Evolutionary Ecology Research, 2005, **7**: 453–478

Correspondence between tooth shape and dietary biomechanical properties in insectivorous microchiropterans

Alistair R. Evans* and Gordon D. Sanson

School of Biological Sciences, Monash University, Clayton Campus, Victoria 3800, Australia

ABSTRACT

Question: Do the biomechanical properties of the diet influence the tooth shape of insectivores? We examined dietary 'intractability', the extent to which structural strength, toughness and stiffness of a food are increased, roughly equivalent to 'hardness'.

Hypotheses: The following three factors may cause discrepancies in tooth form in animals with different diets: (1) optional functional form; (2) risk of tooth fracture; and (3) amount of wear.

Data studied: Functional parameters of molar shape based on engineering principles for three intractable- and three tractable-feeding microbats.

Conclusions: There were no consistent differences in the functional parameters with diet. However, discrepancies within families indicated that the effectiveness of teeth of intractable feeders tended to be lower. The differences found arguably relate more to the risk of tooth fracture and increased wear. It appears that increased structural strength is the main difference in intractable diets, requiring greater robustness of the teeth, which reduces the functional efficacy.

Keywords: dietary properties, functional dental morphology, hardness, insectivory, shear ratio, teeth.

INTRODUCTION

The nutritional ecology of an animal is a vital component of its interaction with the environment, including its ability to acquire and process food. Dental and masticatory adaptations to specific food sources are particularly significant (Turnbull, 1970; Lucas, 1979). To directly explain the evolution of these adaptations, we must be able to define them in biomechanical terms. The current study examines the guild of insectivores. Until recently, workers tended to treat mammalian insectivores as a homogeneous group with respect to dietary habits, but more modern investigations have largely repudiated this misconception. We can consider there to be two aspects to this dietary heterogeneity.

---

* Address all correspondence to Alistair R. Evans, Institute of Biotechnology, University of Helsinki, PO Box 56 (Viikinkaari 9), FIN-00014 Helsinki, Finland. e-mail: arevans@fastmail.fm

First, insectivores do not feed randomly on the invertebrate community available to them. Many species of insectivores consume invertebrates in different proportions to their measured frequency in the habitat (e.g. Buchler, 1976; Anthony and Kunz, 1977; Swift and Racey, 1983; Brigham and Saunders, 1990; Fenton *et al.*, 1998b; Pavey and Burwell, 1998; Menzel *et al.*, 2000) or appear to specialize on particular invertebrates, including beetles, moths and spiders [the diet of an 'insectivore' here includes any invertebrates, including spiders and earthworms (Ross, 1967; Black, 1972, 1974; Whitaker and Black, 1976; Vaughan, 1977; Warner, 1985; Schulz, 2000); but see Arlettaz and Perrin (1995), Fenton (1995) and Findley (1993) for arguments against selectivity and competition in bats; and see Kunz (1988) regarding difficulties in insect sampling].

Second, the animals eaten by insectivores are diverse in their biomechanical properties. Substantial variability exists both among the components within a single invertebrate and among different types of invertebrates in terms of the material properties of strength, toughness, stiffness and 'hardness' (Evans and Sanson, 2005). Previous studies that have investigated the feeding adaptations of insectivores have most often used 'hardness' as a criterion for differentiation of the diet (Freeman, 1979, 1981a, 2000; Strait, 1993c; Dumont, 1995). However, because of the difficulty in defining and measuring 'hardness' in insects, we advocate the use of 'intractability', which is the extent to which the structural properties of structural strength, toughness and stiffness are increased (Evans and Sanson, 2005). Using punch tests, in which a metal punch is driven through insect cuticle and the force and energy required are measured, Evans and Sanson (2005) found that the punch strength and work to punch are higher in intractable invertebrates than tractable ones.

We presume that both of these aspects of heterogeneity, the diversity of invertebrates eaten by insectivores and the diversity of biomechanical properties of the invertebrates, contribute to the morphological differences between insectivores that specialize on prey with particular biomechanical properties. This follows from selection for anatomical features that can deal with the physical demands of acquiring and comminuting food. 'Hard' feeding in insectivores has been found to correlate with skull morphology [thick jaws, well-developed sagittal crests, higher condyles and coronoid processes, wide skull widths relative to skull length (Freeman, 1979, 1981a, 1984, 1988, 2000; Rodríguez-Durán *et al.*, 1993; Jacobs, 1996)], relative molar size [larger M^1 and M^2 but smaller M^3 (Freeman, 1979; Rodríguez-Durán *et al.*, 1993)], gross molar morphology [lower 'shear ratio' of lower molars (Strait, 1991, 1993c)], molar microwear [greater pitting on occlusal surfaces (Strait, 1993a)] and molar enamel thickness [thicker enamel (Dumont, 1995)] when compared with soft feeding. To a large extent, these epitomize differences found between other dietary groups that vary in 'hardness' (Jolly, 1970; Kinzey, 1974; Rosenberger and Kinzey, 1976; Andrews, 1981; Kay, 1981; Teaford, 1985; Grine, 1986; Ravosa, 2000). 'Hardness' in these studies most likely describes foods with high structural strength and stiffness – and perhaps toughness (Evans and Sanson, 2005) – but in most of them a specific definition for dietary hardness was not provided.

Although the use of crests is advantageous in fracturing tough foods due to the need to propagate cracks through them (Lucas and Luke, 1984), the precise form and arrangement of both the crest edge and the surrounding tooth surface will have an immense influence on the function and effectiveness of any crest. For the most part, previous studies have not attempted to examine or explain differences in such fine-scale molar morphology between these two guilds. This study will use engineering principles that relate the various aspects of insectivore molar shape to function to provide a sounder basis for relating tooth shape to function, as detailed in Evans (2003, in press) and Evans and Sanson (2003, in press). The functional parameters relate the shapes of cusps and crests to the force or energy required for penetration or forced crack propagation of tough foods.

A brief description of the parameters is as follows:

- *tip sharpness*: radius of curvature at the tip of a cusp;
- *cusp sharpness*: volume of a cusp to a given distance from the tip;
- *cusp occlusion relief*: space behind a point at which a cusp occludes;
- *edge sharpness*: radius of curvature of a crest;
- *rake angle*: angle of leading face of a crest to a line perpendicular to the direction of movement;
- *crest relief*: space behind the edge of a crest;
- *approach angle*: angle of the long axis of a crest to a line perpendicular to the direction of movement;
- *capture area*: area enclosed by a crest for capturing food;
- *fragment clearance*: the ability of a cusp–crest structure to direct food off the rake surface.

Figure 1a provides a schematic representation of the functional parameters.

The null hypothesis examined in this study is that there is no difference in tooth shape and function, as indicated by the functional dental parameters, between intractable and tractable insectivores. We present three main hypotheses to explain any difference between the intractable and tractable insectivores: (1) that the optimal functional form of the dentition for comminuting intractable and tractable insects differs, leading to selection for different functional shapes in the two groups; (2) that there is a substantial difference in the risk of fracture between insectivores eating intractable and tractable diets that has led to an increased robustness in the dentition of intractable feeders; and (3) that there is a substantial difference in the amount of wear that occurs in intractable and tractable insectivores that has selected for increased dental material to resist wear. These three hypotheses are not mutually exclusive and are elucidated in the Discussion.

We examined the relationships between tooth form and diet of invertebrates with varying biomechanical properties in intractable–tractable species pairs in three families of Microchiroptera. Differences between tooth forms indicate a functional and/or adaptive response to the biomechanical properties of foods (Lucas, 1979; Vinyard *et al.*, 2003). Convergence of species with comparable dietary specialization onto a similar dental form supports the contention that there is a functional relationship between the tooth form and diet (Ridley, 1983; Harvey and Pagel, 1991; Strait, 1993c; Dumont, 1995; Freeman, 2000).

METHODS

Study species

We examined three pairs of confamilial species [*Molossus ater* and *Nyctinomops macrotis* – Molossidae; *Eptesicus fuscus* and *Plecotus townsendii* – Vespertilionidae; *Hipposideros diadema* and *Rhinolophus blasii* – Rhinolophidae, following Simmons (1998) with regard to subfamily status of Rhinolophinae and Hipposiderinae]; each pair has a species with an intractable diet (defined as having a diet with a high proportion of beetles or other invertebrates with an intractable, highly sclerotized exoskeleton) and a tractable diet (low proportion of invertebrates with intractable exoskeletons and high proportion of tractable invertebrates, e.g. moths, caterpillars, earthworms). Table 1 shows the reported diets of the

Table 1. Diets of the intractable (I) and tractable (T) feeding species examined in this study

Family	Diet class	Diet	Reference
Molossidae			
Molossus ater	I	11.5% individuals Coleoptera; $n = 1$, D	Pine (1969)
		Coleoptera, Orthoptera, Hymenoptera; $n = 1$, F	Howell and Burch (1974)
		Mostly Coleoptera, few moth scales; $n = 4$, F	Freeman (1981b)
		37.5% occurrence Coleoptera; $n = 8$, D	Marques (1986)
		97.5% volume Coleoptera; $n = 2$, D	Bowles *et al.* (1990)
		74.0% volume Coleoptera; $n = 18$, F	Fenton *et al.* (1998c)
Nyctinomops macrotis	T	100% volume Lepidoptera; $n = 1$, D	Ross (1967)
		98% occurrence, 86.1% volume Lepidoptera; $n = 49$, D	Easterla and Whitaker (1972)
		100% volume Lepidoptera; $n = 4$, F	Freeman (1981b)
Vespertilionidae			
Eptesicus fuscus	I	36.1% fragments Coleoptera; $nf \approx 300$, C	Hamilton (1933)
		80% volume Coleoptera; $n = 10$, D	Phillips (1966)
		$\geq$25% occurrence Coleoptera; $n = 12$, D	Ross (1967)
		49.6% volume Coleoptera; $n = 184$, D	Whitaker (1972)
		84% occurrence Coleoptera; $n = 165$, F	Black (1974)
		34.4% volume Coleoptera; $n = 30$, D	Whitaker *et al.* (1977)
		72% occurrence Coleoptera; $n = 25$, D	Silva-Taboada (1979), cited in Rodríguez-Durán *et al.* (1993)

