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Frugivorous and animalivorous bats (Microchiroptera): dental and cranial adaptations

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ABSTRACT: The most derived fruit-eating bats have small canines, wide palates and molars with a distinctive labial rim. Paracone and metacone have moved from a dilambdodont position in the middle of the tooth to the labial side of the tooth where they form the labial cutting edge. Along with the well-developed and close fitting labial cutting edges of the premolars and canines, this cutting edge skirts nearly the entire perimeter of the palate. The labial rim of the lower teeth fit inside the labial rim of the upper teeth like two cookie cutters nesting one inside the other. Frugivores have a greater allocation of tooth area at the anterior end of the toothrow, while animalivorous species have more at the posterior end of the toothrow. The area occupied by canines of predators of struggling prey is greater than that for bats that eat non-struggling prey like fruit. In addition, frugivores have wider palates than long while many carnivores have longer palates than wide. Omnivores appear to have a more equal allocation of space to more kinds of teeth, particularly the incisors and non-molariform premolars, on the toothrow than do frugivores or animalivores. The mechanical nature of different food items is discussed and the suggestion made that describing foods in terms of their texture may be more important in tooth design than whether they are fruit or insect or vertebrate.

KEY WORDS: Microchiroptera, frugivory, animalivory, omnivory, tooth patterns, tooth areas, jaws, functional morphology, food textures.

CONTENTS

INTRODUCTION

There has long been an interest in the pattern and design of mammalian teeth and jaws and how that design is correlated with diet. Because the natural diet of wild mammals is seldom or superficially known, the work emphasizes a descriptive morphological approach. More re-

cently, with increased knowledge of diet and with the idea that the mechanical nature of foods must greatly influence design (Lucas, 1979), the ecological viewpoint is being greatly enhanced. Tooth design and dietary or eco-morphological studies have been particularly popular with students of primates (Kay, 1975, 1978; Kay & Covert, 1984; Lucas, 1979; Lucas & Luke, 1984; Lucas, Corlett & Luke, 1985, 1986; Maier, 1984), carnivorans both recent and fossil (Emerson & Radinsky, 1980; Radinsky, 1981; Van Valkenburgh & Ruff, 1987), and bats (Freeman, 1979, 1981, 1984; Reduker, 1983).

Microchiropteran bats are a rich source of functional morphological work because these bats exploit a wide diversity of foods from vertebrates and insects to fruit, nectar and blood. This study examines the design of jaws and teeth of fruit-eating bats and correlates it with their diets. Several of the bats in this study are from the well-studied tropical forests of Costa Rica and Panama. The remaining species are rare, unusual and have virtually unknown food habits. From the relationship of morphology and diet of the first group of bats, projections are made about the diets of the second group. In addition, comparisons are made with animalivorous (insectivorous and carnivorous) species that have been examined earlier (Freeman, 1984).

Although the cusp pattern of a frugivore's teeth is recognizable as being that of a frugivore, the mechanical nature of the frugivorous food item is not obvious. However, there must be common physical properties in fruit that cause the features in the teeth that we recognize. Lucas (1979) believes that study of the design of jaws and teeth is actually a study of different apparatuses that break up different foods. Only by considering and understanding the essential mechanical properties of different foods can different dentitions and mastication, the mechanical breakdown of foods, be understood. Following this line of reasoning it would make sense to categorize diet by its physical property rather than by its taxon (Lucas, 1979; Lucas & Luke, 1984). A cat for example would occupy the soft, brittle food niche and man would occupy the hard, brittle niche. An omnivore would be able to process both hard and soft foods.

