Functional Ecology

The better to eat you with: functional correlates of tooth structure in bats

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Summary

1. Mammalian dental morphology and function are strongly linked to diet. Within mammals, phyllostomid bats are the most diverse family in terms of dietary ecology and thus represent a unique opportunity in which to investigate relationships between diet, tooth structure, feeding performance and behaviour.

2. Previous studies have focused on how specific aspects of dental morphology relate to diet. Here we use a comprehensive approach to describe 3D dental topography through a measure called dental complexity. Using phyllostomids as a model system, we investigate the functional significance of molar complexity with respect to prey breakdown of insect-eating species. We generated complexity data from 3D laser scans of molars from 17 species. We quantified feeding performance (ability to break down insects) and behaviour (number of chews) by conducting feeding experiments on 11 species using native prey.

3. Frugivores were found to have the highest molar complexity, which is related to biting into and crushing fruit pulp. Lower complexity of insectivore and omnivore molars can be related to the presence of crests specialized for shearing insect exoskeleton. Increases in the complexity of these shearing teeth translated into higher performance in prey breakdown (smaller exoskeleton particles), but chewing behaviour also played an important functional role.

4. Our results highlight the importance of morphology and behaviour in determining feeding performance, which potentially contributes to resource partitioning within this diverse group of mammals.

Key-words: dental complexity, diet, feeding performance, molars, Phyllostomidae

Introduction

The utility of teeth in assessing dietary adaptations and mammalian evolutionary relationships was accurately summarized by the father of comparative anatomy, Georges Cuvier (1769–1832): 'show me your teeth and I will tell you who you are' (Bergqvist 2002). Still today, the scope of comparative dental anatomy spans extant and extinct species, as many fossils are represented only by their dentition and scientists often use dental morphology to infer the diets of extinct species (e.g. Pilbeam *et al*. 2008; Ungar, Grine & Teaford 2008; Pabbington 2009). Although mammalian teeth are similar in their basic components, they exhibit a great diversity in number, size and shape that seems to be strongly correlated with diet (reviewed in Lucas 1979; Lucas & Peters 2007). In fact, numerous mammalian trophic adaptations are often described in terms of molar dentition, from insectivorous species with dilambdodont molars specialized for crushing insect exoskeleton, to herbivores with selenodont molars that are good for grinding plant material. Dietary ecology seems to have shaped the evolution of molar morphology to the point that some dental traits may have evolved numerous times in association with diet (Hunter & Jernvall 1995). At a proximal scale, tooth morphology can have an effect on an animal's nutrient intake and digestibility and thus strong selective pressures should act on tooth shape and function (Lanyon & Sanson 1986; Bezzobs & Sanson 1997; Pérez-Barbería & Gordon 2001; McArthur & Sanson 2009).

Teeth can be viewed as tools that have primarily evolved for breaking apart food (Evans & Sanson 2003). As with any

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tool, tooth shape determines how well it will function. Functional morphologists have taken two main approaches to investigate the implications of tooth shape for tooth function. On one hand, they create digital and physical models of teeth and test their effectiveness in breaking down materials of different properties (e.g. Evans & Sanson 1998, 2003, 2006; Ang, Lucas & Tan 2006; Anderson & LaBarbera 2008; Evans & Fortelius 2008). On the other hand, researchers take morphological measurements of teeth and conduct comparative studies and relate morphological differences to dietary ecology. These studies mostly include comparisons of size, such as relative crest lengths (e.g. Anthony & Kay 1993; Strait 1993a; Ungar & Kay 1995; Dumont, Strait & Friscia 2000; Kay 2005; Hogue & Ziashakeri 2010), ratios of dental parts (e.g. Seligsohn 1977; Gingerich & Schoeninger 1979; Yamashita 1998; Kay 2005) or tooth types (e.g. Weller 1968; Freeman 1984; Vizcaíno 2009). Studies of tooth shape are less common (but see Bailey 2004; Lazzari *et al.* 2008; Wood *et al.* 2007). Taking the study of shape one step further, Evans *et al.* (2007) developed a non-homology based technique to characterize the 3D topography of tooth rows. This relatively new measure, called tooth complexity, provides a more detailed three-dimensional description of occlusal surface shape than can be accomplished through traditional 2D measurements of molar cusps. Viewing teeth as tools, increasing complexity is thought to add extra tool components or 'breakage sites' that function in the breakdown of resistant food items. Accordingly, mammals that specialize in a carnivorous diet have less complex molars than mammals specializing in tough plant material (Evans *et al.* 2007).