		52.6% volume Coleoptera; *n* = 60, D; 37.7% volume Coleoptera; *n* = 177, F	Whitaker *et al.* (1981)
		90.5% occurrence Coleoptera; *n* = 21, D, F	Griffith and Gates (1985)
		89% occurrence Coleoptera; *n* = 18, D, F	Warner (1985)
		5.0% individuals Coleoptera; *np* = 395, F	Brigham (1990)
		66.6% occurrence, 54.5% volume Coleoptera; *n* = 14, F	Brigham and Saunders (1990)
		100% occurrence Coleoptera; *n* = 3, F	Rodríguez-Durán *et al.* (1993)
		73.7% volume Coleoptera; *np* = 546, F; 57.9% volume Coleoptera; *np* = 1300, F	Whitaker (1995)
		100% occurrence, 78% volume Coleoptera; *n* = 3, F	Carter *et al.* (1998)
		57.0% volume Coleoptera; *n* = 181, F	Hamilton and Barclay (1998)
		17.7% volume Coleoptera; *np* = 75, F	Verts *et al.* (1999)
		81.0% volume Coleoptera; *np* = 120, F	Menzel *et al.* (2000)
Plecotus townsendii	T	92.1% occurrence Lepidoptera; *n* = 38, D, F	Ross (1967)
		100% occurrence, 99.7% volume Lepidoptera; *n* = 16, D	Whitaker *et al.* (1977)
		100% occurrence and volume Lepidoptera; *n* = 1, D	Whitaker *et al.* (1981)
		97.1% volume Lepidoptera; *np* = 1222, F	Dalton *et al.* (1986)
		95.6% volume, 100% occurrence Lepidoptera; *np* = 447, F; 90.9% fragments, C	Sample and Whitmore (1993)
Rhinolophidae			
Hipposideros diadema	I	≥58.3% occurrence Coleoptera; *n* = 12, D	Vestjens and Hall (1977)
		100% occurrence Coleoptera; *n* = 1, D	Nabhitabhata (1986)
		97.2% occurrence Coleoptera; *np* = 140; 37.7% prey remains	Pavey and Burwell (1997)
Rhinolophus blasii	T	100% occurrence and volume Lepidoptera (winter); *n* = 4, D; 100% occurrence, 96.5% volume Lepidoptera (summer); *n* = 30, D	Whitaker and Black (1976)

Note: % occurrence = proportion of samples containing insect; % volume = proportion of volume of insect in sample; % individuals = proportion of individual insects in sample; % fragments = proportion of culled fragments.

Abbreviations: D, digestive system contents; F, fecal analysis; C, culled fragments of prey (e.g. wings); *n*, number of individuals sampled; *np*, number of fecal pellets sampled; *nf*, number of culled fragments.

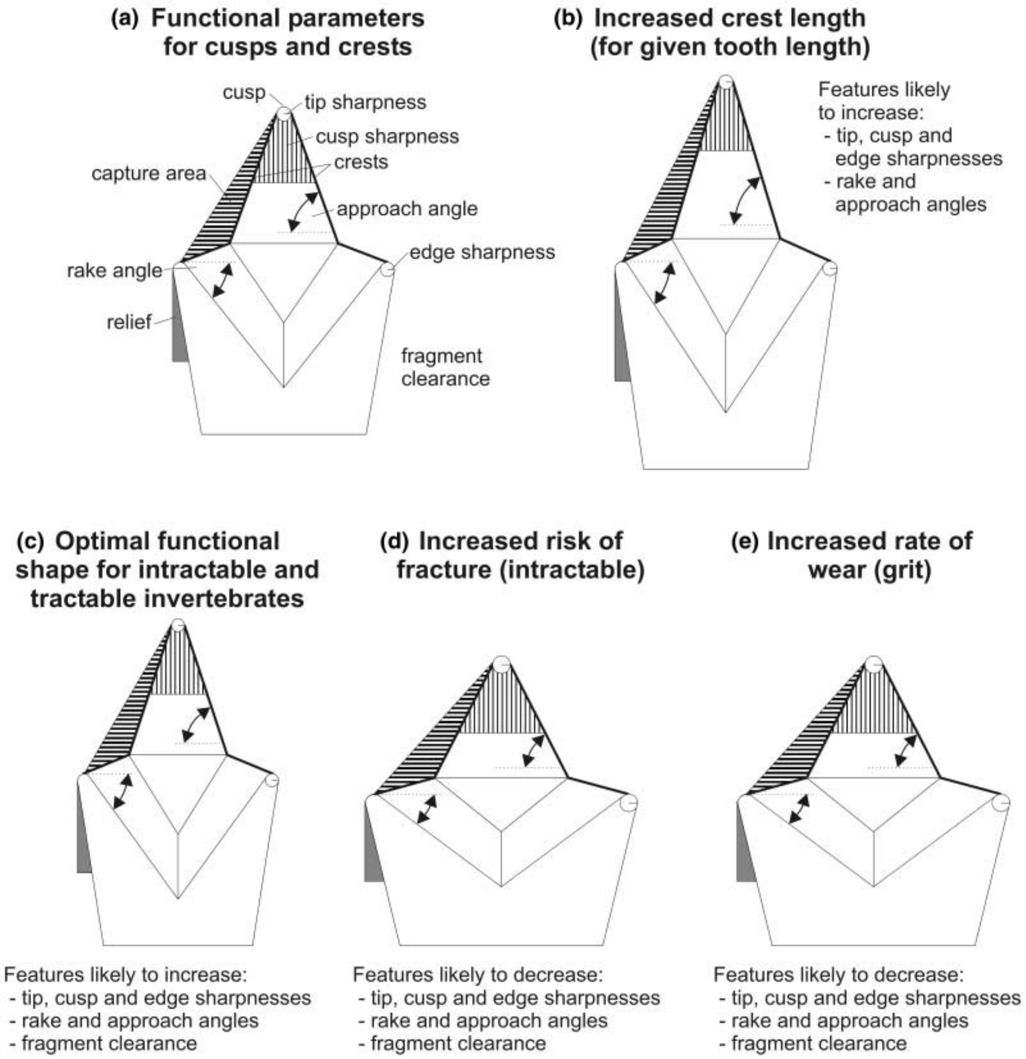

Fig. 1. (a) Eight functional parameters are depicted schematically for a cusp/crest structure, such as the paracone with pre- and postparacristae. (b) An increase in the length of the crest (for a given tooth basal area or tooth length) is likely to lead to increases in several of the functional parameters. (c)–(e) Comparison of the expected tooth shapes for the three hypotheses discussed in the text: the optimal tooth shape for comminuting intractable and tractable invertebrates (c); increased resistance to tooth fracture when feeding on intractable invertebrates (d); increased tooth wear for a diet with high levels of grit (e). Differences between the models and features such as tip and edge sharpnesses are exaggerated. The diagram does not purport to represent the exact method of measurement for the parameters.

six species. Intractable species may also consume a reasonable number of moths, and are usually considered more ‘generalist’ than tractable feeders (Freeman, 1981a, 1984; Warner, 1985; Strait, 1993c). We examined five specimens of each species, using only unworn or very lightly worn specimens, apart from three of the *H. diadema* specimens that were slightly more worn due to limited availability of unworn specimens.

The museum numbers of the examined specimens are as follows: *M. ater*: AMNH 92565, 92566, 92567, 92573, 92574; *N. macrotis*: AMNH 6740, 132773, 169546, 173661, 176096; *E. fuscus*: AMNH 139509, 258269, 258270, MVZ 99527, 112487; *P. townsendii*: AMNH 170802, 170803, 170806, MVZ 103873, 106001; *R. blasii*: AMNH 54413, 239591, 239592, MVZ 99994, 101000; *H. diadema*: AM 3497, 15201, 20077, 20090, 20102 (where AMNH = American Museum of Natural History, New York; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; and AM = Australian Museum, Sydney, NSW).

Functional parameters

The procedures for moulding, casting and confocal imaging of teeth and for the measurement of the nine functional parameters are in line with Evans *et al.* (2001) and Evans (in press). We took measurements from the upper second molar of five individuals of each of the six species. The following measurements were taken for the four ectoloph crests on the upper molar (pre- and postparacrista, pre- and postmetacrista): rake angle, crest relief (wear land area, relief volume and relief angle), approach angle and capture area (see Fig. 2 for

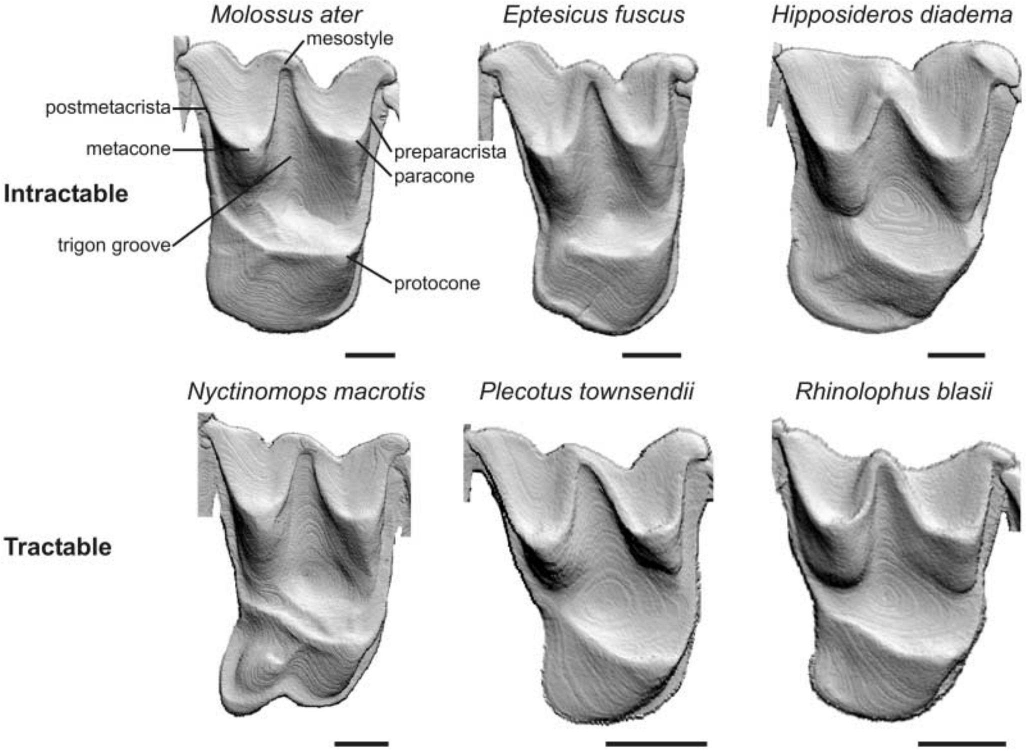

Fig. 2. Shaded relief reconstructions of upper second molars of six microchiropteran species. Some of the important features of the tooth are indicated on the *Molossus ater* molar. Scale bars = 500 μm.

the general features of the molars). We measured cusp sharpness for the paracone and metacone, fragment clearance for the paracone and metacone basins, and cusp occlusion relief for the mesostyle/trigon groove. We measured tip sharpness and edge sharpness for the metacone and postmetacrista respectively.

