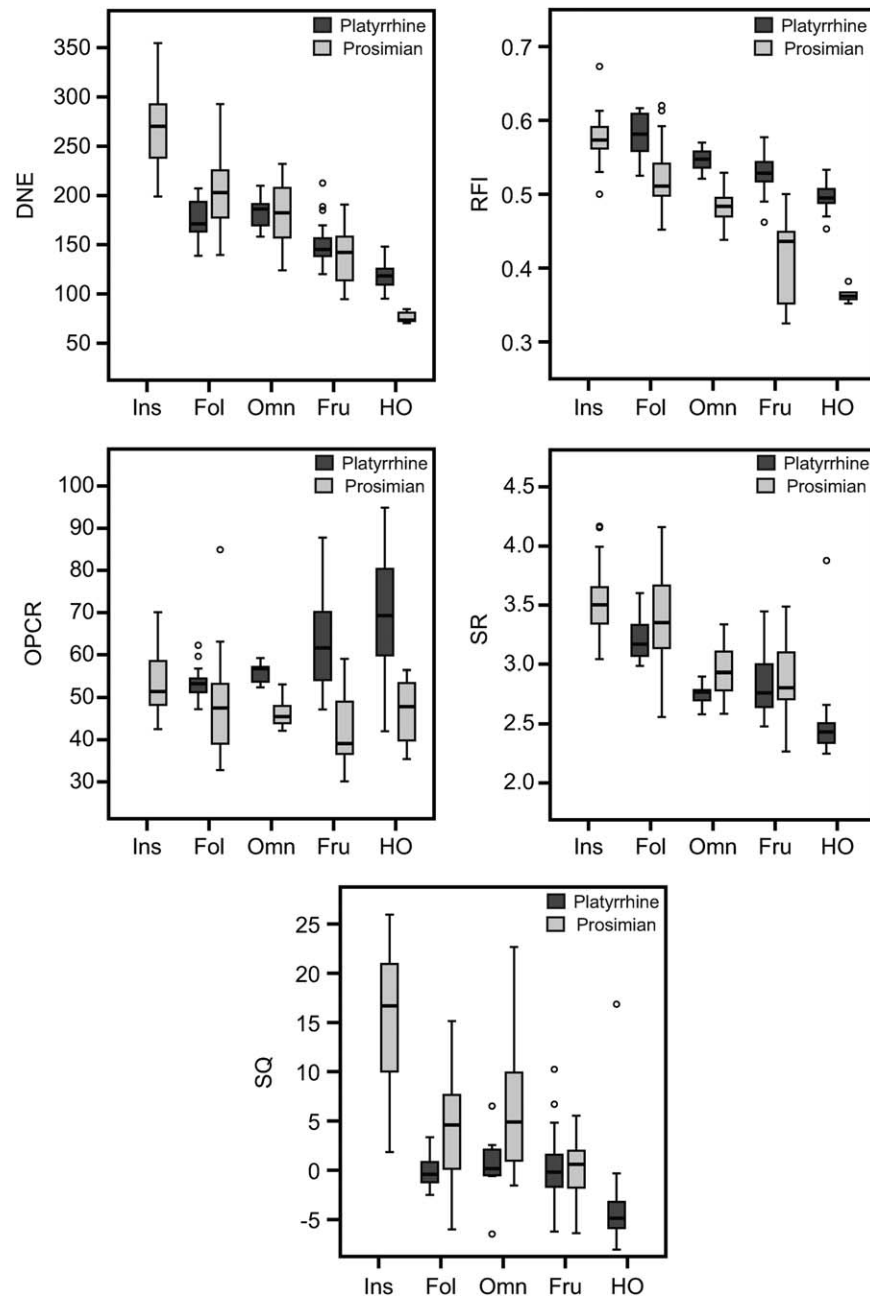


Fig. 2. Box plots of DNE, RFI, OPCR, SR, and SQ for platyrrhine and prosimian diet groups. In: insectivory; Fo: folivory; Om: omnivory; Fr: frugivory; HO: hard-object feeding.

between folivores and frugivores ($P > 0.999$). In terms of total pairwise comparisons, OPCR and SQ evinced the lowest number of significant comparisons with 4 and 3 respectively out of 6.

Phylogenetic regressions

Correlation of variables (including M_2 area) after taking phylogeny into account was assessed as a first step in probing the phylogenetic independence of topographic variables, SR, and SQ (Table 4). SQ is significantly correlated with all other variables, including area, and is in fact the only variable to correlate with area. Other correlations are limited, with DNE significantly correlating

with RFI and SR, and RFI significantly correlating with SR as well. OPCR correlates only with SQ. These results are distinct from the findings of Bunn et al. (2011) who found correlations between all variables (not including molar area) in the prosimian sample alone with a standard tips approach (i.e., with no consideration of phylogenetic relationships among taxa).

Phylogenetic ANOVA

Phylogenetic independence of variables was examined by comparing phylogenetic ANOVAs performed on species means to standard one-way ANOVAs as a baseline comparison (Tables 5 and 6). Listed species means in

TABLE 2. Descriptive statistics of dental topographic metrics of platyrrhines and prosimians by diet

Dietary category	<i>N</i>	DNE		RFI		OPC		SR		SQ	
		Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error
Platyrrhine sample											
Insectivory	0										
Folivory	20	174.618	4.730	0.580	0.006	53.375	0.749	3.202	0.037	−0.019	0.356
Omnivory	10	184.275	5.059	0.547	0.005	55.775	0.711	2.753	0.028	0.564	1.035
Frugivory	40	148.848	2.880	0.529	0.004	62.275	1.457	2.817	0.035	0.013	0.497
Hard-object feeding	41	118.657	2.016	0.496	0.002	69.668	2.129	2.457	0.039	−4.103	0.613
Total	111	145.531	2.751	0.528	0.003	62.816	1.171	2.748	0.032	−1.463	0.362
Prosimian sample											
Insectivory	28	264.068	7.398	0.575	0.006	52.793	1.194	3.537	0.053	14.969	1.337
Folivory	43	204.306	5.291	0.519	0.006	47.300	1.533	3.37	0.055	4.076	0.809
Omnivory	22	180.600	6.600	0.481	0.005	46.036	0.606	2.950	0.043	6.208	1.317
Frugivory	22	138.977	6.078	0.411	0.012	42.050	1.694	2.853	0.065	0.025	0.651
Hard-object feeding	6	75.89	2.272	0.364	0.004	46.783	3.293	—	—	—	—
Total	121	195.579	5.412	0.498	0.007	47.361	0.771	3.231	0.038	6.361	0.716