A discussion of the physical properties of animal prey was introduced in an earlier paper (Freeman, 1984). An insect or an exoskeletal item is a soft package with a cuticle, a stiff brittle covering, while endoskeletal items or vertebrate prey are soft solids covering hard brittle solids. Although these two foods present different processing problems, both have tough coverings-cuticle and skin, respectively (Currey, 1970). To initiate any breakdown of foods, cracks, major structural clefts, must be made or driven into the foods (Lucas et al., 1985). 'Tough' materials are materials that resist crack propagation and the best tools to use to fracture tough items are blades because not only must the blade tip be able to start the initial crack, it must also remain in the crack, drive it to fracture the item, and reduce it to two or more smaller fragments (Lucas, 1979; Lucas & Luke, 1984). The same is true for soft solids where blades become very important in cutting skin and muscle. This is why carnivores have a bladelike carnassial pair and, I presume, why carnivorous bats have lengthened interlophs (also the metastylar ridge; see Freeman, 1984). Another feature in the design of the teeth of animalivorous bats is larger canines that function to subdue and consume struggling prey (Turnbull, 1970; Freeman, 1979, 198 1, 1984).

The outer skin of a fruit can be hard, tough or soft and the insides can range between hard

or extremely soft. A comon fruit structure is a moderately tough 'skin', a soft fleshy pulp and a very hard inner coat to protect the seed. This is a drupe (ex. apricot; Bold, 1973). There are also berries, simple and compound (grapes); pomes (apples); aggregate fruits (strawberries) ; and multiple fruits (mulberry; Bold, 1973; see also Van Roosmalen, 1984). Some fruit may be large relative to the size of the bat's head and some may consist of many small little fruits on a single stalk (like the fruits of Piper). Indeed, Gardner (1977) mentions guava fruits measuring up to 64 mm at greatest diameter and weighing over 50 g being carried off by Artibeus jamaicensis (weighs 47–55 g). The diameter is about 2.5 times the length of the skull of this species.

Fruit is difficult to evaluate not only because of the variation in structure but particularly because of the variation in ripeness when plucked or eaten. Because of ripening a fruit changes in a short period of time from being a brittle solid to being a ductile solid (Lucas, 1979; Mohsenin, 1986). Competitive interactions among bats could potentially hinge on the ripeness of fruit and morphology of jaws and teeth. Bats with robust skulls and teeth could be foraging not-quite-ripe fruits and be temporally displaced from bats with moderately robust skulls and teeth, while bats with the least robust skull and teeth could be eating soft, ripe or overripe fruit. However, nutrition is closely correlated with ripeness, and in one study Fleming, Williams, Bonaccorso & Herbst (1985) have shown that ripeness greatly influences when the fruits of *Muntingia calabura* are picked by bats. So, a fruit can be large or small, hard or soft, but one feature that makes it different from insectivorous and carnivorous prey is that the fruit does not struggle to get free. At least one of the functions of the canine teeth, that of subduing struggling prey, may not apply here. However, the plucking and transporting of enormous fruits, relative to the size of the head of the bat, may require the same canine adaptations as those that eat struggling animals.

Several authors have discussed the nature of a frugivore's teeth and have recognized similar features in phyllostomid and pteropid bats and in cebid monkeys (Slaughter, 1970; Rosenberger & Kinzey, 1976). These mammals have "rather flatter molars . . . with a variably high rim surrounding an inner depression" (Lucas, 1979). The feature common in molar form may well have to do with the ability to express juice from the fruit, and some of these mammals may extract the juice and spit out the pulp and seeds (Constantine, 1970; Lucas, 1979). Lucas & Luke (1984: 287) describe this as a mortar and pestle system with the curvature of the pestles more acute than that of the mortars to allow juice to escape:

A final general pattern of breakdown [of the pestle and mortar system] involves failure but without necessarily any comminution. In this pattern a plastic flowing 'juice' (defined very broadly) is contained within a compartment. Opening the compartment releases the 'juice'. The juice in many ripe fruits contains much of the easily available nutrients of the food and this is contained in microscopic turgid cells which in themselves are stiff and easily broken. A scalpel blade could break only a very few of the cells (of a ripe skinned pear for example) with each subdivision. On the other hand, a pestle and mortar, being very blunt, can easily hit many cells at once . . . bursting them and liberating juice very rapidly. Sharp structures are slower than blunt ones for this particular process.

In addition, some stenodermine phyllostomid bats press the bolus of masticated fruit against their ridged hard palates with their tongues to squeeze out the juice (Morrison, 1980; Bonaccorso & Gush, 1987).