Despite advances in describing trends in the morphology of teeth that are associated with diet, few studies have directly measured how interspecific differences in tooth morphology translate into differences in feeding performance in animals in the wild. In the context of molar complexity, we define feeding performance as the ability to break down prey items during feeding, which is an essential step for efficient processing and absorption of nutrients by the digestive tract (e.g. Beauchemin *et al.* 1994, Kay & Sheine 2005). In addition to tooth morphology, differences in feeding performance could also be the result of differences in chewing behaviours (e.g. chewing speed, number of chews per prey item). This type of behavioural modulation could lead to functional equivalence of very different morphologies, possibly obscuring the relationship between dental morphology and feeding performance.

Here we use Neotropical leaf-nosed bats (family Phyllostomidae) to investigate the relationship among tooth complexity, feeding behaviour, performance and diet. Phyllostomid bats offer a unique model system for answering these questions because their outstanding dietary radiation is accompanied by high diversity in tooth morphology (Freeman 2000; Fig. 1). In particular, the consumption of plants appears to have played a major role in phyllostomid diversification and seems to have influenced the morphology of molars (E.R. Dumont *et al.*, unpublished data; Freeman 2000; Jones, Bininda-Emonds & Gittleman 2005), which are

the teeth mostly used to process food (Dumont 1999; Santana & Dumont 2009). Therefore, the transition from insectivory to frugivory is of particular interest in investigating changes in dental morphology and their potential association with the diversification of the family.

Complexity measures (Evans *et al.* 2007) of molar tooth shape were used to test the hypothesis that molar complexity reflects specialization to different diets. Plant material requires more mechanical processing than insects because many fruits consumed by bats contain fibrous material and seeds in addition to pulp. Thus, we predict that molar complexity will increase from insectivorous, to omnivorous and frugivorous species. We also hypothesize that molar complexity impacts feeding performance and behaviour. Among species that feed on insects, we predict that higher molar complexity (more cutting surfaces) will be correlated with higher performance in insect breakdown (smaller exoskeleton particles in faecal pellets). We also predict that insectivorous species with higher molar complexity will chew their prey less than species with lower complexity.

Materials and methods

TOOTH COMPLEXITY

We investigated interspecific differences in the complexity of 3D shape of molar teeth through geographic information system analysis (Evans *et al.* 2007). We obtained these measures from voucher specimens of the insectivorous and omnivorous bats used in the feeding behaviour observations (below) and for which we collected faecal samples. In addition to these, we included specimens of frugivorous species from collections to expand the scope of our analysis (Table 1).

One upper and one lower tooth row of each specimen were scanned using a Surveyor RPS-120 probe (Laser Design Inc., Minneapolis, MN, USA) following Smith & Strait (2008). Scans were conducted using a step size (the distance from one data point to the next) of 0·01 mm, and included occlusal, lingual and buccal views. These views were merged together prior to analysis. Point cloud data from laser scans were imported into Geomagic v. 11 (Geomagic, Research Triangle Park, NC, USA) to model and manually orient the scans to maximize crown–base projection. Scans were oriented with the X-axis increasing in the buccal direction, the Y-axis increasing in the anterior direction, and the Z-axis increasing in the occlusal direction. Only molar tooth rows were kept for the analyses. This is because phyllostomids use these teeth predominantly to process prey (Dumont 1999; Santana & Dumont 2009), and because complete tooth rows would give a better estimation of the overall processing capacity than single teeth.

We imported 3D objects as text files from Geomagic into Surfer-Manipulator (Evans & Fortelius 2008; http://users.monash.edu.au/~arevans/software.html). This software converted the files into digital elevation (grid) files, removed undercuts, scaled image resolution and ran tooth complexity analyses. Because differences in size can influence complexity measures, we scaled all tooth rows to the same length of 150 data rows following Evans *et al.* (2007). Topographic (contour) maps were then generated with contours of twice the X and Y resolutions. Orientation maps were generated from the topographic maps by determining the orientation at each grid point as being one of eight compass directions (e.g. north, southwest, etc.). We used
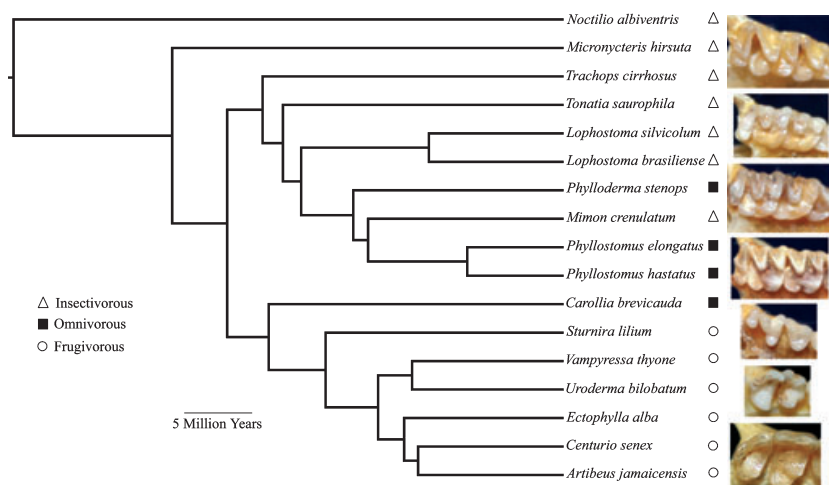
Fig. 1. Evolutionary relationships and dietary habits of the species included in this study. Pictures of the upper right molars of some species are included to illustrate the dental diversity within the family (from top to bottom: *Trachops cirrhosus*, *Lophostoma brasiliense*, *Mimon crenilatum*, *Phyllostomus hastatus*, *Carollia brevicauda*, *Vampyressa thyone* and *Artibeus jamaicesis*). Phylogeny pruned from E.R. Dumont *et al.* (unpublished data).