TABLE 3. Two-way ANOVA results for dental topographic metrics of platyrrhines and prosimians by taxonomic grouping and diet factors, $\alpha = 0.05$

Factor	df	F	P
DNE			
Group	1	2.061	0.152
Diet	4	113.610	<0.001
Group \times diet	3	10.740	<0.001
RFI			
Group	1	303.344	<0.001
Diet	4	129.821	<0.001
Group \times diet	3	12.303	<0.001
OPCR			
Group	1	88.858	<0.001
Diet	4	8.757	<0.001
Group \times diet	3	7.969	<0.001
SR			
Group	1	7.786	<0.001
Diet	4	55.060	0.006
Group \times diet	2	1.224	0.296
SQ			
Group	1	15.333	<0.001
Diet	4	37.986	<0.001
Group \times diet	2	4.400	0.013

Table 5 differ between the standard ANOVAs and phylogenetically informed ANOVAs because the algorithm employed by CAPER uses PGLS to produce an estimate of group means weighted based on tree structure and evidence of autocorrelation with respect to that structure. Estimates of standard error are also re-weighted in this way. For all variables except SQ, re-weighted species means follow the same pattern as non-weighted means. For DNE, RFI, and SR, mean values decrease progressively from a high point in insectivores to folivores, omnivores, frugivores, and hard-object feeders. For OPCR, values decrease from insectivores to folivores and omnivores, but increase in frugivores and hard-object feeders. In contrast, the patterns of SQ differ between re-weighted and non-weighted means. Notably, the re-weighted group mean of folivores for SQ is lower than that of omnivores or frugivores, contra expectations.

Using standard one-way ANOVAs on species means substantially reduces statistical power; however, species

means of all shape variables vary significantly by dietary category overall. Phylogenetic ANOVAs on species means demonstrate that DNE, RFI, SR, and SQ continue to vary significantly by dietary category when phylogeny is taken into account, but that OPCR does not. This means that diet-grouping no longer explains variance in OPCR when phylogenetic interdependence is accounted for and that previously apparent differences are likely related to differential oversampling of certain dietary categories in some clades relative to other clades.

Bonferroni-corrected post hoc comparisons of standard ANOVAs indicate little significant differentiation between specific dietary category pairs for most variables, with the exception of DNE and SQ where relatively high numbers of significant post hoc comparisons exist (Table 6). Post hoc comparisons of phylogenetic ANOVAs differ from those of standard ANOVAs. DNE, OPCR, and SR evince one less significant post hoc comparison each, while only three significant comparisons are found for SQ compared to five in the standard ANOVA. Meanwhile, the number of significant comparisons actually increases for RFI, from three to five. This suggests that RFI is more capable of partitioning dietary-group related variance when phylogenetic interdependence is accounted for than when it is not, while DNE and other variables are less effective at doing so.

Discriminant function analysis

To further investigate dental topographic variation by diet within and between platyrrhines and prosimian samples, multiple discriminant function analyses were performed employing the platyrrhine sample alone, the prosimians alone, and platyrrhines and prosimians combined (Figs. 3 and 4; Table 7). Of the DFAs employing dental topographic metrics individually or only in conjunction with M_2 area, those including DNE are generally the most successful at predicting diet. RFI has success similar to DNE in the noncombined groups, though notably less success in the combined sample. OPCR is the least reliable in predicting diet. Compared with DFAs employing topographic metrics individually, adding M_2 area to analyses always increases success in prediction. The second discriminant function in all cases is overwhelmingly driven by M_2 area.

TABLE 4. PGLS correlations between variable pairs

Variables	Correlation	<i>P</i>	<i>t</i> -Value	Lambda	AIC	BIC	logL
DNE~RFI ^a	0.703	<0.001	8.52	0.907	-196	-188	102
DNE~OPCR	0.688	0.2327	1.21	0.980	523	530	-257
DNE~SR ^a	0.797	<0.001	6.78	0.986	485	493	-239
DNE~Area	0.647	0.1122	-1.62	0.978	515	523	-254
RFI~OPCR	0.688	0.9989	0.00	0.980	-158	-151	83
RFI~SR ^a	0.812	<0.001	6.69	0.959	-196	-188	102
RFI~Area	0.644	0.9712	0.04	0.981	-164	-157	86
OPC~SR	0.854	0.8213	0.23	0.795	368	376	-180
OPC~Area	0.726	0.7286	-0.35	0.795	368	376	-180
SR~Area	0.614	0.9338	0.08	1.000	46	53	-19
SQ~RFI ^a	0.909	0.0014	3.40	0.973	279	271	-132
SQ~DNE ^a	0.685	<0.0001	5.60	0.966	272	279	-132
SQ~OPC ^a	0.604	0.0404	2.11	1.006	282	289	-137
SQ~SR ^a	0.889	<0.0001	5.93	0.988	258	265	-125
SQ~Area ^a	0.617	0.0254	-2.31	0.993	280	288	-136

^aSignificant correlation, $P < 0.05$.