Bats with elongate, narrow rostra and diminutive teeth are recognizable as nectarivorous-pollenivorous bats. But what exactly is the nature of nectar and pollen and how does that affect tooth pattern? The teeth are diminutive which is a characteristic seen in insectivorous carnivorans (aardwolf and sloth bear) and other ant-eating mammals where the tongue does most of the work. If the canines and other teeth are used at all, what are they used for? Finally, is it possible to characterize an omnivorous food habit from morphological features alone? From a food texture standpoint an omnivore would be able to eat hard and soft items. Omnivory may involve a more equal allocation of space for the different teeth on the toothrow and enable the owner of the teeth to take a wider variety of foods. I have lumped non-animalivorous microchiropteran bats into one category, frugivory. However, there appear to be morphological features in this small sample of bats with a diversity of food habits that indicate the predominant food habit, whether it be frugivory, nectarivory-pollenivory, or omnivory. There are also features that give some idea of the ripeness of fruits taken by frugivores.

MATERIALS AND METHODS

Selected species of fruit-eating bats of the family Phyllostomidae were compared with insectivorous and carnivorous species from seven families (Appendix 1; Freeman, 1984). A general comparison of 32 measurements or characteristics thought to be functionally important to feeding were taken on all 45 species. Characters are listed and described in Appendix 2 and any differences with methods in previous work are noted. Additional areal quantities—area of canines and incisors, area of palate and total tooth area—were taken on a subset of 30 species. Most measurements were taken with dial calipers under a dissecting microscope. Other measurements were taken from drawings. I drew the occlusal surfaces of both toothrows and the entire palate under a camera lucida and measured the relevant area with a polar planimeter and angles with a protractor. Because of structural differences among the different families, the palatal area had to be modified. The posterior border in all species was drawn at a line connecting the anteriormost curves of the two posterior emarginations on either side of the nasal passage while the anterior border in those species with a deep anterior palatal emargination or very slender premaxillaries (and sometimes could be missing) was drawn connecting the anteriormost margin of the maxillae (Fig. 1). Otherwise the palatal area includes that area within the outermost perimeter of all the teeth. Areas of each kind of tooth—incisors, canines, premolars, molars—and the raised stylar shelf of P^4–M^2 or M^3 were taken and compared with total palatal area. A simple measurement of the openness of the parabolic arch formed by the upper toothrows, the curvature of bite, was to draw an angle that inscribed the outermost edges of the canines and P^4 or the next outermost tooth on each side. This effectively described bats with widely spread toothrows and produces a large angle. Bats with narrowly spread or parallel toothrows produce a small angle (Fig. 1).
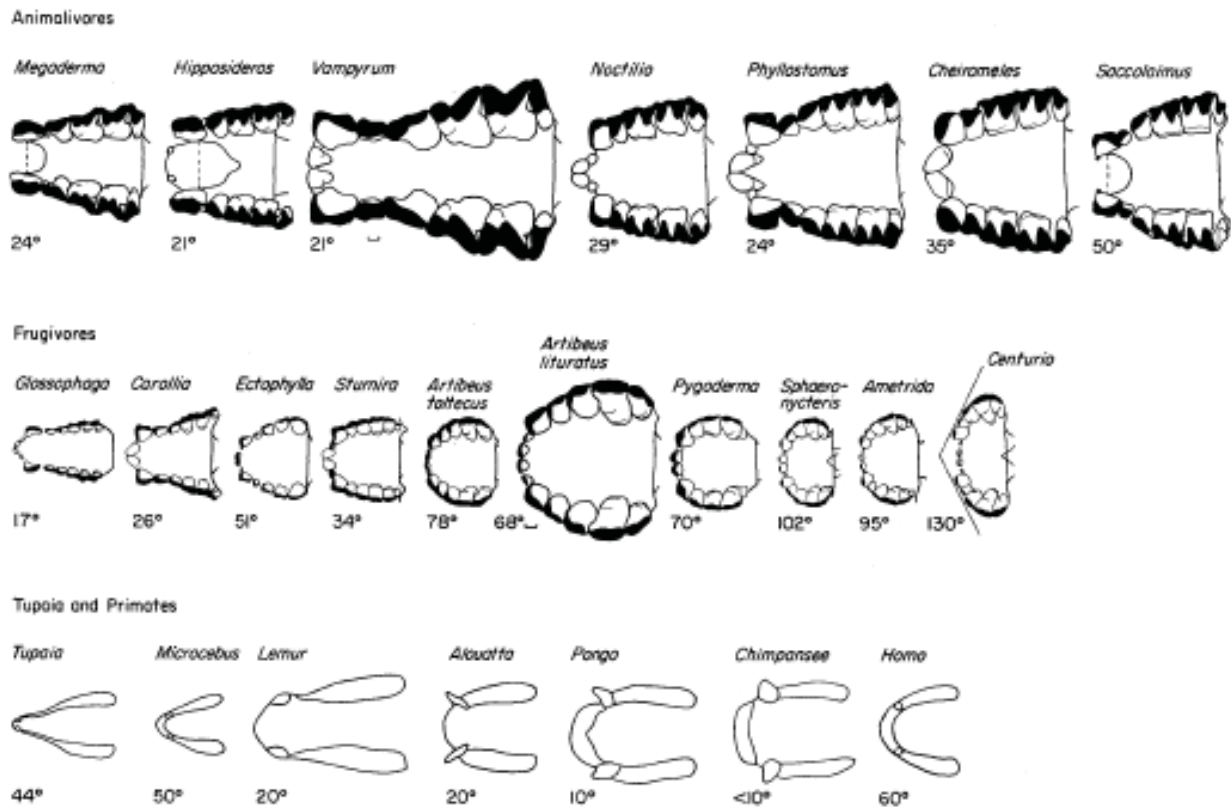
Figure 1. The palates of seven animalivorous and ten frugivorous microchiropterans drawn to the same scale and the outlines of palates of *Tupaia* and six species of primates (not to scale; taken from Hershkovitz, 1977). **A** simple indication of the width of the arc of the palate (curvature of bite) is by inscribing the palate with an angle as shown for *Centurio* and described in text. Magnitude of this angle is listed beneath each palate. The limits of the modified palatal area that is described in Materials and Methods is also illustrated. The stylar shelf is in black.