Table 1. Sample sizes and complexity (OPC) of the lower and upper molars for the species included in this study

Species	Species	*N* behaviour	*N* feeding events	*N* complexity	Complexity lower molars	Complexity upper molars
Lophostoma brasiliense	Insectivore	3	17	3	259·0 ± 11·31	405·0 ± 2·83
Lophostoma silvicolum	Insectivore	4	43	2	174·5 ± 21·92	352·5 ± 10·61
Micronycteris hirsuta	Insectivore	3	23	3	169·0 ± 6·93	308·0 ± 14·00
Mimon crenulatum	Insectivore	4	29	3	223·0 ± 24·98	330·0 ± 4·58
Noctilio albiventris	Insectivore	2	4	2	330·0 ± 66·47	410·5 ± 82·73
Tonatia saurophila	Insectivore	7	57	3	179·0 ± 24·88	301·0 ± 32·42
Trachops cirrhosus	Insectivore	5	18	3	195·3 ± 24·01	362·5 ± 56·66
Carollia brevicauda	Omnivore	14	40	3	226·0 ± 67·91	337·0 ± 65·64
Phylloderma stenops	Omnivore	2	19	2	203·5 ± 6·36	343·0 ± 1·41
Phyllostomus elongatus	Omnivore	3	29	2	207·5 ± 38·89	378·0 ± 97·58
Phyllostomus hastatus	Omnivore	5	29	2	158·0 ± 12·73	281·5 ± 40·31
Artibeus jamaicensis	Frugivore	–	–	2	409·5 ± 45·96	589·0 ± 26·87
Centurio senex	Frugivore	–	–	2	516·5 ± 0·71	907·0 ± 1·41
Ectophylla alba	Frugivore	–	–	2	424·5 ± 44·55	603·0 ± 113·14
Sturnira lilium	Frugivore	–	–	2	335·0 ± 80·61	518·5 ± 58·68
Uroderma bilobatum	Frugivore	–	–	2	338·5 ± 21·92	556·5 ± 55·86
Vampyressa thyone	Frugivore	–	–	2	524·0 ± 5·66	779·0 ± 212·13

Values for complexity are means ± SD.
OPC, orientation patch count.

these orientation maps to quantify the number of 'tools' on the crown, by subdividing the surface of each model into patches based on slope orientation, with a minimum patch size of two grid points. Contiguous points with the same orientation were grouped together as a patch. The number of these patches is the orientation patch count (OPC; Evans *et al.* 2007; Fig. 2).

FEEDING BEHAVIOUR AND PERFORMANCE

We collected individuals from 10 insectivorous and omnivorous phyllostomid species (Table 1) and one species from a sister family, *Noctilio albiventris* (Noctilionidae), by placing mist nests in forested areas in Venezuela and Panama (February–April and June–July, 2007). Only adult males and adult non-pregnant, non-lactating females were studied; all other individuals were released immediately. Upon capture, we placed bats in separate cloth bags to obtain faecal

samples corresponding to their natural diet, measured the bats' mass using a spring scale and transported them to a base camp. All procedures involving live animals were approved by the Institutional Animal Care and Use Committee at the University of Massachusetts, Amherst, USA (protocol # 26-10-06).