We measured tooth length as the distance from the anterior end of the preparacrista to the posterior point of the postmetacrista. SV3, or (skull volume)$^{1/3}$, was used as a measure of body size, where skull volume was estimated as (condylocanine length × occipital height × zygomatic breadth).

Cusp sharpness is a measure of the volume of a cusp to a given distance from its tip. Any measurement of cusp sharpness will vary greatly depending on the distance from the tip from which the volume is measured – that is, the cusp volume to the same absolute distance from the tip for large and small teeth of isometric shape will differ. However, if we scale the distance from the tip according to a measure of size, then we can avoid this problem. Therefore, we used three different methods for defining the distance from the tip in the calculation of cusp sharpness, with a smaller and larger value for each method: constant distance from cusp tip (100 and 400 μm); fraction of the tooth length (3/50 and 1/5 × tooth length); and multiple of SV3 (10 and 30 × SV3). Other measurements that used a constant (such as 100 μm along rake surface for rake angle) varied much less than cusp volume if the distance over which the parameter was measured was scaled with size. We measured tip and edge sharpnesses for constant tooth area (400 μm^2) and crest length (100 μm) respectively.

Statistical methods and size correction

We tested for differences between intractable and tractable feeders in each family for the quantitative features using Mann-Whitney *U*-tests in Systat for Windows Version 10.0 (SPSS, Inc.) using raw values of rake and approach angles, and for other quantitative measures divided by SV3 or tooth length (tip, cusp and edge sharpnesses, capture area and cusp occlusion relief). Qualitative features (relief wear land, volume and angle, and fragment clearance) were tested with Fisher's exact tests using SPSS for Windows Version 10.0 (SPSS, Inc.). The statistical significance for all tests was set at $P = 0.05$.

Recently, there have been debates in the literature as to the best practice for size correction when examining hypotheses correlating morphological features with particular feeding behaviours (e.g. Dumont, 1997; Vinyard *et al.*, 2003). Dumont (1997) advocated using the geometric mean of all variables to standardize for size, but Vinyard *et al.* (2003) defended the use of ratios with a biomechanically relevant dimension such as jaw length rather than geometric mean techniques. Their opposing methods led to conflicting conclusions regarding morphological adaptations for nectar feeding by gouging. Comparing 11 statistical techniques for size-adjustment, Jungers *et al.* (1995) found that the only measures that correctly grouped geometrically identical animals together were members of the Mosimann family of shape ratios, which make use of the geometric mean (Mosimann, 1970; Mosimann and James, 1979). However, we are not sure of the applicability of these methods when using a mixed data set (linear, area, volume and angular measurements, and qualitative data). Therefore, we decided to use principal components analysis on the logged data.

We carried out principal components analyses (PCAs) using Systat. Volume (mm^3) and area (mm^2) measures were reduced to linear measures by cube and square root respectively, and then all quantitative values were logged. We undertook analyses for functional parameters relating to the following three groups of variables: (1) the entire data set (including SV3 and tooth length, which were included in all analyses, and the three methods for calculating cusp sharpness); (2) all parameters, except for cusp sharpness, using only the cusp sharpness measurements based on SV3 (i.e. excluding the constant and tooth length measurements); (3) all parameters, except for cusp sharpness, using only the cusp sharpness measurements based on tooth length (i.e. excluding the constant and SV3 measurements). Relief angle and wear land were omitted from the principal components analyses when there was no variation in these parameters among species.

RESULTS

Figure 2 shows the gross molar morphology for the six species. The measurements for the nine functional parameters are given in Tables 2–4. There were no consistent differences in the tooth functional parameters between intractable and tractable feeders within families (Table 5). We found no significant difference within families for tip and edge sharpnesses (divided by either SV3 or tooth length) or any of the qualitative variables (relief parameters and fragment clearance). The molossid and rhinolophid intractable feeders tended to have larger rake angles than the tractable feeders, but this was not the case for the vespertilionids. In addition, there were significant differences within the vespertilionids and rhinolophids for most measures of cusp sharpness, but not within the molossids. Approach angle, cusp occlusion relief and capture area were significantly different in only some of the intra-familial comparisons. The low number of families prevents us from using a sign test, as was done by Dumont (1995), although for all measurements of rake angle, the species mean of the tractable feeder was higher than that of the intractable feeder.

The three PCA plots all showed very similar distribution of the species, so only the plot including all variables will be discussed (Fig. 3). Factor 1 correlated with cusp sharpness measurements based on SV3 and tooth length ($r = 0.963$ to 0.981), tooth length (0.953), SV3 (0.948), constant cusp sharpness (0.876 to 0.913), rake angles (preparacrista −0.832; postmetacrista −0.721), capture areas (0.676 to 0.813) and fragment clearance (−0.724). Factor 1 separated the intractable and tractable feeders – this may be largely due to body size differences, as some of these variables represent size (SV3 and tooth length), and so we may consider it to be a size factor. Factor 2 in general separated the intractable and tractable feeders within each family; however, the molossid and vespertilionid intractable feeders generally had lower Factor 2 scores, but the rhinolophid intractable feeder (*Hipposideros diadema*) had a higher Factor 2 score than the tractable feeder (*Rhinolophus blasii*). Approach angles were the only parameters highly correlated with Factor 2 ($r = -0.765$ to −0.905). Factors 1 and 2 explained 52.99% and 15.31% of the variance respectively.

DISCUSSION

Three hypotheses

We postulated three possible reasons for any differences found between the tooth form of the intractable and tractable insectivores. The first hypothesis is that the optimal functional form may differ for an intractable and tractable invertebrate diet. Where there are extensive differences in the biomechanical properties of foods, the optimal tools to divide them are predicted to differ dramatically (Osborn and Lumsden, 1978; Lucas, 1979; Lucas and Luke, 1984). The diversity of biomechanical properties among invertebrates is low compared with the vast

Table 2. Functional parameters relating to cusps (mean ± standard error) for paracone and metacone for six species of intractable and tractable feeding bats

		Species					
	Cusp	*M. ater*	*N. macrotis*	*E. fuscus*	*P. townsendii*	*H. diadema*	*R. blasii*
Tooth length (μm)		1938.88 ± 12.44	1751.07 ± 6.77	1511.20 ± 15.65	1091.89 ± 4.82	2139.33 ± 29.87	1228.60 ± 8.84
SV3 (μm)		13.18 ± 0.03	12.34 ± 0.07	10.90 ± 0.07	8.95 ± 0.04	14.36 ± 0.26	9.68 ± 0.03
Tip sharpness (μm)	me	40.08 ± 2.72	33.36 ± 1.70	24.97 ± 1.15	16.56 ± 0.34	26.50 ± 1.56	15.89 ± 0.49
Cusp sharpness to 100 μm	pa	1420.53 ± 54.50	1313.58 ± 53.33	1559.52 ± 76.09	750.04 ± 14.94	1629.04 ± 67.63	853.09 ± 18.19
(10^3 μm^3)	me	1312.44 ± 57.02	1259.88 ± 78.04	1474.96 ± 87.04	620.21 ± 25.38	1682.09 ± 50.57	811.96 ± 13.67
Cusp sharpness to 400 μm	pa	27.84 ± 1.18	21.11 ± 0.62	28.43 ± 1.41	12.09 ± 0.41	39.43 ± 1.25	15.46 ± 0.56
(10^6 μm^3)	me	24.62 ± 0.63	19.64 ± 0.63	24.66 ± 1.09	9.77 ± 0.34	39.13 ± 0.93	14.64 ± 0.45
Cusp sharpness to 3/50 tl	pa	1965.10 ± 93.26	1453.92 ± 65.04	1297.30 ± 81.80	329.26 ± 7.76	2946.64 ± 160.95	459.25 ± 13.85
(10^3 μm^3)	me	1849.73 ± 91.08	1395.91 ± 85.84	1224.57 ± 85.23	257.11 ± 13.14	3017.75 ± 134.61	434.99 ± 12.33
Cusp sharpness to 1/5 tl	pa	26.04 ± 1.28	16.03 ± 0.51	15.45 ± 0.89	3.33 ± 0.07	47.10 ± 2.27	5.20 ± 0.19
(10^6 μm^3)	me	23.19 ± 0.82	15.17 ± 0.52	13.97 ± 0.76	2.86 ± 0.10	46.05 ± 1.82	4.97 ± 0.14
Cusp sharpness to 10 × SV3	pa	2540.36 ± 88.36	2025.11 ± 100.52	1879.50 ± 107.48	607.77 ± 14.50	3899.63 ± 291.02	800.63 ± 21.20
(10^3 μm^3)	me	2420.71 ± 76.46	1950.81 ± 122.25	1759.12 ± 102.38	495.63 ± 23.33	3992.06 ± 267.15	760.94 ± 16.27
Cusp sharpness to 30 × SV3	pa	27.07 ± 1.07	18.06 ± 0.71	18.18 ± 0.94	5.07 ± 0.16	48.93 ± 3.35	7.40 ± 0.28
(10^6 μm^3)	me	24.02 ± 0.55	16.96 ± 0.67	16.28 ± 0.74	4.33 ± 0.16	47.46 ± 2.79	7.14 ± 0.23

Note: $n = 5$ for all species (except for tip sharpness measurements of *M. ater* and *N. macrotis*, where $n = 4$).
Abbreviations: me, metacone; pa, paracone; tl, tooth length.

range of all mammalian diets (including bone, meat, skin, grass, leaves, stems, fruit, nectar and blood), but still contains considerable variety. Evans and Sanson (2005) concluded that the cuticle of intractable insects is structurally tougher than that of tractable insects. However, both types require reasonable amounts of energy to fracture, either because of crack-stopping mechanisms in the stiff cuticle so that there is very little brittle fracture, or because of their ductility. A significant commonality of both types is that their internal organs are generally ductile and relatively tough. In addition, the complex structural nature of an invertebrate means that multiple initiations of fracture are required to divide it completely – cracks do not self-propagate through the whole animal. Therefore, both intractable and tractable types of invertebrates will require cusps to initiate crack propagation and crests to force the propagation of cracks through the entire animal, and we argue that dealing with toughness is probably the principal objective of insectivore teeth. A mortar and pestle would not efficiently divide invertebrates, as it would require large amounts of force. Such excess force may be available to large-bodied animals that eat insects but not to small insectivores.