TABLE 1. Bats that are extremes on the reduced major axes (s.d. = standard deviation units). Each measurement is plotted against SIZE

Measurement	−3.00 s.d.	−2.00 s.d.	−1.75 s.d.	+1.75 s.d.	+2.00 s.d.
CCL		Centurio senex Noctilio leporinus		Glossophaga soricina	
MTR		C. senex Trachops cirrhosus G. soricina	Sphaeronycteris toxophyllum	Macrotus californicus Saccolaimus peli	
ZYG					Chiromeles torquatus
C–C WID		M. californicus	Vampyrum spectrum	Lasiurus borealis	Nyctalus lasiopterus
M–M WID	G. soricina			C. senex	
UP CANIN			M. californicus	Peropteryx kappleri	Rhinolophus rufus Hipposideros commersoni commersoni
TEMP D		Carollia perspicillata G. soricina	Pygoderma bilabiatum V. spectrum S. peli		
TEMP L		Nycteris grandis N. lasiopterus N. leporinus			Rhinolophus blasii
TEMP HT		Eumops underwoodi Ametrida centurio S. toxophyllum	Taphozous nudiventris	C. senex	N. leporinus
MASS O	C. senex				
MASS D	Otomops martiensseni		G. soricina Hipposideros commersoni gigas		S. peli
P–M ROW		C. senex P. bilabiatum			
LO CANIN				Tadarida brasiliensis	H. c. commersoni E. underwoodi
DENT L		C. senex S. toxophyllum	N. leporinus A. centurio		