To record the bats' behaviour during insect-feeding, we transferred each bat to a small, wire mesh enclosure ($40 \times 60 \times 60$ cm) and used tweezers to offer live, native scarabeid beetles (Coleoptera: Scarabaeidae, length: 13.93 ± 0.21 mm, width: 7.02 ± 0.10 mm). These insects have been reported to be part of the diet of the insectivorous and omnivorous phyllostomids included in this study (Gardner 1977; Ferrarezi & Gimenez 1996; Aguirre *et al.* 2003; Giannini & Kalko 2004) and bats usually ate the beetles eagerly. We recorded the bats' feeding behaviour using a digital video camera with night vision (Sony DCR-TRV730 Digital-8 Camcorder, Sony, USA). Feeding trials ended once the bats were satiated, typically after ingesting several
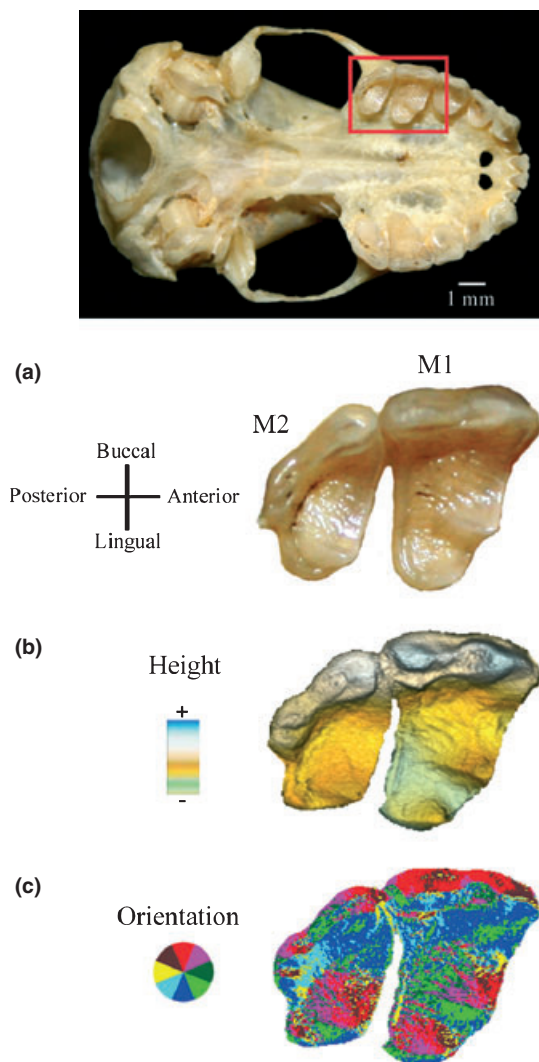
Fig. 2. Occlusal view of the upper dentition of a frugivorous phyllo-stomid (*Artibeus jamaicesis*, top) and the steps followed in the tooth complexity analysis. From laser scans of the upper molars (a) an occlusal reconstruction of the molar tooth row (b) is processed to determine surface orientation (c). Orientation of the surfaces is indicated by colour as shown on the colour wheel. This allows the measurement of orientation patch count (OPC, the number of coloured patches).

beetles. We analysed the videos of feeding behaviour by watching them at slow speed and quantifying the total number of chews each bat used to eat a beetle. We used this measure (chews per beetle) as an indicator of the amount of processing needed given a particular molar structure. Numbers of chews per beetle were averaged to obtain means for each individual bat and across individuals to obtain species means.

After the feeding trials were completed, bats were transferred from the enclosure to a clean cloth bag. Holding the bats for 2–6 h in this bag allowed us to gather faecal samples corresponding predominantly to insects ingested during the feeding behaviour trials. In all cases, used bags were allowed to dry for at least 24 h to avoid damaging the faecal pellets during removal. After this period, faecal pellets were carefully removed in the laboratory using fine tweezers and transferred to Eppendorf centrifuge tubes for storage.

We randomly selected a few faecal pellets (1–2 g) from each sample. These were placed on a Petri dish with distilled water for a few hours until the exoskeleton particles could be teased apart using needles or fine forceps and pieces were evenly distributed over the surface of the water. We placed a grid under the Petri dish and used a random number generator to choose quadrants from which to collect particles; samples were collected under a dissecting microscope and placed on a paper tissue to dry. We separated at least 20 particles per faecal pellet and included only flat cuticle pieces that were relatively uniform in thickness. Wing, limb, head capsule and irregularly shaped fragments were not included as they often did not meet this requirement. To quantify feeding performance, we measured the size and thickness of the exoskeleton particles. As chitin is mostly indigestible by mammals (Altman & Dittmer 1968), smaller particles indicate a better performance in breaking down the insects with the teeth. We measured particle size by taking a digital picture of the particles along with a millimetric scale and using ImageJ (National Institutes of Health, Bethesda, MD, USA) to outline each particle's perimeter and calculate its area. Exoskeleton thickness and insect hardness are positively correlated (Evans & Sanson 2005; this paper), thus thicker particles indicate a more physically demanding prey, or parts of the prey. As this could influence insect breakdown, we also measured the thickness of each exoskeleton particle to account for this factor. Thickness of each particle was measured using a digital micrometer head with hemi-spherical attachments (Mitutoyo IP65; Mitutoyo Corporation, USA) (Evans & Sanson 2005). Particle size and thickness data were averaged across individuals to obtain species means. We found that particle size and thickness were correlated ($R^2 = 0.470$, $P = 0.010$), and only used particle size as a measure of performance in subsequent analyses.