TABLE 5. Data from phylogenetically informed ANOVA

Variable	Lambda	df	MS	<i>F</i>	<i>P</i>	Ins(9)	Fol(16)	Om(6)	Frug(14)	HO(7)
DNE	OA	47	841.6	27.59	<0.0001	242.5	205.7	173.0	147.6	112.2
DNE	0.931	47	30.1511	6.272	<0.0001	246.2	196.9	178.8	154.6	121.1
RFI	OA	47	0.0022	7.08	0.0002	0.568	0.533	0.482	0.483	0.475
RFI	0.961	47	0.000036	16.75	<0.0001	0.559	0.543	0.510	0.468	0.443
OPCR	OA	47	108.2	3.795	0.009	52.75	47.67	46.05	55.45	63.83
OPCR	0.755	47	1.9321	0.3354	0.889	52.62	50.56	50.87	53.34	56.40
SR	OA	47	0.175	12.88	<0.0001	3.37	3.34	2.94	2.80	2.12
SR	0.996	47	0.0047	7.467	<0.0001	3.17	3.08	2.78	2.74	2.16
SQ	OA	46	19.5	13.79	<0.0001	11.40	2.92	4.80	-0.290	-3.72
SQ	0.986	46	0.6972	4.244	0.003	11.59	3.70	6.44	3.98	1.57

For each variable, the upper row represents the ordinary ANOVA (OA), while the second row is the PGLS version run using the Caper package in R. Mean values for different dietary groups are given in the five right-most column, with sample sizes given in parentheses after the abbreviation for the group name in the column heading. Lambda is a measure of phylogenetic signal with ~1 representing a perfect fit between data and a Brownian motion model of change in values through evolution, and 0 representing no phylogenetic structuring. df, degrees of freedom; MS, mean square error within groups; *F*, *f*-statistic for ANOVA; *P*, probability that within-within group variation is the same as between group variation.

Analyses involving multiple topographic variables and M_2 area generally demonstrate high rates of success in diet prediction. DFA of DNE, RFI, OPCR, and second-molar area on the prosimian sample achieve a success rate of 82% (Fig. 3). Adding SR and SQ to that analysis further increases success to 85%. In this analysis, the first discriminant function explains 73% of variance and is driven by DNE followed by RFI, while the second function is largely a size vector explaining 24.9% of variance. In this analysis, there are clear separations between dietary groups, with certain overlap between frugivores and other groups, and folivores and insectivores.

The success rate of the DFA including DNE, RFI, OPCR, and M_2 area of the platyrrhine sample comparatively is 93%, increasing to 94% when SR and SQ are incorporated. The first discriminant function correlates primarily with RFI and DNE, explaining 73% of variance. The second discriminant function explains 22% of variance, and is again related mostly to size. There is stark separation for the most part in this analysis, with the only overlap existing between the frugivores and hard-object feeders.

The success rate for the DFA of the combined sample is lower at 77% (Fig. 4), increasing to 80% with the addition of SR and SQ. The first discriminant function here, explaining again 73% of variation, differs from the anal-

ysis of the separated samples in that it is correlated largely with DNE and only very slightly with RFI. This is consistent with results comparing standard and phylogenetic ANOVA. The second discriminant function, explaining 20% of variance, is related primarily to M_2 area. Examining the distribution of specimens over the first and second discriminant functions, there is strong overlap between platyrrhines and prosimians with similar dietary preferences, as expected for an adaptively related characteristic such as dental topography. Prosimians vary more and exhibit extreme values for discriminant functions relative to platyrrhines, as befitting their overall trend of greater shape variation.

One thing that emerges from the foregoing analyses is the confusing state of observations surrounding RFI: both it and DNE are highly effective for diet prediction in separated platyrrhine and prosimian samples, and RFI also correlates strongly with DNE. However, RFI is relatively ineffective at predicting diet when the platyrrhine and prosimian samples are combined while DNE remains effective; and finally, taking into account the phylogenetic distance matrix from the combined sample allows a substantial increase in the number of significant post hoc comparisons for RFI, but not DNE. To examine these findings further, two DFAs are presented: RFI with M_2 area, and DNE with M_2 area (Fig. 5). The first and second discriminant functions are highly

TABLE 6. Results of post hoc comparisons

Data	DNE ^a	DNE	RFT ^a	RFT	OPCR ^a	OPCR	SR ^a	SR	SQ ^a	SQ
Ins vs. Fol	36.834 (2.5/0.02)	49.317 (2.9/0.006)	0.034 (2.6/0.016)	0.016 (0.9/0.40)	5.076 (1.4/0.17)	2.056 (0.4/0.69)	0.028 (0.2/0.83)	0.098 (0.5/0.63)	8.48 (3.57/0.002)	7.89 (3.1041/0.002)
Ins vs. Om	69.487 (3.5/0.003)	67.399 (5/0.0001)	0.086 (7.1/0.0001)	0.049 (3.5/0.001)	6.696 (3.6/0.003)	1.748 (0.4/0.71)	0.425 (2.6/0.021)	0.396 (2.9/0.005)	6.60 (1.85/0.087)	5.15 (2.94/0.005)
Ins vs. Frug	94.912 (7.5/0.0001)	91.608 (5.8/0.0001)	0.085 (3.5/0.002)	0.091 (5.2/0.0001)	-2.697 (0.6/0.56)	-0.727 (0.2/0.88)	0.565 (4.9/0.0001)	0.43 (2.2/0.03)	11.69 (5.59/0.0001)	7.61 (3.21/0.002)
Ins vs. HO	130.32 (7.6/0.0001)	125.092 (6.2/0.0001)	0.093 (4.9/0.0002)	0.115 (5.1/0.0001)	-11.083 (2.4/0.031)	-3.786 (0.7/0.51)	1.246 (3.7/0.002)	1.016 (4/0.0002)	15.12 (4.68/0.0004)	10.02 (3.021/0.004)
Fol vs. Om	32.653 (2.2/0.04)	18.082 (1.9/0.06)	0.051 (3.3/0.003)	0.033 (1.7/0.09)	1.62 (0.4/0.71)	-0.308 (0.8/0.42)	0.397 (3.2/0.005)	0.298 (1.5/0.15)	-1.88 (-0.90/0.38)	-2.74 (1.07/0.29)
Fol vs. Frug	58.078 (6/0.0001)	42.291 (3.5/0.0009)	0.051 (2.6/0.016)	0.075 (5.9/0.0001)	-7.773 (1.8/0.082)	-2.783 (0.7/0.47)	0.536 (6/0.0001)	0.332 (2.8/0.008)	3.21 (2.72/0.011)	-0.28 (0.18/0.86)
Fol vs. Ho	93.486 (7.2/0.0001)	75.775 (4/0.0002)	0.058 (3.2/0.004)	0.099 (4.6/0.0001)	-16.159 (3.2/0.004)	-5.842 (1.1/0.29)	1.217 (4.8/0.0001)	0.918 (3.9/0.0003)	6.64 (3.72/0.001)	2.13 (-0.68/0.50)
Om vs. Frug	25.425 (2.5/0.024)	24.209 (0.6/0.57)	0 (0/0.992)	0.042 (1.6/0.11)	-9.393 (1.7/0.11)	-2.476 (0.3/0.76)	0.139 (1.5/0.149)	0.034 (0.6/0.56)	5.09 (3.68/0.002)	2.46 (1.003/0.32)
Om vs. HO	60.833 (4.8/0.0006)	57.693 (2.7/0.009)	0.007 (0.3/0.75)	0.066 (2.8/0.008)	-17.779 (3.3/0.007)	-5.534 (0.9/0.38)	0.82 (2.1/0.061)	0.619 (2.4/0.023)	8.52 (4.097/0.002)	4.87 (1.41/0.17)
Frug vs. HO	35.408 (4.3/0.0004)	33.484 (1.9/0.06)	0.007 (0.2/0.81)	0.024 (1.2/0.23)	-8.386 (1.4/0.186)	-3.059 (0.6/0.53)	0.681 (2.7/0.015)	0.586 (2.6/0.011)	3.43 (4.97/0.0001)	2.41 (-0.83/0.41)
^b Sig	6	5	3	5	1	0	4	3	5	3