Intractable and tractable insects are substantially different in the structural strength and stiffness of the cuticle (Evans and Sanson, 2005). In terms of tooth function, this will probably only be relevant to tip and edge sharpnesses. If strength were increased, it would be further advantageous to increase tip and edge sharpnesses to enhance the stress induced in the food. However, Lucas (1982) argued that if stiffness were also increased, the area of contact between tooth and food would not be greatly increased, maintaining higher stress in the food. This does not negate the inference that tip sharpness should still be as high as possible (demonstrated by applications such as emergency hammers with extremely sharp points for breaking glass in the case of an accident), only that the risk of fracture may be increased (which is dealt with in the next hypothesis). An increase in stiffness may affect the ease with which concave crests capture food, but it is difficult to predict whether this would encourage a larger or smaller capture area.

Therefore, for both foods, the optimal cusp will have low tip and cusp sharpnesses, which will minimize the force and energy required to penetrate and drive through the food (Fig. 1c), as demonstrated for both intractable and tractable invertebrates (Evans and Sanson, 1998). There should be relief behind points of cusp occlusion. For crests, edge sharpness, rake and approach angles and fragment clearance should be maximized, and crest relief and capture should be present (Fig. 1c). Therefore, we expect no substantial difference in the optimal shapes for comminuting both intractable and tractable insects, which would not lead to any difference in dental form. Note that the result of this analysis would differ if the hard food was also significantly brittle for a large proportion of the food, where a mortar and pestle arrangement would be advantageous (Lucas and Luke, 1984).

Our prediction for similar optimal tooth shapes for intractable and tractable insectivores differs from that of Strait (1993c). Strait predicted that the optimal tooth shape for 'hard' eaters will have short crests to minimize the area of contact between the crest and food. She also reasoned that 'soft' feeders could manage with longer crests because a 'soft' diet is weaker, and critical fracture stress could still be achieved with a higher contact area. However, crests are not oriented parallel to the food (Evans and Sanson, 1998); in fact, longer crests (for a given basal area and tooth length) require an increase in the height of the cusp and will tend to give higher tip, cusp and edge sharpnesses and larger approach and rake angles (Fig. 1b). Feeding on both intractable and tractable foods would select for these functional features, which may be particularly important for tractable feeders, where the

Table 3. Functional parameters relating to upper molar ectoloph crests [mean ± standard error, or median (minimum, maximum) for qualitative data] for six species of intractable and tractable feeding bats

		Species					
	Crest	*M. ater*	*N. macrotis*	*E. fuscus*	*P. townsendii*	*H. diadema*	*R. blasii*
Edge sharpness (μm)	pomec	19.45 ± 1.2	12.35 ± 0.71	15.63 ± 0.89	9.61 ± 0.79	13.52 ± 1.28	16.11 ± 1.44
Rake angle (°)	prpac	−7.35 ± 0.46	11.56 ± 2.43	18.02 ± 3.99	37.65 ± 1.23	8.69 ± 4.58	40.21 ± 0.89
	popac	−7.00 ± 1.24	11.62 ± 1.20	8.73 ± 3.04	22.25 ± 0.57	23.25 ± 3.97	30.69 ± 3.19
	prmec	−1.03 ± 1.26	15.24 ± 1.80	13.78 ± 2.96	25.61 ± 1.66	15.92 ± 2.70	35.45 ± 2.86
	pomec	−11.20 ± 1.64	8.07 ± 2.58	10.36 ± 3.57	23.59 ± 3.19	9.55 ± 2.28	40.94 ± 1.31
Relief – wear land (qual)	prpac	2 (1, 2)	1 (1, 1)	2 (1, 2)	1 (1, 1)	1 (1, 1)	1 (1, 1)
	popac	1 (1, 2)	1 (1, 1)	1 (1, 3)	1 (1, 1)	1 (1, 1)	1 (1, 1)
	prmec	1 (1, 1)	1 (1, 1)	1 (1, 2)	1 (1, 1)	1 (1, 1)	1 (1, 1)
	pomec	1 (1, 1)	1 (1, 2)	1 (1, 1)	1 (1, 1)	1 (1, 1)	1 (1, 1)
Relief – volume behind crest (qual)	prpac	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)
	popac	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)
	prmec	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)
	pomec	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)	3 (3, 3)
Relief – angle (qual)	prpac	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)
	popac	2 (2, 2)	2 (2, 2)	2 (1, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)
	prmec	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)
	pomec	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)	2 (2, 2)

Approach angle (°)	prpac	39.12 ± 0.65	32.47 ± 0.92	41.49 ± 0.74	33.27 ± 0.34	26.70 ± 0.47	25.20 ± 1.04
	popac	37.02 ± 0.67	37.29 ± 0.51	42.27 ± 0.52	41.52 ± 0.35	30.11 ± 0.44	36.67 ± 0.37
	prmec	36.23 ± 0.66	27.55 ± 0.47	35.96 ± 0.68	30.35 ± 0.59	24.35 ± 0.47	29.81 ± 0.78
	pomec	36.30 ± 0.63	32.14 ± 0.35	37.03 ± 0.91	37.21 ± 0.68	25.30 ± 0.77	26.86 ± 0.64
Capture area (10^3 μm^2)	prpac	43.15 ± 1.58	67.22 ± 3.75	43.05 ± 1.79	23.41 ± 0.80	61.67 ± 2.66	20.84 ± 1.65
	popac	134.38 ± 5.13	136.06 ± 4.45	93.19 ± 3.88	50.37 ± 1.45	134.50 ± 5.86	83.77 ± 2.13
	prmec	68.01 ± 2.68	74.16 ± 2.02	57.73 ± 2.96	32.66 ± 1.77	47.02 ± 1.97	30.48 ± 1.13
	pomec	105.04 ± 4.69	99.04 ± 1.00	91.24 ± 4.51	60.44 ± 0.99	115.55 ± 5.63	64.02 ± 2.23

Note: $n = 5$ for all species. Crests: prpac, preparacrista; popac, postparacrista; prmec, premetacrista; pomec, postmetacrista. Wear land: 1, small wear land; 2, moderate; 3, large. Volume of space behind crest: 1, small volume; 2, moderate; 3, large. Relief angle: 1, 0° relief angle; 2, small relief angle; 3, large relief angle.

Table 4. Cusp occlusion relief (mean ± standard error) and fragment clearance (median, with minimum and maximum in parentheses) for paracone and metacone basins and trigon groove for six intractable and tractable feeding species

		Species					
	Feature	*M. ater*	*N. macrotis*	*E. fuscus*	*P. townsendii*	*H. diadema*	*R. blasii*
Cusp occlusion relief (μm)	mesost	108.29 ± 2.39	76.88 ± 4.19	164.92 ± 4.26	47.54 ± 3.63	87.18 ± 14.19	71.76 ± 3.17
Fragment clearance (qual)	paba	2 (2, 2)	2 (2, 2)	2 (2, 3)	3 (3, 3)	3 (2, 3)	3 (3, 3)
	meba	2 (2, 2)	2 (2, 2)	2 (2, 3)	3 (3, 3)	3 (2, 3)	3 (3, 3)

Note: n = 5 for all species.
Abbreviations: mesost, mesostyle; paba, paracone basin; meba, metacone basin.

Table 5. Results of statistical comparisons of functional parameters within three microchiropteran families given as *P*-values

		Family		
	Feature	Molossidae	Vespertilionidae	Rhinolophidae
(a) Angles				
Rake angle	prpac	0.016 *	0.117 NS	0.028 *
	popac	0.009 **	0.175 NS	0.917 NS
	prmec	0.028 *	0.076 NS	0.028 *
	pomec	0.028 *	0.175 NS	0.009 **
Approach angle	prpac	0.028 *	0.009 **	0.465 NS
	popac	0.917 NS	0.917 NS	0.009 **
	prmec	0.009 **	0.009 **	0.076 NS
	pomec	0.028 *	0.917 NS	0.917 NS
(b) Divided by SV3				
Tip sharpness	me	0.248 NS	0.175 NS	0.602 NS
Cusp sharpness to 10 × SV3	pa	0.602 NS	0.028 *	0.009 **
	me	0.754 NS	0.009 **	0.009 **
Cusp sharpness to 30 × SV3	pa	0.117 NS	0.009 **	0.009 **
	me	0.251 NS	0.009 **	0.009 **
Cusp occlusion relief	mesost	0.028 *	0.009 **	0.347 NS
Edge sharpness	pomec	0.076 NS	0.175 NS	0.117 NS
Capture area	prpac	0.009 **	0.117 NS	0.347 NS
	popac	0.251 NS	0.117 NS	0.028 *
	prmec	0.117 NS	0.251 NS	0.028 *
	pomec	0.465 NS	0.917 NS	0.175 NS
(c) Divided by tooth length				
Tip sharpness	me	0.248 NS	0.465 NS	0.917 NS
Cusp sharpness to 3/50 tl	pa	0.917 NS	0.047 *	0.117 NS
	me	0.917 NS	0.016 *	0.047 *
Cusp sharpness to 1/5 tl	pa	0.175 NS	0.016 *	0.009 **
	me	0.465 NS	0.009 **	0.009 **
Cusp occlusion relief	mesost	0.175 NS	0.009 **	0.175 NS
Edge sharpness	pomec	0.117 NS	0.465 NS	0.076 NS
Capture area	prpac	0.175 NS	0.754 NS	0.009 **
	popac	0.009 **	0.602 NS	0.754 NS
	prmec	0.009 **	0.465 NS	0.009 **
	pomec	0.602 NS	0.047 *	0.016 *
(d) Qualitative data				
Relief – wear land	prpac	1.000 NS	0.444 NS	1.000 NS
	popac	1.000 NS	1.000 NS	1.000 NS
	prmec	1.000 NS	1.000 NS	1.000 NS
	pomec	1.000 NS	1.000 NS	1.000 NS

Table 5.—*continued*

		Family		
	Feature	Molossidae	Vespertilionidae	Rhinolophidae
Relief – volume behind crest	prpac	1.000 NS	1.000 NS	1.000 NS
	popac	1.000 NS	1.000 NS	1.000 NS
	prmec	1.000 NS	1.000 NS	1.000 NS
	pomec	1.000 NS	1.000 NS	1.000 NS
Relief – angle	prpac	1.000 NS	1.000 NS	1.000 NS
	popac	1.000 NS	1.000 NS	1.000 NS
	prmec	0.167 NS	0.167 NS	1.000 NS
	pomec	1.000 NS	1.000 NS	1.000 NS
Fragment clearance	paba	1.000 NS	0.167 NS	0.444 NS
	meba	1.000 NS	0.167 NS	0.444 NS

Note: (a) angle data; (b) parameters divided by SV3; (c) parameters divided by tooth length (tl). (a)–(c) Mann-Whitney *U*-test; (d) Fisher's exact test. Abbreviations as in Tables 2–4. Significance: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$; NS, not significant.