STATISTICAL ANALYSES

In order to ensure statistical independence across the species data, we tested all variables for phylogenetic inertia by comparing the Akaike Information Criterion (AICc) scores of four evolutionary models that we considered likely to match the data (lambda, delta, early burst, white noise; Harmon *et al.* 2008). These models were fitted to the data while using a pruned version of the E.R. Dumont *et al.* (unpublished data) species-level phyllostomid phylogeny (Fig. 1). This phylogeny was estimated based on sequences of mitochondrial, ribosomal, cyto-chrome b, partial mitochondrial cytochrome oxidase, and partial nuclear recombination activating genes from 147 species exemplars. Tree topology and branch support differed minimally between Maximum likelihood and Bayesian analyses carried out by Dumont *et al.* Functions contained in the libraries ape, geiger, picante and GLM in R (R Development Core Team 2010) were used to run phylogenetic analyses. The model with lowest AICc was a 'white noise' model (i.e. all species drawn from the same normal distribution, or 'no phylogenetic signal', Harmon *et al.* 2008), and therefore we carried out the subsequent analyses without phylogenetic adjustments.

To test differences in tooth complexity related to diet, species were classified into one of three dietary categories following published dietary information (Aguirre *et al.* 2003; Da Silva, Gaona & Medellin 2008; Ferrarezi & Gimenez 1996; Gardner 1977; Giannini & Kalko 2004; Snow, Jones & Webster 1980; Van Cakenberghe, Herrel & Aguirre 2002; Table 1). We used a one-way analysis of variance (ANOVA) to investigate whether 'diet' (insectivorous, frugivorous, omnivorous) had a significant impact on molar complexity (OPC). In this ANOVA model, OPC for either the lower or upper molars was the dependent variable, and 'diet' was designated as the fixed factor. *Post hoc* pairwise comparisons with a Bonferroni correction were performed to further investigate which and how dietary categories differed in OPC.

Linear regressions were used to investigate the relationship among tooth complexity, feeding behaviour (number of chews) and feeding performance (particle size). Given that larger bats require fewer chews to fully process their insect prey ($R^2 = 0.513$, $\beta = -1.940$, $t_{11} = -3.248$, $P = 0.009$), we used residuals of a linear regression of log number of chews on log body mass as size-corrected number of chews in subsequent analyses. Variables were log-transformed to ensure linearity.

To investigate if and how increases in tooth complexity and size-corrected number of chews resulted in higher performance in insectivorous and omnivorous phyllostomids, we used multiple linear regressions of particle size (response variable) on size-corrected number of chews, molar OPC, and their interaction (predictor variables). We conducted two separate multiple regressions using the OPC data for the upper and lower molars, and a third regression using the sum of the upper and lower OPC. Number of chews and molar complexity were not correlated ($P > 0.05$). All statistical analyses were run in SPSS (v. 12.0 for Windows; SPSS Inc., Chicago, IL, USA).

Results

TOOTH COMPLEXITY AND DIET

When comparing tooth complexity across dietary categories, phyllostomids with different diets were found to differ significantly in the complexity of their lower and upper molars (lower molars: $R^2 = 0.757$, MS = 88831.39, $F_{2,14} = 21.790$, $P < 0.0001$; upper molars: $R^2 = 0.745$, MS = 190101.75, $F_{2,14} = 20.423$, $P < 0.0001$). Frugivores have significantly higher tooth complexity than insectivores and omnivores (Table 1, Fig. 3; $P < 0.0001$). Tooth complexities in insectivores and omnivores were not significantly different ($P = 0.998$).

TOOTH COMPLEXITY, CHEWING BEHAVIOUR AND FEEDING PERFORMANCE

Size-corrected number of chews and upper molar complexity significantly predicted the size of the exoskeleton particles in faecal pellets (Table 2). The interaction between number of chews and complexity was also significant in all regressions. Increasing complexity in insectivorous and omnivorous bats allowed them to generate smaller exoskeleton particles in their faecal pellets (Fig. 4a,b; lower molars: $R^2 = 0.613$, $F_{1,9} = 14.270$, $P = 0.004$; upper molars: $R^2 = 0.320$, $F_{1,9} = 4.231$, $P = 0.07$). Bats also generated smaller particles by chewing their prey more (Fig. 4c, $R^2 = 0.458$, $F_{1,9} = 7.619$, $P = 0.022$). When compared to insectivores, omnivores seemed to generate relatively larger exoskeleton particles in their faecal pellets, however sample sizes are too small to test this statistically.