For each variable, the asterisked column represents the ordinary ANOVA

(OA), while the nonasterisked column is the PGLS version run using the Capser package in R. In each cell the results of the comparisons are given. The first number is the difference in the mean value of the groups being compared. Within parentheses, the number in front of the backslash is the *t*-statistic for a Student's *t*-test. The number after is the probability of no difference between means. Bolded cells are significant at $P \leq 0.05$ with a Bonferroni applied [10 comparisons per variable means corrected critical value is (0.05/10) = 0.005].

^aStandard (not phylogenetically informed) ANOVA.

^bSig column tallies the number of significant post hoc comparisons associated with each ANOVA.

correlated with DNE and RFI in each analysis respectively, and so are depicted as the *x*-axis in their respective visualizations. Much more overlap between dietary

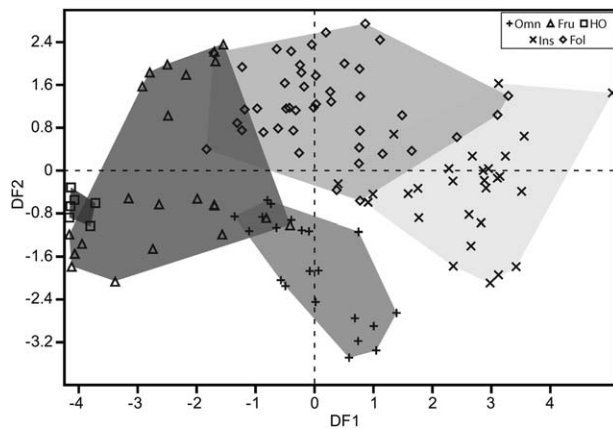


Fig. 3. Discriminant function analyses of diet by topographic metrics and molar area for prosimians alone.

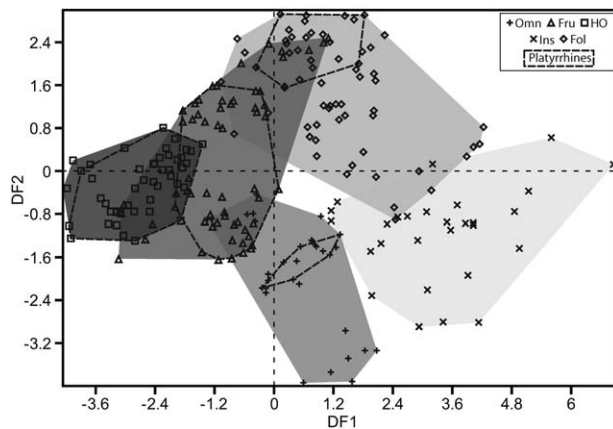


Fig. 4. Discriminant function analyses of diet by topographic metrics and molar area for platyrrhines and prosimians.

categories is clear when considering relief compared to curvature. When dietary groups are differentiated by taxonomic grouping, the reason for this is apparent: platyrrhines of a given diet category tend to have higher relief than their prosimians counterparts but similar curvature. Higher relief across the board in platyrrhines causes overlap between dietary groups when platyrrhines and prosimians are combined, while similar curvature in platyrrhines and prosimians keeps dietary groupings relatively distinct. Thus one might say there is a “group level offset” in relief between platyrrhines and prosimians.

To further examine prosimians and platyrrhines in the context of each other, platyrrhine diets were predicted from a DFA employing DNE, RFI, OPCR, and M_2 area trained on the prosimian sample (Fig. 6a). The reverse was also performed, predicting dietary category of prosimians from a platyrrhine DFA (Fig. 6b). Neither of these analyses is very effective. Predicting platyrrhine diets from a prosimian analysis yields a 19% success, while predicting prosimians from platyrrhines is somewhat more successful with a success rate of 36%. In the latter case, it should be noted that for the purposes of comparing platyrrhines to prosimians, no platyrrhines were coded as “insectivores” (as explained in Methods). When prosimian insectivores are removed from this analysis, the success rate of predicting prosimians from platyrrhines increases to 48%. When these discriminant analyses are plotted, the clustering in each case shows the same broad pattern: platyrrhines cluster relatively tightly toward the center while prosimians spread out at the extremes.