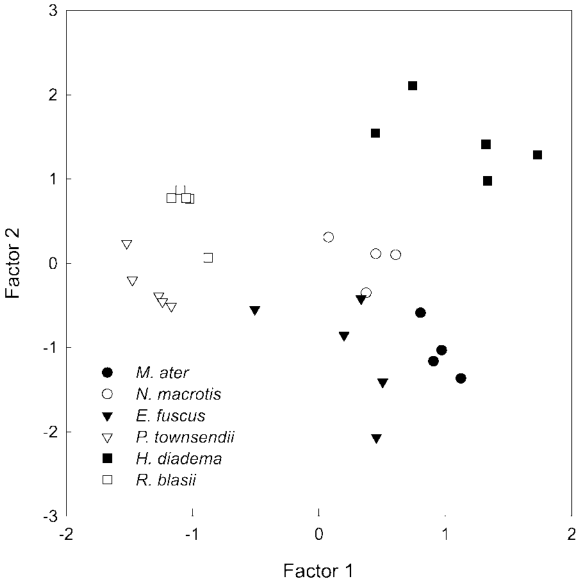

Fig. 3. PCA (Factor 1 *vs* Factor 2) plot for all functional parameters for three intractable (solid symbols) and three tractable (open symbols) feeding species of microchiropterans. Circles, molossids; triangles, vespertilionids; squares, rhinolophids.

high ductility of the food makes penetration and cutting difficult. The presence of other constraints, particularly on the intractable feeder tooth form, is likely to be responsible for any reduction in these parameters and so for a less effective tooth.

The second hypothesis is that the greater force required to fracture intractable insects increases the risk of tooth fracture. The greater structural strength of intractable foods would require greater bite forces in intractable feeders. Stress in the tooth could be reduced by increasing the structural integrity and robustness of the dental components. A decrease in the height and/or an increase in the width or length of the tooth or individual cusps would achieve this. In terms of functional parameters, this would most likely lead to decreased tip, edge and cusp sharpnesses, and smaller rake and approach angles (Fig. 1d). Capture area and fragment clearance may be reduced. Cusp occlusion relief and crest relief may be diminished, as these features would tend to reduce tooth strength, but perhaps only marginally. Selection for increased resistance to higher bite forces is likely to result in differences in enamel thickness, which is greater in intractable feeders than congeners (e.g. Dumont, 1995), and in enamel structure (e.g. Koenigswald *et al.*, 1987).

Bats are reasonably likely to incur tooth fracture and loss during their lifetime [7.7% of individuals have at least one broken tooth, 19.9% at least one missing or broken tooth (Fenton *et al.*, 1998a)]. Extreme differences in the strength and hardness of the diet can have an effect on the risk of fracture, as was found between bone-feeding and meat-feeding carnivores (Van Valkenburgh, 1988). In the case of intractable and tractable insectivores, the increased risk may be very slight, or easily overcome by an increase (possibly only minor) in sturdiness. However, it is unlikely to be great enough to cause a significantly higher rate of tooth fracture, given the lack of significant effect of differences in broad dietary categories among bats (animal, blood, fruit and nectar) on tooth fracture. This differs from the situation in large carnivores, which appear to have reached a structural limit in strengthening the canines (Van Valkenburgh, 1988).

The third hypothesis posits that differences in tooth form may result from differential wear from intractable and tractable diets. It has apparently been assumed that the hard exoskeleton of beetles is more likely to cause wear than the softer exoskeleton of other invertebrates, such as moths, larvae and the like (Strait, 1993c). 'Hardness' can be defined as the ability of one material to scratch or penetrate another (Lowrison, 1974; Evans and Sanson, 2005). Hardness values for invertebrate skeletons are substantially below those of enamel and dentine. This is supported by some comparative values for hardness from Vickers (V), microvickers (mv) and Knoops (K) tests, the results of which are not directly comparable (Lowrison, 1974) – invertebrates: tibia 8.3 $\text{kg}\cdot\text{mm}^{-2}$, abdominal tergite 23.9 $\text{kg}\cdot\text{mm}^{-2}$, mandible 36.4 $\text{kg}\cdot\text{mm}^{-2}$ [V (Hillerton *et al.*, 1982)]; leaf-cutting ant 52.1 $\text{kg}\cdot\text{mm}^{-2}$ [V (Edwards *et al.*, 1993)] and ~100 $\text{kg}\cdot\text{mm}^{-2}$ [microindentation and atomic force spectroscopy (Schofield *et al.*, 2002)]; teeth: human dentine and enamel 74 and 393 $\text{kg}\cdot\text{mm}^{-2}$ respectively [K (Waters, 1980)]; macropodine enamel 270–379 $\text{kg}\cdot\text{mm}^{-2}$ [mv (Palamara *et al.*, 1984)]; koala dentine and enamel 122 and 410 $\text{kg}\cdot\text{mm}^{-2}$ respectively [K (Young *et al.*, 1990)]. It would thus appear unlikely that the increase in hardness from tractable to intractable invertebrates would greatly increase wear, even though softer materials can cause wear given sufficient force (Bayer, 1994; Puech *et al.*, 1981).

A more likely cause of wear in insectivores is siliceous grit, which may be on the outer surface of the invertebrate or in its gut. We can consider several factors that would influence the amount of grit: the habitat (terrestrial or aerial) and diet of the invertebrate, and the intractability of the cuticle. An invertebrate that lives in soil (e.g. burrowing beetle or cricket) will have more dirt in and on its body than one that lives its life in the air, only occasionally alighting on a surface (e.g. moth or trichopteran). A herbivore or detritivore (e.g. beetle or earthworm) may also ingest large amounts of soil, or phytoliths from plant leaves, that firstly wear the beetle's mandibles, and when ingested and masticated by a bat, subsequently wear the bat's teeth. This contrasts with the non-abrasive diet of a fluid feeder (e.g. moth). The intractability of the exoskeleton is also likely to be influential: a beetle with intractable mandibles will almost certainly consume harder and more abrasive foods than a fluid feeder.

These factors indicate that a beetle will probably be associated with more grit than a moth. Coupled with the greater bite force of intractable insectivores, this may also increase the rate of wear. The result is that beetle-eaters may experience more dental wear than moth-feeders, but not for the simple reason that a beetle's exoskeleton is 'harder' or more intractable and directly wears the teeth. It is interesting to note that those insectivores that have the least exposure to wear-causing grit (due to their aerial habitat) are also the most long-lived, suggesting that increased longevity may be caused (or at least enabled) by lower tooth wear rates in microchiropterans compared with terrestrial insectivorans and marsupial insectivores (Jürgens and Prothero, 1987). This needs to be examined using data relating to the influence of tooth wear on longevity in these groups.

Increased wear would select for features that improve wear resistance, such as a greater amount of dental material available for wear. This may have a similar appearance to increased robustness, and have the functional parameter characteristics described above (Fig. 1e). Thicker enamel would also be advantageous in this situation because of its greater resistance to wear compared with dentine. It is geometrically possible for robust teeth that resist wear (with large dental volume and low cusp sharpness) to have high tip and edge sharpnesses. This means that 'sharp' and 'robust' are not necessarily mutually exclusive for some functional parameters, as has been assumed [hard-eating 'should be associated with robust rather than sharp teeth because hard, brittle items would rapidly dull a sharp blade' (Freeman, 1988, p. 268)]. Greater wear may blunt cusps and crests, reducing tip and edge sharpnesses, but it will not necessarily select for lower tip and edge sharpnesses in the unworn state. Sharpness in the unworn state could be as high as possible (without increasing the risk fracture), regardless of whether wear dulls the sharp edge later.

This study has shown that there are no general trends in the differences in the functional parameters of teeth for the families Molossidae, Vespertilionidae and Rhinolophidae. The large amount of variability in many of the characters, compounded by the small sample size, may disguise any broad patterns between species. For instance, the great deal of variability in rake angle in vespertilionids may explain the lack of significant difference in that parameter. The qualitative measurements of some of the characters may be too imprecise to reveal differences, as we found no significant differences in these parameters. For instance, we may expect a correlation between fragment clearance and rake angle (as a larger rake angle will tend to improve the flow of food off the rake surface), but this was not apparent. In addition, the suite of functional parameters used by intractable and tractable feeders within each family may differ.

Body size is most probably a confounding factor here, in that the scaling of these features is not isometric and perhaps differs to some extent among the families. The first factor of the principal components analysis correlates highly with SV3 and tooth size. The second differentiates the intractable and tractable feeders in each family according to approach angle: the tractable feeder in Molossidae and Vespertilionidae and the intractable feeder in Rhinolophidae have higher approach angles. This means that approach angle does not necessarily follow changes in other parameters as closely as implied by Fig. 1. This shows that various features of the teeth can to some extent be varied independently (see Evans and Sanson, 2003), and the situation is not as simple as that modelled in Fig. 1.

Strait (1993c) and Dumont (1995) found that there was no consistent value of shear ratio or enamel thickness that distinguishes all intractable feeders from tractable feeders regardless of the phylogenetic relationships. The same appears to be true for the functional parameters measured in this study.

The differences that are apparent within families will tend to decrease the functional effectiveness of the intractable feeder (e.g. smaller rake angle, but was not significantly different in vespertilionids). Hypothesis 1 predicts no variance in tooth form, and so the lack of difference in many of the functional parameters may be due to the similar function of intractable and tractable invertebrate dentitions. We can interpret the differences that do exist as being due to an increase in the robustness of the dentition. This robustness may be due to either increased risk of fracture (Hypothesis 2) or increased wear (Hypothesis 3). The result, though, is overall decreased effectiveness of the molars of intractable feeders, meaning that greater force and/or energy would be required for the teeth to function. However, the increased bite force of intractable feeders will allow them to compensate to some extent for this decreased effectiveness.