Discussion

MOLAR COMPLEXITY AND DIET: CRUSHING/GRINDING VS. SHEARING MOLARS

There is strong evidence that diet and the biomechanical properties of foods influence the morphology and function of
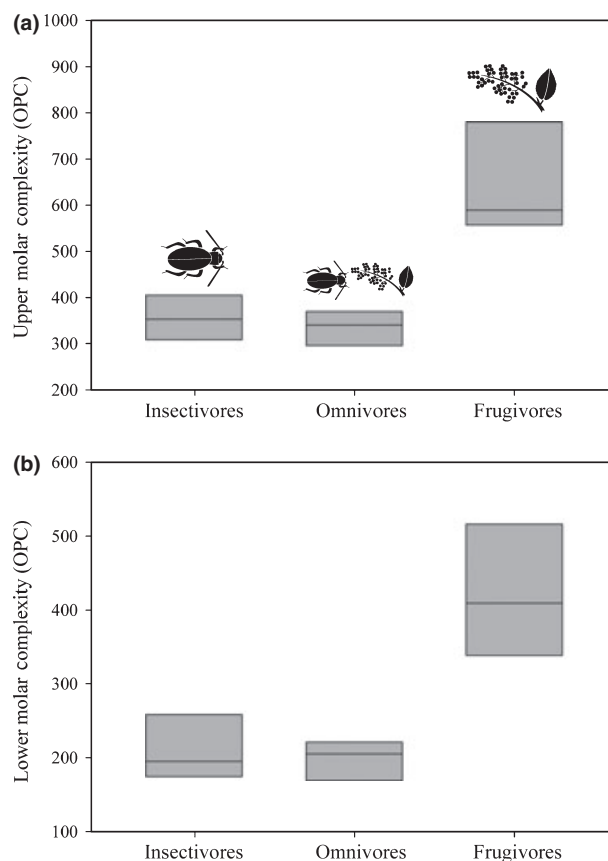

Fig. 3. Complexity of the upper (a) and lower (b) molars measured through orientation patch count (OPC) across dietary groups. Boxes represent 95% confidence intervals around the mean (solid line).

the feeding apparatus of animals (e.g. Freeman 1988; Perez-Barberia & Gordon 1999; Herrel & Holanova 2008; Herrel *et al.* 2009). For mammals in particular, the consumption of plant resources seems to have dramatically shaped the evolution of cranial and dental morphologies (Freeman 1988; Anapol & Lee 1994; Janis 1995; E.R. Dumont *et al.*, unpublished data). Our results indicate that fruit consumption in primarily frugivorous phyllostomids is associated with elevated molar complexity when compared to the less-derived insectivores and omnivores, even though the latter have third upper and lower molars. This finding is consistent with complexity trends in carnivorans and rodents, where plant-eating species have a higher complexity than carnivorous species (Evans *et al.* 2007). Higher tooth complexity is characteristic of dentitions bearing more edges that can be used to cut, crush and break down plant material during mastication. In the case of frugivorous phyllostomids, high complexity seems to be the product of relatively small stylar shelves, sharp stylar cusps, and especially crenulations of the tooth enamel (Figs 1 and 2). In some species, the sharp stylar cusps form a continuous cutting edge with the canines and premolars that would be useful in biting through fruit skin and pulp (Freeman 1988). Crenulations in the molar enamel could contribute to crushing fruit pulp or seeds (e.g. Norconk, Grafton & Conklin-Brittain 1998) by providing points of higher stress

Table 2. Results from a multiple regression of exoskeleton particle size on the complexity of the upper and lower molars, and size-corrected number of chews

Variables	Estimate	SE	t	P
Upper molars				
OPC	0·002	0·001	3·182	0·012*
Residual number of chews	8·409	1·865	4·509	0·002*
OPC × residual number of chews	−0·025	0·005	−4·892	0·001*
Lower molars				
OPC	0·001	0·001	1·018	0·339
Residual number of chews	2·121	1·000	2·119	0·066**
OPC × residual number of chews	−0·012	0·004	−2·821	0·022*
Upper ± lower molars				
OPC	0·001	0·001	2·011	0·070**
Residual number of chews	4·652	1·403	3·315	0·010*
OPC × residual number of chews	−0·001	0·002	−3·822	0·005*

*$P < 0.05$, **$P < 0.1$.
OPC, orientation patch count.

during mastication. Such changes in the surface of small molars are hard to measure, thus our results also highlight the utility of OPC for describing molar microstructure. Overall, high molar complexity would contribute to thorough processing of plant material for more efficient bacterial digestion in the intestines. Furthermore, many species of frugivorous phyllostomids chew fruit pulp for prolonged periods of time to extract fruit juices, and spit out the indigestible fibrous material (Morrison 1980). High molar complexity could be linked to this behaviour as well.