DISCUSSION

Of the major primate groups, dental topographic analysis has been least applied thus far to the parvorder Platyrrhini. This study sought to determine whether dental topography of platyrrhine lower second molars reflects dietary preference, hypothesizing a trend in which, for all variables (relief, curvature, and shear) folivores possessed the highest values followed by insectivores/omnivores, frugivores, and hard-object feeders. The hypothesis is strongly supported by significant

TABLE 7. Successful classification percentages for DFAs of platyrrhine, prosimian, and combined samples

Analysis	Platyrrhines (n = 111)		Prosimians (n = 121)		Combined (n = 232)	
	Success (%)	Cross-validated (%)	Success (%)	Cross-validated (%)	Success (%)	Cross-validated (%)
DNE	67.6	65.8	62.8	61.2	62.9	62.5
RFI	71.2	70.3	56.2	55.4	28.9	24.6
OPCR	44.1	43.2	38.8	35.5	36.2	36.2
SR	70.3	70.3	44.3	44.3	55.3	55.3
SQ	57.7	57.7	53.0	52.2	50.0	50.0
DNE/M2	85.6	82.0	77.7	75.2	73.7	72.8
RFI/M2	82.0	80.2	73.6	71.1	48.7	45.7
OPCR/M2	60.4	57.7	62.0	61.2	50.9	50.9
SR/M2	82.9	79.3	69.6	68.7	74.8	73.9
SQ/M2	77.5	73.9	66.1	64.3	60.2	60.2
DNE/RFI/OPCR	85.6	82.0	65.3	61.2	66.4	65.9
DNE/RFI/OPCR/M2	92.8	91.9	81.8	80.2	76.7	74.6
DNE/RFI/OPCR/SR	90.1	87.4	69.6	67.0	73.0	73.0
DNE/RFI/OPCR/SR/M2	93.7	93.7	84.3	84.3	77.9	77.9
DNE/RFI/OPCR/SQ	86.5	84.7	78.3	74.8	70.8	70.6
DNE/RFI/OPCR/SQ/M2	95.5	91.9	85.2	83.5	77.9	76.1
DNE/RFI/OPCR/SR/SQ/M2	93.7	91.9	85.2	84.3	81.0	79.6

differences in relief, curvature, complexity, and shear between dietary-category groups in platyrrhines and high numbers of significant pairwise comparisons between platyrrhine dietary preference groups. The very high predictive success rate of DFAs on platyrrhine-only sample further supports this conclusion, as analyses incorporating second-molar area, SR, and SQ were able to achieve success rates of almost 94%. In essence, dental topography reflects dietary preferences in the living platyrrhines considered here. This finding is consistent with Ledogar et al.'s (2013) observation that dental

topography differentiates platyrrhine seed predators *Pithecia*, *Chiropotes*, and *Cacajao* from non-seed predators *Aotus* and *Callicebus*. It also generally reflects similar findings of dental topography correlating with feeding choices in many other primate taxa (M'Kirera and Ungar, 2003; Ulhaas et al., 2004; Boyer, 2008; Bunn and Ungar, 2009; Bunn et al., 2011).

Phylogenetic comparisons

Results of correlation analyses incorporating phylogeny indicate that curvature, relief, and shear are significantly correlated with each other. This echoes the observation of Bunn et al. (2011) that DNE, RFI, SR, and SQ are all interrelated, although their correlation analyses did not account for phylogeny. Relatively longer or larger shearing crests result in increased degrees of these three shape aspects, and appear to be the best qualitative explanation for this inter-relationship. Contrary to the observations of Bunn et al. (2011), curvature and relief are not more closely related to each other than either is to shear. A close relationship between curvature and relief would be expected due to their ability to capture variation in features unique to particular taxa (e.g., additional cusps), their shared sensitivity to increases in cusp and shearing crest sharpness, and their reflection of the number and extent of such features on a molar surface. Comparatively, shear is mostly increased by the lengthening of crests or enlargement of cusps. In this case, the relatively low correlation between DNE and RFI may result from a clade-level offset in RFI values between prosimians and platyrrhines (discussed below).

Phylogenetic ANOVAs confirm that when phylogenetic data are available, curvature, relief, and shear measured as SR vary according to dietary groupings in a similar fashion to that observed by previous phylogenetically ignorant analyses (Boyer, 2008; Bunn et al., 2011; Godfrey et al., 2012). In other words, neither phylogenetic spottiness in sampling of dietary groups nor clade level offsets have spuriously led to significant differences in diet-group differences in morphology. Although SQ was still found to vary significantly by diet after accounting for phylogeny, the lower number of significantly separated dietary post hoc pairs is surprising. The increase in the number of significantly separated dietary post hoc pairs that results for RFI when phylogeny is incorporated suggests the existence of a phylogenetic offset in

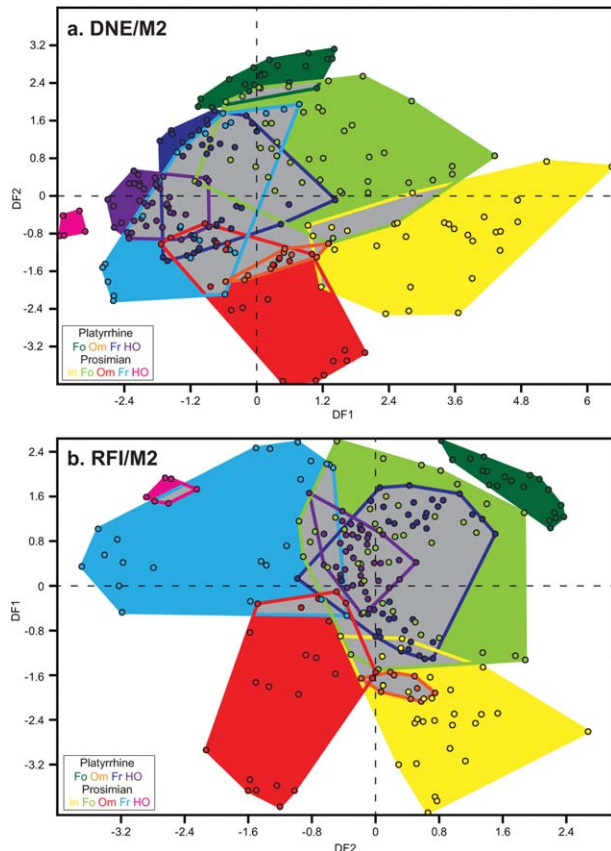


Fig. 5. Discriminant function analyses of diet by DNE/molar area and RFI/molar area for platyrrhines and prosimians.