Therefore, tractable feeders are better able to maintain an efficient tooth form due to the fewer constraints placed upon them; intractable feeders build a more robust tooth to cope with additional demands (tooth fracture and wear). The greater jaw musculature that was already required by feeding on intractable foods (Freeman, 1979) means that they can generate sufficient bite force for their teeth to function, but this in turn is likely to produce greater wear and to some extent compound the effect.

The extreme changes in function with wear that were apparent following wear in *Chalinolobus gouldii* (Evans, in press) are much greater than any among different species in this study. It would appear, then, that to some extent wear is a more influential factor in tooth form than biomechanical properties *per se*, at least within insectivores. This may mean that the rate of wear is not dramatically different between the two feeding types considered here [at least compared with herbivorous tooth forms (Evans, 2003)], but an increase in wear may still have an effect on tooth form.

The main difference induced by the greater intractability of the diet is likely to be increased bite force and the consequences that flow from this. This has been supported by other studies investigating 'hardness' (Freeman, 1979; Dumont, 1999; Aguirre *et al.*, 2003). The diets of insectivores may be largely limited by the bite force they can generate (see Evans, 2003). A larger bite force is likely to increase the risk of fracture and tooth wear.

Biomechanical properties and tooth form in previous studies

Freeman (1979, 1981a) found a significant difference in the sizes of the molars in 'hard' and 'soft' feeders. In 'hard' feeders, the first and second molars were larger and the third molar smaller, often lacking the premetacrista that was present in the soft feeders, creating a 'V' ectoloph instead of a 'W' or 'N'. The length of the premetacrista of the M^3 was the most significant molar determinant of dietary hardness found by Rodríguez-Durán *et al.* (1993). These differences by themselves do not reveal a lot about the comparative function of the molars. Later studies found that hard-feeding bats were more wide-faced than soft-feeding bats (Freeman, 1984, 1988, 1998, 2000). These bats were distinct from soft-feeding insectivorous and carnivorous bats, which form a continuous group. The reduction in the size of the M^3 and the wide faces brings the teeth closer to the fulcrum, increasing leverage (Freeman, 1995).

There is a suite of possible explanations for the difference in relative size of the molars. First, it may relate to the number of contact points along the molar row. When penetrating intractable foods, minimizing the contact area between the food and teeth decreases the force required. Either reducing the overall number or increasing the spacing between them, ensuring fewer cusps will contact an object of a given size, will reduce the contact area. Intractable feeders have achieved this by reducing the number of cusps on the third molar (where the metacone is now absent) and spacing the remaining cusps out along the tooth row. However, the effect of decreasing the number of cusps in contact may only be minor.

Similarly, the greater number of cusps in tractable feeders may be an advantage. Although more cusps will distribute the force over a larger area and thereby reduce the effective stress, the lower structural strength of tractable invertebrates should mean that this does not considerably impede the insectivore. An increase in the number of penetration points and therefore locations at which cracks are initiated will aid the initiation and propagation of cracks through a ductile material.

Concurrent with the reduction in cusp number is an increase in the size of the first and second molars. If the increase in tooth size were isometric, then the tip sharpness would decrease in absolute terms due to a larger radius of curvature. However, if the elastic modulus of the food is increased and animals have a diet that is stiffer (higher intractability), the contact area between tooth and food is not greatly enlarged [as discussed above (Lucas, 1982)]. Therefore, an animal consuming foods of higher intractability could afford to have blunter teeth.

The use of a relative measure of crest length, such as shear quotient and shear ratio, is a commonly used method in dietary inference, particularly in primates (Kay and Hylander, 1978; Kay *et al.*, 1978; Covert, 1986; Benefit and McCrossin, 1990; Strait, 1991, 1993b,c, 2001; Anthony and Kay, 1993; Williams and Covert, 1994; Ungar and Kay, 1995; Dumont *et al.*, 2000; Kirk and Simons, 2001). However, such measures do not reveal a great deal about comparative function concerning the shape or orientation of the crest and its associated rake and relief surfaces.

As tractable invertebrates are still relatively tough, greater crest lengths will be advantageous for tractable feeders, as this will tend to increase tip, edge and cusp sharpnesses, and rake and approach angles (Fig. 1b). The decrease in crest length in intractable feeders found by Strait (1993c) is most probably related to increased probability of fracture and/or wear. The difference in shear ratio between folivores/insectivores and frugivores found by Strait (1993b) is probably due to the relative importance of crests in fracturing their food. Longer crests will also increase the quantity of food processed by crests. It is likely that there are also associated improvements in the mechanical efficiency of the crests (e.g. increased rake angles, capture areas, approach angles) that are not as important in a frugivorous dentition.

A potential source of discrepancy between Strait's (1993c) study and the current investigation is that shear ratio was measured for the lower molars in the former and the functional parameters were measured for the upper molars in the latter. It is unlikely that there would be significantly greater difference between intractable and tractable feeders in the lower molars than the upper molars, as the teeth must still maintain occlusion. It is possible, however, that the protoconid of the lower tooth shows a greater variation in height and therefore crest length than the upper ectoloph crests while still being able to occlude with the upper crests.

We also measured the two-dimensional (2-D) and three-dimensional (3-D) crest lengths of the ectoloph crests, standardizing the total crest length by either SV3 (CL/SV3) or tooth length (CL/TL). Total crest length was only significantly different for 2-D and 3-D CL/TL and 2-D CL/SV3 for molossids [Kruskal-Wallis (KW) test statistic = 1, $P = 0.016$; KW = 3, $P = 0.047$; KW = 1, $P = 0.016$, respectively] and for 3-D CL/SV3 for vespertilionids [KW = 25, $P = 0.009$]; all other tests showed $P > 0.05$. Thus, crest length of the upper ectoloph crests also does not reveal consistent differences between intractable and tractable feeders.

Yamashita (1998) carried out an extremely interesting investigation on the correlations between several biomechanical properties of the diet and tooth form in five lemur species. Two of the hypotheses that were tested were: (1) crest length would be positively correlated with shear strength – 'longer crests would be able to drive crack propagation in tougher leaves' (Yamashita, 1998, p. 178); and (2) radius of curvature would be positively correlated with food hardness. We will now examine these two hypotheses and the findings of that paper in light of the above discussions.

(1) The mechanical test used to measure 'shear strength' was a punch test. We have interpreted the results of these as a measure of structural strength (Evans and Sanson, 2005). Yamashita (1996, p. 357) provides a similar interpretation: 'Shear strength is not a substitute for fracture toughness, which measures the work of fracture. It is simply a measure of the breaking stress of a material placed under a shearing load'. Therefore, we cannot test a hypothesis regarding the toughness of leaves from this test. If strength were measured by these tests, we may expect that there would be a negative rather than positive correlation between shear strength and crest length due to increased robustness of the tooth form related to risk of tooth fracture and increased wear.

Despite the punch test measuring structural strength, if the foods measured by Yamashita (1996, 1998) can be considered intractable, structural toughness would also be higher in those foods with high structural strength. This still does not mean that we would expect a correlation between dietary toughness and crest length. If a food were sufficiently tough that crests are required to drive a crack through it (i.e. it is not fragile or brittle), increasing the toughness further would not encourage longer crests. A longer crest (all other functional parameters being the same) would not help to propagate cracks in a tougher food; it would only increase the amount of food divided, which in itself may be an advantage but it is not what was advocated by Yamashita (1996, 1998).

In addition, an increase in the structural strength of foods would raise the force required to drive the crest through the food. A longer crest would hinder this further, as the stress induced in the food by the crest driving through it will be lower for a given applied force. If sufficient food to maintain the animal's metabolism is divided by a given crest length and the toughness of the food were further increased [as is the situation envisaged by Yamashita (1998)], then we may expect that the crest length would not be increased.

The findings of Yamashita (1998) did not support this hypothesis, finding a negative correlation between shear strength and crest length. In contrast, we would expect this to be the case given the alternatives discussed above, such as increased robustness due to the higher strength of foods.

(2) The prediction that radius of curvature would be correlated with food hardness is in accord with the approach in this study. However, the method by which radius of curvature was measured in Yamashita's (1998) study is suspect. Pilot studies for the present study showed that the measurement of radius of curvature depends greatly on the resolution at which it is measured (unpublished data). Yamashita (1998) does not specify the resolution at which the radius of curvature was measured – that is, how far B and C are from A in figure 3

of Yamashita (1998). This is crucial to the answer obtained. We measured tip and edge sharpness at the highest possible resolution (1 μm) for the confocal microscope set-up because of this issue.

In addition to the points raised above about the specific hypotheses, we should view the results of the mechanical tests of Yamashita (1996, 1998) with caution, as they were not carried out under a constant loading speed, and so will potentially vary due to the viscoelasticity of foodstuffs.

Additional differences in tooth form

The tractable feeders display further differences from the intractable feeders that the nine functional parameters do not quantify. We can interpret some of these as adaptations for improved fracture of tough, ductile foods. In *Nyctinomops macrotis*, the rake surface of the protocone crests is concave (Fig. 2). This would improve the rake angle of these crests (which was not quantified in the current study). The buccal edges of these grooves meet the lingual face of the bases of the paracone and metacone. This would direct flow of some food cut on the protocone crests into the embrasure between teeth rather than into the talon basin. Fracture of tough, ductile food is unlikely to be efficiently accomplished through the mortar and pestle action of the talon basin (Lucas and Luke, 1984), and may impede centric occlusion of the molars when the food is largely incompressible. We did not find this grooved rake surface in the other molossid *Molossus ater*, nor in any of the other species.

The lower molars of *Rhinolophus blasii* have distinct sharp notches in the paracristid (and sometimes protocristid). This notching improves the approach angle of the crests and the efficiency of cutting at the end of a stroke (similar to a carnassial notch in carnivores). In intractable feeders, this notch is not as emphasized.

In several of the tractable feeders, the relief surface consisted of a thin wear land (attrition facet) along the crest edge, behind which the relief surface was slightly concave. This was particularly noticeable for the postmetacrista and preparacrista. Such an arrangement will improve relief behind a crest, as was noted in *Chalinolobus gouldii* (Evans, in press). However, once a moderate amount of wear has occurred, the thin band along the crest edge is removed, leading to an increase in the width of the wear land and a slight decrease in the amount of relief. This suggests that teeth that undergo significant wear would be less likely to have such a feature, as it would create large wear lands at higher wear states. Since this feature only occurs in tractable feeders, this may indicate that they are less prone to tooth wear than intractable feeders, but this is not conclusive.