Although insectivorous and omnivorous phyllostomids consume diverse prey types (i.e. insects and other arthropods, vertebrates, fruit), they do not differ in molar complexity and exhibit relatively low complexity values when compared to frugivores. Insects are the primary food source for the insectivorous and omnivorous species we studied, and thus the similarities in their molar complexity could be related to specialization towards finely breaking down insect cuticle. Even though the physical properties of exoskeleton vary across insect taxa (dry specimens: Hepburn & Chandler 1980; Hillerton 1984; fresh insects: Freeman & Lemen 2007), molars with shearing crests seem to be the most effective shape for cutting cuticle and exposing the edible contents inside the insect's body. Both tough (e.g. beetles) and ductile (e.g. caterpillars) prey can be well-subdivided by sharp blades that continuously drive cracks through these solids, despite their hardness or tendency to deformation (Strait 1993a, b; Evans & Sanson 1998). The shearing crests present in insectivorous and omnivorous phyllostomids (Fig. 1, top pictures) return lower values of molar complexity, a trend that is similar to that found on other mammals that consume animal prey (Evans *et al.* 2007). Note however, that the OPC values reported here for insectivores and omnivores are much higher than those of carnivorans and rodents (50–350 patches, Evans *et al.* 2007). This raises the issue of potential historical effects that led phyllostomid bats to have elevated complexity relative to
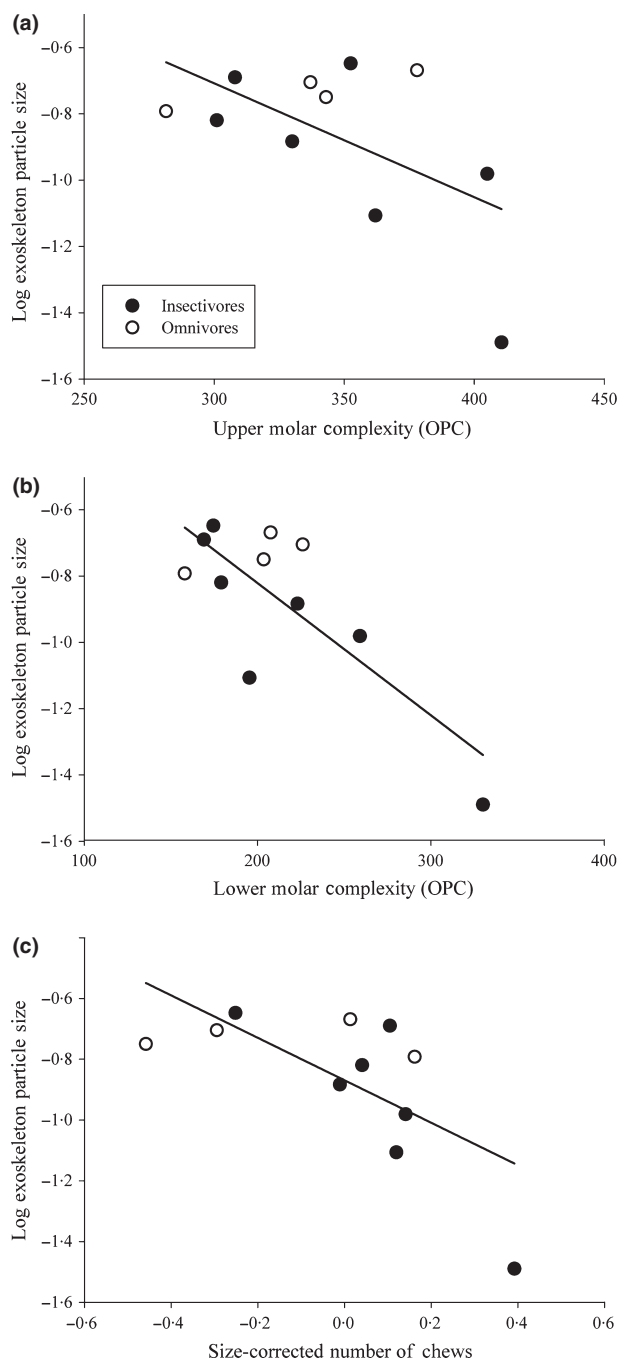
Fig. 4. The relationship between the complexity of the upper (a) and lower (b) molars, number of chews (c) and exoskeleton particle size in faecal pellets from insectivorous and omnivorous phyllostomids.

other mammals. Further comparative studies are necessary to evaluate this possibility.