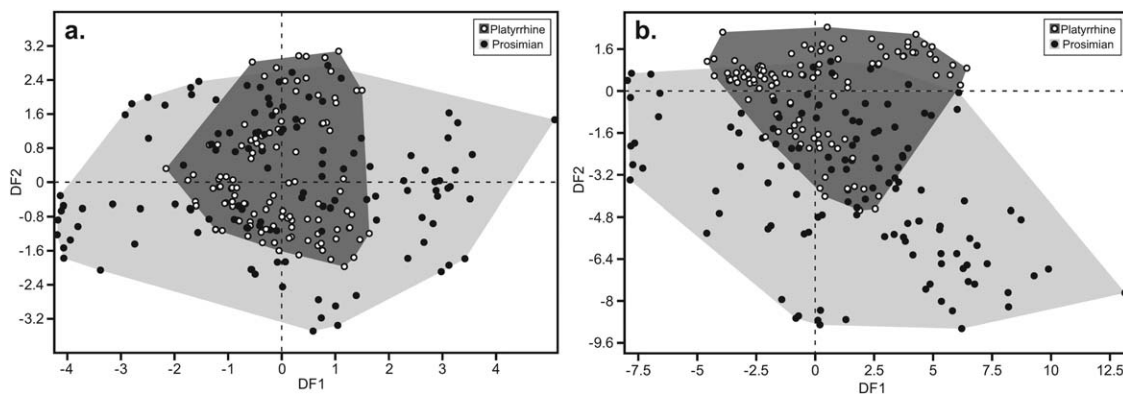


Fig. 6. Discriminant function analyses of diet by dental topographic metrics for (a) platyrrhines predicted by prosimian baseline and (b) prosimians predicted by platyrrhine baseline.

RFI mean and/or variance in the data set that masks a more fundamental relationship between diet and RFI (discussed in more detail below).

Boyer's (2008) analysis found that dietary preference in a wide sample of prosimians, dermopterans, and scandentians was well reflected by RFI in both standard and phylogenetically informed statistics; however, his prediction that RFI might be free of confounding phylogenetic offsets across primates is not supported here. However, we suggest a functional explanation for the differences between platyrrhine and prosimian groups below.

Curvature was equally effective at differentiating diet pairs regardless of whether phylogeny was accounted for, except in the case of omnivores and hard-object feeders. Phylogenetic ANOVA on curvature did not separate omnivores from hard-object feeders significantly, with a *p*-value of 0.009 (Bonferroni-corrected critical value was determined to be 0.005). This may suggest that differences in functional demands between omnivores and hard-object feeders do not consistently select for differences in curvature. On the other hand, with a Bonferroni-corrected [α] level of 0.005, this *P* value may be considered "marginally significant" and this result may be consistent with other dietary-pair separations by curvature.

OPCR is more problematic. Phylogenetic ANOVAs suggest that differences in OPCR in this sample are not explained by the dietary categories used here, after phylogeny was accounted for in the statistical methods used. This means that it is difficult to interpret variance between taxa in complexity observed here as resulting from functional selective pressures. Complexity is high in certain platyrrhine genera, namely pitheciines and likely related to large amounts of molar enamel crenulation (Ledogar et al., 2013). Similarly high degrees of complexity are seen in the prosimians, but only in the bamboo-eating lemur, *Prolemur simus* (Zohdy et al., 2009; Bunn et al., 2011). Both the pitheciines and *Prolemur* consume highly fibrous and mechanically resistant foods such as seeds and bamboo pith respectively, but they are not considered as members of the same dietary categories—possibly revealing some of the inherent problems of using categories based on food types rather than food mechanical properties. Possible functional relationships between high complexity and the mechanical requirements of breaking down these foods have been discussed in previous studies (Bunn et al., 2011; Ledogar et al., 2013), but an analysis with dietary groups configured to include both pitheciines and *Hapalemus* (and to recognize the potential for similarity in functional demands they face) has yet to be executed. It is also possible that dental complexity has been adaptive for different biological roles between the two primate radiations because of other constraints including environmental differences as well as potentially different developmental limitations/possibilities that have diverted similar selective regimes down different paths in the two radiations.

Comparing platyrrhine and prosimian dental topography

Our results suggest that variation in dental topography reflects variation in feeding preferences in living platyrrhines. Prior analyses have concluded the same for strepsirrhines and tarsiers (Boyer, 2008; Bunn et al., 2011). Given this, we asked how platyrrhine dental topographic variation relative to diet compares to that of

strepsirrhines and tarsiers. Phylogenetic informed statistics (see Discussion above) has answered this to some degree, but the question can be considered further. If these two groups have similar correspondence between dietary preference and dental topography this demonstrates the power of these methods to reveal diet in extinct primate taxa. Additionally, it suggests some fundamental conclusions about the form-function link in primate molars. On the other hand, if dental topography is widely dissimilar in these groups, this could suggest specific differences in the adaptive "toolboxes" of platyrrhine and prosimian molar teeth with possible evolutionary or behavioral significance. A primary research goal of this study has been to examine these issues.