Three of the *Hipposideros diadema* specimens had undergone more wear than the other two. The enamel on the rake surface was worn away to approximately 100 μm from the crest edge along the length of the ectoloph crests. In general, the five specimens of *H. diadema* group together on PCA plots (Fig. 3), so it appears that on the whole this small amount of wear does not affect the shape of the teeth. The two unworn specimens have higher Factor 2 values, giving greater separation from the *R. blasii* specimens. There is a profound difference in rake angle between these specimens though, which indicates that this is probably the main variable affected by wear at this early stage.

CONCLUSIONS

We did not find consistent significant differences between intractable and tractable feeders in three microchiropteran families. However, the differences found within families indicated that the effectiveness of teeth of intractable feeders tended to be lower. This may be due to an increased risk of fracture or rate of tooth wear in intractable feeders, but not due to any predicted difference in the ideal tooth form of these two dietary groups.

Increased structural strength appears to be the main difference in intractable diets. This probably leads to increased bite force by enlarged musculature, and increased risk of fracture and wear, resulting in greater robustness of the teeth that reduces the functionality of the tooth. These conflicting forces are not as apparent in tractable feeders, which in general had more advantageous functional characteristics compared with intractable feeders.

ACKNOWLEDGEMENTS

We wish to thank John Rensberger, Betsy Dumont and an anonymous reviewer for helpful comments which improved the manuscript. Thanks also to Sandy Ingleby and Tish Ennis (Australian Museum), Chris Norris and Bob Randall (American Museum of Natural History), Jim Patton and Chris Conroy (Museum of Vertebrate Zoology), and Michael Carlton and Linda Gordon (National Museum of Natural History) for their generous loan of specimens under their care.

REFERENCES

Aguirre, L.F., Herrel, A., Van Damme, R. and Matthysen, E. 2003. The implications of food hardness for diet in bats. *Funct. Ecol.*, **17**: 201–212.

Andrews, P. 1981. Species diversity and diet in monkeys and apes during the Miocene. In *Aspects of Human Evolution* (C.B. Stringer, ed.), pp. 25–61. London: Taylor & Francis.

Anthony, E.L.P. and Kunz, T.H. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, **58**: 775–786.

Anthony, M.R.L. and Kay, R.F. 1993. Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. *Am. J. Sci.*, **293A**: 356–382.

Arlettaz, R. and Perrin, N. 1995. The trophic niches of sympatric sibling *Myotis myotis* and *M. blythii*: do mouse-eared bats select prey? *Symp. Zool. Soc. Lond.*, **67**: 361–376.

Bayer, R.G. 1994. *Mechanical Wear Prediction and Prevention*. New York: Marcel Dekker.

Benefit, B.R. and McCrossin, M.L. 1990. Diet, species diversity and distribution of African fossil baboons. *Kroeber Anthropol. Soc. Pap.*, **71/72**: 77–93.

Black, H.L. 1972. Differential exploitation of moths by the bats *Eptesicus fuscus* and *Lasiurus cinereus*. *J. Mammal.*, **53**: 598–601.

Black, H.L. 1974. A north temperate bat community: structure and prey populations. *J. Mammal.*, **55**: 138–157.

Bowles, J.B., Heideman, P.D. and Erickson, K.R. 1990. Observations on six species of Free-tailed Bats (Molossidae) from Yucatan, Mexico. *Southwest. Nat.*, **35**: 151–157.

Brigham, R.M. 1990. Prey selection by Big Brown Bats *Eptesicus fuscus* and Common Nighthawks *Chordeiles minor*. *Am. Midl. Nat.*, **124**: 73–80.

Brigham, R.M. and Saunders, M.B. 1990. The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada. *Northwest Sci.*, **64**: 7–10.

Buchler, E.R. 1976. Prey selection by *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Am. Nat.*, **110**: 619–628.

Carter, T.C., Menzel, M.A., Krishon, D.M. and Laerm, J. 1998. Prey selection by five species of vespertilionid bats on Sapelo Island, Georgia. *Brimleyana*, **25**: 158–170.

Covert, H.H. 1986. Biology of early Cenozoic primates. In *Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy* (D.R. Swindler and J. Erwin, eds.), pp. 335–359. New York: Alan R. Liss.

Dalton, V.M., Brack, V., Jr. and McTeer, P.M. 1986. Food habits of the big-eared bat, *Plecotus townsendii virginianus*, in Virginia. *Virginia J. Sci.*, **37**: 248–254.

Dumont, E.R. 1995. Enamel thickness and dietary adaptation among extant primates and chiropterans. *J. Mammal.*, **76**: 1127–1136.

Dumont, E.R. 1997. Cranial shape in fruit, nectar, and exudate feeders: implications for interpreting the fossil record. *Am. J. Phys. Anthropol.*, **102**: 187–202.

Dumont, E.R. 1999. The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): an experimental study. *J. Zool.*, **248**: 219–229.

Dumont, E.R., Strait, S.G. and Friscia, A.R. 2000. Abderitid marsupials from the Miocene of Patagonia: an assessment of form, function, and evolution. *J. Paleontol.*, **74**: 1161–1172.

Easterla, D.A. and Whitaker, J.O., Jr. 1972. Food habits of some bats from Big Bend National Park, Texas. *J. Mammal.*, **53**: 887–890.

Edwards, A.J., Fawke, J.D., McClements, J.G., Smith, S.A. and Wyeth, P. 1993. Correlation of zinc distribution and enhanced hardness in the mandibular cuticle of the leaf-cutting ant *Atta sexdens rubropilosa*. *Cell Biol. Int.*, **17**: 697–698.

Evans, A.R. 2003. Functional dental morphology of insectivorous microchiropterans: spatial modelling and functional analysis of tooth form and the influence of tooth wear and dietary properties. PhD thesis, Monash University, Melbourne, VIC.

Evans, A.R. in press. Connecting morphology, function and tooth wear in microchiropterans. *Biol. J. Linn. Soc.*

Evans, A.R. and Sanson, G.D. 1998. The effect of tooth shape on the breakdown of insects. *J. Zool.*, **246**: 391–400.

Evans, A.R. and Sanson, G.D. 2003. The tooth of perfection: functional and spatial constraints on mammalian tooth shape. *Biol. J. Linn. Soc.*, **78**: 173–191.

Evans, A.R. and Sanson, G.D. 2005. The biomechanical properties of insects in relation to insectivory: cuticle thickness as an indicator of insect ‘hardness’ and ‘intractability’. *Aust. J. Zool.*, **53**: 9–19.

Evans, A.R. and Sanson, G.D. in press. Spatial and functional modeling of carnivore and insectivore molariform teeth. *J. Morphol.*

Evans, A.R., Harper, I.S. and Sanson, G.D. 2001. Confocal imaging, visualization and 3-D surface measurement of small mammalian teeth. *J. Microsc.*, **204**: 108–118.

Fenton, M.B. 1995. Constraint and flexibility – bats as predators, bats as prey. *Symp. Zool. Soc. Lond.*, **67**: 277–289.

Fenton, M.B., Waterman, J.M., Roth, J.D., Lopez, E. and Fienberg, S.E. 1998a. Tooth breakage and diet: a comparison of bats and carnivorans. *J. Zool.*, **246**: 83–88.

Fenton, M.B., Cumming, D.H.M., Rautenbach, I.L. *et al.* 1998b. Bats and the loss of tree canopy in African woodlands. *Conserv. Biol.*, **12**: 399–407.

Fenton, M.B., Rautenbach, I.L., Rydell, J. *et al.* 1998c. Emergence, echolocation, diet and foraging behavior of *Molossus ater* (Chiroptera: Molossidae). *Biotropica*, **30**: 314–320.

Findley, J.S. 1993. *Bats: A Community Perspective*. Cambridge: Cambridge University Press.

Freeman, P.W. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. *J. Mammal.*, **60**: 467–479.

Freeman, P.W. 1981a. Correspondence of food habits and morphology in insectivorous bats. *J. Mammal.*, **62**: 166–173.

Freeman, P.W. 1981b. A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution. *Fieldiana Zool.*, **7**: 1–173.

Freeman, P.W. 1984. Functional cranial analysis of large animalivorous bats (Microchiroptera). *Biol. J. Linn. Soc.*, **21**: 387–408.

Freeman, P.W. 1988. Frugivorous and animalivorous bats (Microchiroptera): dental and cranial adaptations. *Biol. J. Linn. Soc.*, **33**: 249–272.

Freeman, P.W. 1995. Nectarivorous feeding mechanisms in bats. *Biol. J. Linn. Soc.*, **56**: 439–463.

Freeman, P.W. 1998. Form, function, and evolution in skulls and teeth of bats. In *Bat Biology and Conservation* (T.H. Kunz and P.A. Racey, eds.), pp. 140–156. Washington, DC: Smithsonian Institution Press.

Freeman, P.W. 2000. Macroevolution in Microchiroptera: recoupling morphology and ecology with phylogeny. *Evol. Ecol. Res.*, **2**: 317–335.

Griffith, L.A. and Gates, J.E. 1985. Food habits of cave-dwelling bats in the central Appalachians. *J. Mammal.*, **66**: 451–460.

Grine, F.E. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Human Evol.*, **15**: 783–822.

Hamilton, I.M. and Barclay, R.M.R. 1998. Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southeastern Alberta. *J. Mammal.*, **79**: 764–771.

Hamilton, W.J. 1933. The insect food of the big brown bat. *J. Mammal.*, **14**: 155–156.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Hillerton, J.E., Reynolds, S.E. and Vincent, J.F.V. 1982. On the indentation hardness of insect cuticle. *J. Exp. Biol.*, **96**: 45–52.

Howell, D.J. and Burch, D. 1974. Food habits of some Costa Rican bats. *Revista de Biologia Tropical*, **21**: 281–294.

Jacobs, D.S. 1996. Morphological divergence in an insular bat, *Lasiurus cinereus semotus*. *Funct. Ecol.*, **10**: 622–630.

Jolly, C.J. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man*, **5**: 5–26.

Jungers, W.L., Falsetti, A.B. and Wall, C.E. 1995. Shape, relative size, and size-adjustments in morphometrics. *Yearbook Phys. Anthropol.*, **38**: 137–161.

Jürgens, K.D. and Prothero, J. 1987. Scaling of maximal lifespan in bats. *Comp. Biochem. Physiol., Part A*, **88A**: 361–367.