COND M1	C. senex	S. taxophyllum	A. centurio	C. perspicillata	G. soricina
COND M3		C. senex	N. leporinus		
			S. taxophyllum		
MAT	C. senex				
	N. leporinus				
MAM	C. senex	S. taxophyllum	C. torquatus	Molossus molossus	
			T. brasiliensis	E. underwoodi	
			T. nudiventris		
			A. centurio		
CORO HT	O. martiensseni				
DENT THIC	N. grandis				
DENT D	G. soricina	H. c. gigas	H. c. gigas	C. perspicillata	P. hilabiatum
		C. perspicillata			
		Eumops perotis			
COND L	O. martiensseni	O. martiensseni	M. californicus	Rhinolophus luctus	
				T. nudiventris	
COND HT	H. c. gigas	Megaderma lyra			
	Macroderma gigas				
	H. c. commersoni				
PALATE	S. peli				
C-I AREA	G. soricina				
P-M AREA			T. brasiliensis	P. kappleri	
			P. kappleri		
SS AREA	P. hilabiatum	C. senex		P. kappleri	
		Sturnira tildae			
DENTAREA	N. grandis		Artibeus toltecus		
			Artibeus phaeotis		
			T. nudiventris		
			H. c. commersoni		
			E. underwoodi		
TEMP VOL	C. senex	G. soricina	H. c. commersoni	R. blasii	
MASS VOL		S. taxophyllum	E. underwoodi		
		A. centurio			
		G. soricina			
TT AREA	R. rufus		R. rufus		

Sample sizes vary. There are ten each of *Artibeus jamaicensis, A. phaeotis, A. toltecus, Carollia perspicillata, Glossophaga soricina,* and *Sturnira lillium;* and five each of *Ametrida, Artibeus lituratus, Centurio, Ectophylla, Pygoderma,* and *Sphaeronycteris.* Care was taken to use specimens of species from the same geographic area for which there is good diet information (primarily the dry tropical forest of Costa Rica). With the exception of *A. lituratus* the other five species in the sample of only five each are not common in collections. These 12 are the frugivorous species. The remaining 33 species are the same insectivorous and carnivorous species as in Freeman (1984) and are represented by a single, adult male specimen. These species are called animalivorous (Appendix 1).

Analyses included simple bivariate plots of each measurement, logged, and plotted against a composite size character (SIZE = sum of the natural logs of condylocanine length, zygomatic breadth, and temporal height) both within species where possible and among species. These plots are reduced major axes rather than regression (Radinsky, 1981; Freeman, 1984) and were used to get an idea of what characteristics might be varying compared to bats I had previously studied. Confidence limits in standard deviation units around the reduced major axis allow me to identify bats that have an extremely short or long measurement. Space does not permit reproducing these bivariate plots but the extremes are listed in Table 1.

Two additional analyses were run on the 12 frugivorous species alone. Principal components analysis was performed to determine the amount of intra- and interspecific variation within and among the 12 species of frugivores. Finally, a correlation coefficient was calculated to determine the strength of the relationship between the SIZE character and the weight of the animal. This last analysis was possible because there is relatively good weight data (based on adequate sample sizes from the same geographic area) for ten of the 12 frugivores.

RESULTS

Interspecific variation is 20 times greater than intraspecific variation in the 12 species of frugivores based on a principal components analysis. Body weights of ten of these species (no weights for *Sphaeronycteris* or *Pygoderma)* are highly correlated with SIZE ($r = 0.9902$). *Sturnira lilium* is bigger than *Carollia perspicillata* on the SIZE axis while the reverse is true according to weight (S.l. = 17.5 g, C.p. = 19.4 g).

Extremes for each measurement versus SIZE are listed in Table 1. *Centurio* and *Noctilio* have particularly short skulls (condylocanine length) and *Trachops* and *Glossophaga* have particularly narrow skulls (zygomatic breadth). *Cheiromeles* has the widest skull. *Centurio* is extreme (greater than 2 or 3 S.D.) in 10 of the 32 measurements (condylocanine length, maxillary toothrow, masseter origin length, molariform row length, dentary length, condyle to M_1, condyle to M_3, moment arm of the temporal, moment arm of the masseter, masseter volume) and slightly less extreme (between 2.00 and 1.75 s.D.) for three more (palatal width, temporal height, stylar shelf area). *Glossophaga* is most extreme in six measurements (zygomatic breath, palatal width, temporal depth, condyle to M_3, dentary depth, molariform row area) and slightly less extreme in four others (condylocanine length, masseter depth, temporal volume and total tooth area). Frugivorous species had the smallest styler shelf areas and shortest molariform rows.