Results suggest that the pattern of platyrrhine dental topographic variation is broadly similar to that of the prosimians sampled here. For most aspects of topography, diet categories within each group relate to each other in the same ways: taxa consuming larger amounts of tough leaf matter or hard insect chitin that require shearing or puncturing respectively tend to possess higher curvature, relief, and shear, and taxa consuming less mechanically resistant fruits or tough, hard objects that require crushing tend to possess lower curvature, relief, and shear. In general, insectivorous primate taxa exhibit higher curvature, relief, and shear than folivores, and these dietary categories can be roughly distinguished from each other on this basis. These general trends suggest these two groups of taxa share a similar relationship between variation in presumably functional molar features and dietary preferences. That is, for both platyrrhines and prosimians, the consumption of more foods that require puncturing and shearing necessitates greater degrees of curvature, relief, and shear from molar occlusal features. Dental complexity reveals a contrary trend where platyrrhine hard-object feeders, rather than extreme folivores exhibit the highest complexity. This speaks to a more stochastic, less unified, relationship between diet and functional morphology in the evolutionary history of dental complexity. In other words, it may be possible that high complexity does not have a singular functional association, or that complexity derived from crenulated enamel may be functionally distinct from complexity derived from the proliferation of cusps and crests.

Additionally, discriminant function analyses demonstrate high accuracy in predicting the diets of "unknown" specimens of platyrrhines and prosimians based on a combined platyrrhine-prosimian sample, correctly identifying 77% of specimens using topographic metrics and molar length. While this is less accurate than predicting the diets of platyrrhine specimens from a platyrrhine-only sample (94%) or prosimian specimens from a prosimian-only sample (82%), it is respectable given the wide variation in both molar form and diet in the combined platyrrhine-prosimian sample. This suggests that these dental topographic methods should be usable to infer diets in fossil specimens, even though the specific configuration of molar features and diets of extinct taxa may fail to match exactly those of any member of the living comparative sample.

Gross differences between topography in platyrrhines and prosimians do exist, however, and point to substantive distinctions between these groups. Across the sample, the platyrrhines we examined evinced greater relief and complexity than the prosimians in general, although both samples exhibited similar curvature and shear.

In addition to comparisons of central tendencies between groups, comparisons of variance in each sample are interesting. Namely, in almost all topographic aspects platyrrhines possess a muted trend of shape variation compared to prosimians. For almost every topographic variable, prosimians occupy the extremes of the topographic range. This can be seen in the comparative plotting of platyrrhines and prosimians in DFA space, where platyrrhines largely nest within the space occupied by prosimians. This further explains the poor performance of predicting the diets of platyrrhine specimens from a prosimian-only sample and the still-poor but higher accuracy of predicting prosimians from a platyrrhine-only sample.

Given that all variables except complexity continue to distinguish dietary groups when phylogeny is accounted for, the explanation for this difference in variance is most likely a complex one. It is probably partly explained by different levels of ecological variance and possibly time for adaptive radiation between these groups to some degree. With fewer committed folivores and insectivores, platyrrhines clearly exhibit less variation in selective conditions regarding feeding preferences, and as a result exhibit lesser molar variation. This is not the whole story though, as the total variance in complexity is actually greater in platyrrhines than strepsirrhines, thereby suggesting the same potential for developing morphological diversity in both groups. A more general explanation is that natural selection has proceeded similarly, but not identically to produce variation in molar teeth through the separate histories of prosimians and platyrrhines: any number of intrinsic contextual and/or developmental, as well as extrinsic environmental variables may have contributed to the development of differences through time.

Another avenue that deserves further examination is observed differences between relief and curvature in platyrrhines and prosimians. Bunn et al. (2011) observed that these two metrics are highly correlated in strepsirrhines. In the DFAs of platyrrhine-only and prosimian-only samples, DNE and RFI explained the highest degrees of variation. In single-variable analyses, DNE and RFI tended to be the most accurate topographic variables for predicting diet from “unknown” specimens and their accuracy percentages tended to be similar. Yet in analyses combining platyrrhines and prosimians into a single sample, curvature continues to explain the highest percentage of variation in the sample while relief unexpectably explains the lowest. This is due to a combination of two factors: similar patterns of relief across dietary groups for platyrrhines and prosimians combined with the aforementioned increased relief in platyrrhines generally compared to prosimians. This results in any given dietary category in the platyrrhine sample exhibiting relief higher than its companion dietary category in the prosimian sample, thus interfering with the ability to predict diet in a sample consisting of platyrrhines and prosimians. Taking the results of the phylogenetic analyses described above into consideration, we interpret this failure of relief to predict diets in a combined sample as a result of squelching from phylogenetic offsets in relief between platyrrhines and prosimians. In other words, platyrrhines and prosimians have different phylogenetic “starting points” when it comes to molar occlusal relief.

There is another distinction between platyrrhine and prosimian molars that may be related to this: relative molar size. It is possible that in a functional sense, the

selective force increasing molar relief is the need to increase tooth longevity (Boyer et al., 2010). Even without having actually calculated values, it seems obvious that hypsodont teeth of browsing and grazing ungulates living today would have extreme relief values. In this scenario, higher relief means that more attrition is required to wear down a tooth, and this may be beneficial in diets consisting of mechanically resistant foods such as leaves and insect chitin that require numerous chewing repetitions, resulting in concomitant tooth-tooth attrition. Another way of thinking about how increasing relief increases tooth longevity is to recognize that increasing relief also increases the absolute amount of tooth enamel available in an animal's lifetime, as well as the relative amount of tooth enamel for an animal of a given body size/tooth size. The prosimians of our sample appear to exhibit larger molars relative to their body mass than do the platyrrhines examined. This was tested using analysis of covariance (ANCOVA) in the program JMP (Supporting Information Table S4). Species means for natural log M_2 area for 14 platyrrhines and 24 prosimians were used as the test variable and averaged male and female natural log body mass reported in Smith and Jungers (1997) was used as the covariate. The interaction effect between body mass and group was nonsignificant ($P = 0.5085$), indicating the slope of the scaling relationship between body mass and M_2 area is the same for both groups. Running the ANCOVA showed a significant group effect on M_2 area ($P = 0.0009$) verifying that platyrrhines have smaller molars for a given body mass than prosimians. This effect is, of course, also implied by literature such as Conroy (1987) in which body mass predictions from teeth based on prosimian taxonomic samples are smaller than those based on “all primates” samples. Therefore greater average relief in platyrrhines and greater molar areas relative to body mass in prosimians may solve the same functional problem of tooth wear in different ways. This phenomenon may be present to a smaller degree among platyrrhines as well—*Pithecia* and *Chiropotes* exhibit topographically similar molars despite higher folivory in *Pithecia*, possibly related to that genus' relatively larger molars. But apparently differences in relief do not affect curvature despite a high correlation between curvature and relief. That small differences in relief do not affect curvature is corroborated by an error study presented by Bunn et al. (2011) in which curvature was calculated on the same tooth multiple times after it was modified by increasing or reducing the amount “non-occlusal surface” material included in the calculation. Thus curvature as an ecological indicator does not seem to relate to tooth longevity. One prediction that stems from this suggestion is that measures of DNE should be more stable in the context of variability in tooth wear than relief.