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

Kay, R.F. and Hylander, W.L. 1978. The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea (Marsupialia). In *The Ecology of Arboreal Folivores* (G.G. Montgomery, ed.), pp. 173–191. Washington, DC: Smithsonian Institution Press.

Kay, R.F., Sussman, R.W. and Tattersall, I. 1978. Dietary and dental variations in the genus *Lemur*, with comments concerning dietary–dental correlations among Malagasy primates. *Am. J. Phys. Anthropol.*, **49**: 119–128.

Kinzey, W.G. 1974. Ceboid models for the evolution of hominoid dentition. *J. Human Evol.*, **3**: 193–203.

Kirk, E.C. and Simons, E.L. 2001. Diets of fossil primates from the Fayum Depression of Egypt: a quantitative analysis of molar shearing. *J. Human Evol.*, **40**: 203–229.

Koenigswald, W.v., Rensberger, J.M. and Pretzschner, H.U. 1987. Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature*, **328**: 150–152.

Kunz, T.H. 1988. Methods of assessing the availability of prey to insectivorous bats. In *Ecological and Behavioral Methods for the Study of Bats* (T.H. Kunz, ed.), pp. 191–210. Washington, DC: Smithsonian Institution Press.

Lowrison, G.C. 1974. *Crushing and Grinding: The Size Reduction of Solid Materials*. London: Butterworths.

Lucas, P.W. 1979. The dental–dietary adaptations of mammals. *N. Jb. Geol. Paläont. Mh.*, **1979**: 486–512.

Lucas, P.W. 1982. Basic principles of tooth design. In *Teeth: Form, Function and Evolution* (B. Kurtén, ed.), pp. 154–162. New York: Columbia University Press.

Lucas, P.W. and Luke, D.A. 1984. Chewing it over: basic principles of food breakdown. In *Food Acquisition and Processing in Primates* (D.J. Chivers, B.A. Wood and A. Bilsborough, eds.), pp. 283–301. New York: Plenum Press.

Marques, S.A. 1986. Activity cycle, feeding and reproduction of *Molossus ater* (Chiroptera: Molossidae) in Brazil. *Boletim do Museu Paraense Emilio Goeldi Serie Zoologia*, **2**: 157–179.

Menzel, M.A., Carter, T.C., Mitchell, B.L. *et al.* 2000. Prey selection by a maternity colony of big brown bats (*Eptesicus fuscus*) in the southeastern United States. *Florida Sci.*, **63**: 232–241.

Mosimann, J.E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *J. Am. Stat. Assoc.*, **65**: 930–945.

Mosimann, J.E. and James, F.C. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution*, **33**: 444–459.

Nabhitabhata, J. 1986. Food of Thai bats: preliminary study of the food habits of insectivorous bats from Thailand. *Courier Forschunginstitut Senckenberg*, **87**: 55–71.

Osborn, J.W. and Lumsden, A.G.S. 1978. An alternative to 'thegosis' and a re-examination of the ways in which mammalian molars work. *N. Jb. Geol. Paläont. Abh.*, **156**: 371–392.

Palamara, J., Phakey, P.P., Rachinger, W.A., Sanson, G.D. and Orams, H.J. 1984. The nature of the opaque and translucent enamel regions of some Macropodinae (*Macropus giganteus, Wallabia bicolor* and *Peradorcas concinna*). *Cell Tissue Res.*, **238**: 329–338.

Pavey, C.R. and Burwell, C.J. 1997. The diet of the diadem leaf-nosed bat *Hipposideros diadema*: confirmation of a morphologically-based prediction of carnivory. *J. Zool.*, **243**: 295–303.

Pavey, C.R. and Burwell, C.J. 1998. Bat predation on eared moths: a test of the allotonic frequency hypothesis. *Oikos*, **81**: 143–151.

Phillips, G.L. 1966. Ecology of the Big Brown Bat (Chiroptera: Vespertilionidae) in northeastern Kansas. *Am. Midl. Nat.*, **75**: 168–198.

Pine, R.H. 1969. Stomach contents of a free-tailed bat, *Molossus ater. J. Mammal.*, **50**: 162.

Puech, P.-F., Prone, A. and Albertini, H. 1981. Mechanical process of dental surface alteration by nonabrasive and nonadhesive friction, reproduced by experimentation and applied to the diet of early man. *Comptes Rendus des Seances de L'Academie des Sciences Serie III, Sciences de la Vie*, **294**: 497–502.

Ravosa, M.J. 2000. Size and scaling in the mandible of living and extinct apes. *Folia Primatol.*, **71**: 305–322.

Ridley, M. 1983. *The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating*. Oxford: Clarendon Press.

Rodríguez-Durán, A., Lewis, A.R. and Montes, Y. 1993. Skull morphology and diet of antillean bat species. *Caribb. J. Sci.*, **29**: 258–261.

Rosenberger, A.L. and Kinzey, W.G. 1976. Functional patterns of molar occlusion in platyrrhine primates. *Am. J. Phys. Anthropol.*, **45**: 281–298.

Ross, A. 1967. Ecological aspects of the food habits of insectivorous bats. *Western Foundation of Vertebrate Zoology*, **1**: 203–263.

Sample, B.E. and Whitmore, R.C. 1993. Food habits of the endangered Virginia big-eared bat in West Virginia. *J. Mammal.*, **74**: 428–435.

Schofield, R.M.S., Nesson, M.H. and Richardson, K.A. 2002. Tooth hardness increases with zinc-content in mandibles of young adult leaf-cutter ants. *Naturwissenschaften*, **89**: 579–583.

Schulz, M. 2000. Diet and foraging behavior of the golden-tipped bat, *Kerivoula papuensis*: a spider specialist? *J. Mammal.*, **81**: 948–957.

Silva-Taboada, G. 1979. *Los murciélagos de Cuba*. Havana: Editorial Academia.

Simmons, N.B. 1998. A reappraisal of interfamilial relationships of bats. In *Bat Biology and Conservation* (T.H. Kunz and P.A. Racey, eds.), pp. 3–26. Washington, DC: Smithsonian Institution Press.

Strait, S.G. 1991. Dietary reconstruction in small-bodied fossil primates. PhD dissertation, State University of New York, Stony Brook, NY.

Strait, S.G. 1993a. Molar microwear in extant small-bodied faunivorous mammals: an analysis of feature density and pit frequency. *Am. J. Phys. Anthropol.*, **92**: 63–79.

Strait, S.G. 1993b. Differences in occlusal morphology and molar size in frugivores and faunivores. *J. Human Evol.*, **25**: 471–484.

Strait, S.G. 1993c. Molar morphology and food texture among small-bodied insectivorous mammals. *J. Mammal.*, **74**: 391–402.

Strait, S.G. 2001. Dietary reconstruction of small-bodied omomyoid primates. *J. Vertebrate Paleontol.*, **21**: 322–334.

Swift, S.M. and Racey, P.A. 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool.*, **200**: 249–259.

Teaford, M.F. 1985. Molar microwear and diet in the genus *Cebus. Am. J. Phys. Anthropol.*, **66**: 363–370.

Turnbull, W.D. 1970. Mammalian masticatory apparatus. *Fieldiana Geol.*, **18**: 147–356.

Ungar, P.S. and Kay, R.F. 1995. The dietary adaptations of European Miocene catarrhines. *Proc. Natl. Acad. Sci. USA*, **92**: 5479–5481.

Van Valkenburgh, B. 1988. Incidence of tooth breakage among large, predatory mammals. *Am. Nat.*, **131**: 291–302.

Vaughan, T.A. 1977. Foraging behaviour of the giant leaf-nosed bat (*Hipposideros commersoni*). *East Afr. Wildlife J.*, **15**: 237–249.

Verts, B.J., Carraway, L.N. and Whitaker, J.O., Jr. 1999. Temporal variation in prey consumed by big brown bats (*Eptesicus fuscus*) in a maternity colony. *Northwest Sci.*, **73**: 114–120.

Vestjens, W.J.M. and Hall, L.S. 1977. Stomach contents of forty-two species of bats from the Australasian region. *Aust. Wildlife Res.*, **4**: 25–35.

Vinyard, C.J., Wall, C.E., Williams, S.H. and Hylander, W.L. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. *Am. J. Phys. Anthropol.*, **120**: 153–170.

Warner, R.M. 1985. Interspecific and temporal dietary variation in an Arizona bat community. *J. Mammal.*, **66**: 45–51.

Waters, N.E. 1980. Some mechanical and physical properties of teeth. In *The Mechanical Properties of Biological Materials: 34th Symposium of the Society for Experimental Biology* (J.F.V. Vincent and J.D. Currey, eds.), pp. 99–135. Cambridge: Cambridge University Press.

Whitaker, J.O., Jr. 1972. Food habits of bats from Indiana. *Can. J. Zool.*, **50**: 877–883.

Whitaker, J.O., Jr. 1995. Food of the big brown bat *Eptesicus fuscus* from maternity colonies in Indiana and Illinois. *Am. Midl. Nat.*, **134**: 346–360.

Whitaker, J.O., Jr. and Black, H. 1976. Food habits of cave bats from Zambia, Africa. *J. Mammal.*, **57**: 199–204.

Whitaker, J.O., Jr., Maser, C. and Keller, L.E. 1977. Food habits of bats of western Oregon. *Northwest Sci.*, **51**: 46–55.

Whitaker, J.O., Jr., Maser, C. and Cross, S.P. 1981. Food habits of eastern Oregon bats, based on stomach and scat analyses. *Northwest Sci.*, **55**: 281–292.

Williams, B.A. and Covert, H.H. 1994. New Early Eocene anaptomorphine primate (Omomyoidae) from the Washakie Basin, Wyoming, with comments on the phylogeny and paleobiology of anaptomorphines. *Am. J. Phys. Anthropol.*, **93**: 323–340.

Yamashita, N. 1996. Seasonal and site specificity of mechanical dietary patterns in two Malagasy lemur families (Lemuridae and Indriidae). *Int. J. Primatol.*, **17**: 355–387.

Yamashita, N. 1998. Functional dental correlates of food properties in five Malagasy lemur species. *Am. J. Phys. Anthropol.*, **106**: 169–188.

Young, W.G., Douglas, W.B. and Robson, S.K. 1990. Differential wear resistance as a function of tooth enamel structure in the koala *Phascolarctos cinereus*. In *Biology of the Koala* (A.K. Lee, K.A. Handasyde and G.D. Sanson, eds.), pp. 145–150. Sydney, NSW: Surrey Beatty & Sons.