IMPLICATIONS OF MOLAR COMPLEXITY AND CHEWING BEHAVIOUR ON INSECT BREAKDOWN

Intra- and interspecific variation in morphology can be related to differences in ecology only when it results in differences in performance (Arnold 1983). This study is the first to examine the functional significance of dental complexity, by

testing measures of performance on animals in the wild that were fed prey items naturally included in their diet. We found support for the prediction that an increase in the complexity of the shearing molars results in higher performance, i.e. finer breakdown of insect cuticle. As noted previously, shearing crests are the most effective shape for breaking down insects, and thus it is not surprising that molars with additional cutting edges, function better in breaking down insect prey (Evans & Sanson 1998). Ecological evidence suggests that cranial morphology and sensory ecology may play important roles in resource partitioning among insectivorous bats (Kingston *et al.* 2000; Aguirre *et al.* 2002; Siemers & Swift 2006). In addition to these factors, our results highlight the possibility that molar structure could contribute to reducing dietary overlap among insect-eating species at a finer scale.

The role of behaviour in modulating performance has been highlighted in several recent studies of feeding in vertebrates (Schulte *et al.* 2004; Wilga, Motta & Sanford 2007; Santana & Dumont 2009). Although tooth complexity is a good predictor of the ability for insectivorous and omnivorous phyllostomids to comminute insects, we also found strong support for the prediction that chewing behaviour is associated with particle size. Independent of body size and tooth complexity, bats that chew more were better able to break apart insects, an action that would contribute to digestion of the insect's internal tissues and thin chitinous parts (Jeuniaux 1961; Cornelius, Dandrifosse & Jeuniaux 1976; Whitaker, Dannelly & Prentice 2004; Kay & Sheine 2005; Moore & Sanson 2009). Ultimately, behavioural differences of this nature could have implications for reducing interspecific competition for resources, as behaviours could fine-tune the function of teeth to the diversity of the physical properties of prey.

POTENTIAL TRADE-OFFS ASSOCIATED WITH OMNIVOROUS DIETS

Many studies examining omnivorous vertebrates describe them as opportunistic herbivores with a generalized morphology that lacks obvious adaptations to partially herbivorous diets (e.g. Van Damme 1999; Cooper & Vitt 2002; Sacco & Van Valkenburgh 2004). Although omnivorous phyllostomids are capable of consuming fruit, their generalized diet might be associated with functional trade-offs that may result in a decreased feeding performance when compared with specialized insectivores and frugivores. If this is the case, then we would expect molar structure to show a generalized morphology (or 'compromise phenotype', Huey & Hertz 1984) that would not converge on neither of the extremes observed in insectivorous and frugivorous species. In the omnivorous phyllostomids examined here, we found no trend towards elevated dental complexity as seen in frugivores. In fact, the molars of the most omnivorous species in the data set, *Phyllostomus hastatus*, are strongly dilambdodont and more similar to the molars of insectivores than to those of frugivores (Freeman 1984; Santos *et al.* 2003). It is possible then that the shearing teeth and high bite forces generated by these bats (Aguirre *et al.* 2002; Santana, Dumont & Davis 2010) could

act together to effectively cut most food items including large fruits, insects, and vertebrate prey. This could reduce the pressure for phenotypic specialization and explain the lack of increased molar complexity. However, whether and how tooth shape restricts the fruit resources that omnivores are able to consume cannot be fully determined until more detailed information on their diet is available. Other dental traits not measured here could also help elucidate whether omnivory is reflected in dental morphology among phyllostomids. In particular, the surface areas allocated to different teeth could be related to the variety of food items these bats consume (Freeman 1988, 1998).

Previous studies suggest that generalists tend to exhibit lower performance in comparison to specialists feeding on the same foods (e.g. Roslin & Salminen 2008). This might provide further support for the presence of trade-offs in omnivores. Omnivorous phyllostomids tend to generate larger exoskeleton particles than insectivores, although more data on other prey types are necessary to confirm this observation. Lower performance however, would not necessarily imply negative consequences. For these bats, being a 'Jack of all diets, master of none' could buffer them from experiencing negative impacts of changing environmental conditions because they are less likely to depend on a specific resource that may become limiting (Eisenberg & Harris 1984; Laurance 1991).

Concluding remarks

The dietary radiation of phyllostomids is unprecedented across mammals and presents a unique system within which to investigate functional correlates of dental structure. By integrating morphological, performance and behavioural data, this study describes how 3D molar structure may be related to the mechanical demands imposed by different diets. We illustrate a trend from relative simplicity of the shearing molars in insectivores and omnivores to high complexity of the crushing molars in frugivores. Our study highlights the functional significance of tooth structure and chewing behaviour in breaking down natural prey and provides the basis for future studies relating 3D tooth structure with feeding performance, niche partitioning, and dietary radiations of mammals.

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