Implications for dental topography

Results here suggest that of the topographic variables considered, DNE may be the most effective metric for predicting diets in broad samples of primates and in novel situations. It is easy to apply and usable for dietary inference even in samples combining very different taxonomic groups and in situations where the similar metric RFI was ineffective. We predict this is also the case for nonprimates, but further study is needed. Comparatively, RFI may be more effective when phylogeny is accounted for, and differences in relief between primate

groups may contribute more to our knowledge of the molar form-function relationship with diet.

A fundamental conclusion demonstrated here relates to the fact that relief seems to be reflecting morphology in a fashion distinct from curvature in the manner in which it differs between platyrrhines and prosimians. Relief and curvature seem to be highly correlated, but results here suggest that they are functionally employed in distinct ways by different groups, and that it is valuable to employ multiple topographic metrics in future analyses.

Shear does not predict dietary preference as well as curvature or relief in most DFAs, regardless of whether SR or SQ is considered. This is explainable by RFI and DNE being “whole-tooth” shape metrics compared to SR/SQ’s relatively more landmark-based approach. But differences in variation of SQ by dietary preference compared with variation in SR are more puzzling. In the platyrrhine-only sample, folivorous *Alouatta* and *Brachyteles* exhibit higher SR than frugivorous genera as per expectations, but lower SQ.

Examining the results of phylogenetically informed analyses further complicate matters. Platyrrhine and prosimian SQ is significantly correlated with second molar area when phylogeny is taken into account, although SR is not. As the allometric size-correction function of SQ (the primary distinction between SQ and SR) is partially intended to ensure that SQ is uncorrelated with body size proxy (Anthony and Kay, 1993), this is curious. Additionally, as mentioned above, the pattern of phylogenetically weighted species means for SQ differs both from standard SQ species means and also SR species means of either type. Furthermore, while SQ significantly varies by diet when phylogeny is accounted for, it has lower efficacy in distinguishing dietary category pairs. It does not seem possible to suggest that these trends can be explained as biological attributes of shear relating to either phylogeny or topography, given that results from SR, another measure of shear, differ so strongly.

Rather, we suggest this is a methodological issue relating to the size-correction function of SQ compared to the ratio of body size proxy of SR. This size-correction function is firmly sample-specific—that is, the size correction function calculated for platyrrhines differs from that of prosimians, and this could affect resulting SQ in unexpected ways. This may explain the surprising results observed here using phylogenetically informed analyses. A possible solution to this obstacle is to recalculate SQ for each analysis with a new permutation of a sample, for example to have platyrrhine-only SQ for analyses involving only platyrrhines and platyrrhine-prosimian SQ for combined analyses. But this would still limit the comparison of SQ across studies, and seems needlessly complex given the simplicity of SR calculation.

CONCLUSIONS

Variation in curvature, relief, and shear of platyrrhine second molars reflects dietary preference. This supports the hypothesis that dental topography is functionally adaptive, that primate species have evolved molar features to increase curvature, relief, and/or shear such as elaborating, elongating, or sharpening cusps and crests in order to overcome the mechanical defenses of food items. Dental topographic variables predict platyrrhine

dietary preferences very accurately, demonstrating that these methods are ideal for paleoecological inference.

Phylogenetic ANOVAs indicate that curvature, relief, and shear continue to be significantly explained by dietary preference when phylogeny is accounted for, but complexity does not. Observed differences in complexity between platyrrhines and prosimians in this sample are best explained by phylogeny rather than functional considerations of diet. Unlike other metrics, relief index explains diet more thoroughly in our combined prosimian-platyrrhine sample when weighted phylogenetically.

Overall, the pattern of variation of platyrrhine dental topography is similar to that of prosimians, although platyrrhines exhibit a muted trend of shape variation. This points to similarity in adaptive landscapes between radiations. Complexity differs, having distinct profiles in platyrrhines and prosimians, but this may result from limitations in our paradigm for categorizing primate dietary preferences. Accuracy in DFAs of combined prosimian-platyrrhine samples is less than in prosimians or platyrrhines alone, but not by much, again underpinning the potential of these methods for inference of fossils whose dietary preferences may vary from those of extant comparative samples.

Differences are present in dental topography between radiations, specifically there exists a clade-level offset in relief where platyrrhines exhibit greater relief overall than prosimians, but similar curvatures. This is the source of reduced effectiveness of relief for inferring diets in standard analyses, but when phylogeny is accounted for, relief is highly effective at distinguishing dietary preference groups in our combined sample. Differences in relief between platyrrhines and prosimians may be related to differences in molar size relative to body size, in that prosimians may have solved a problem of tooth attrition by evolving larger molars while platyrrhines evolved greater relief. Finally, despite expected interrelatedness between relief and curvature, our results suggest they are two distinct aspects of molar shape and deserve further study simultaneously.

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