All frugivores except *Glossophaga* have a wider palate than long. Maxillary toothrow length was used for length but the frugivorous bats would have an even wider palate if a line parallel to the midline of the palate were used as did Radinsky (1981; Fig. 2). Five of the seven carnivorous bats have palates longer than wide. *Nycteris* and *Phyllostomus* do not. *Vampyrum* and *Macroderma* have the narrowest palates, while *Centurio* has the widest relative to maxillary toothrow. *Glossophaga* has the narrowest palate (M-M width) relative to SIZE.
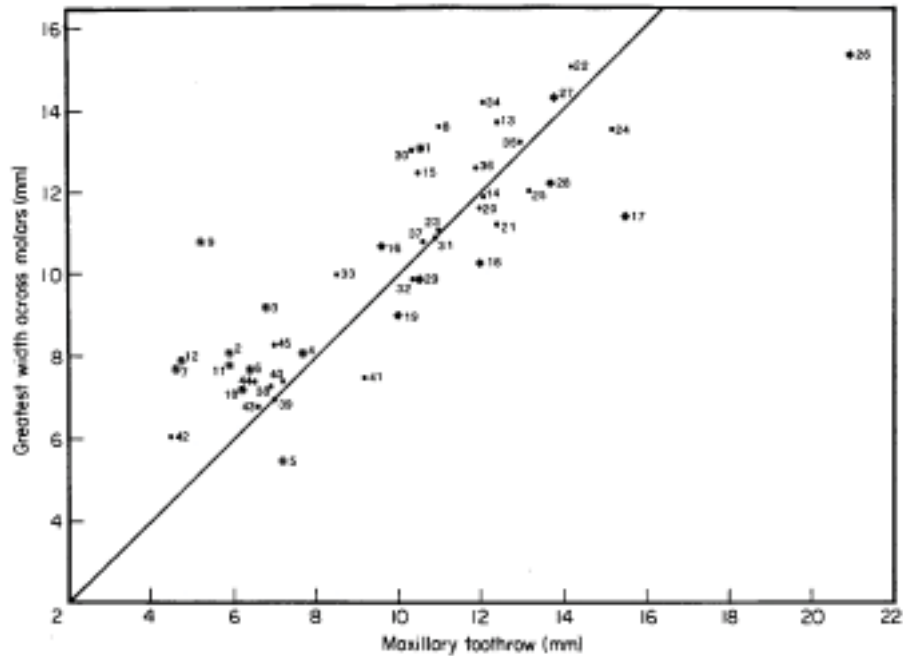

Figure 2. A graph showing the width of palate (M–M WID) versus length of palate (MTR) for all 45 species. The line represents equal widths to lengths. With exception of *Glossophaga,* all frugivores (circled dots) have palates that are wider then long. Six of eight carnivorous species (diamonds) have palates that are longer than wide. Insectivorous species (dots) lie on either side of the line. Numbers correspond to species names listed in Appendix 1.

When total tooth area is plotted against SIZE all the carnivores lie below the reduced major axis indicating they have small areas (Fig. 3). The percentage that the different teeth occupy of total tooth area and the percent that stylar shelf occupies of total tooth area is illustrated in Fig. 4. Averages for each genus are given in Table 2. The stylar shelf of frugivores occupies less than half the space it occupies in animalivores. In a graph of percent stylar shelf of molariform row (P^4–M^2 or M^3) versus percent of total tooth area of palate, there is separation of all frugivores except *Carollia* and illustrates the unique position of *Glossophaga,* a bat with very small teeth (Fig. 5). Carnivorous bats appear to have large tooth areas because many of them have small palates. *Centurio, Ametrida, Sphaeronycteris, Pygoderma,* and *Ectophylla* have the smallest stylar shelves of any bat here, while *Cardioderma* and *Myotis* have the largest.

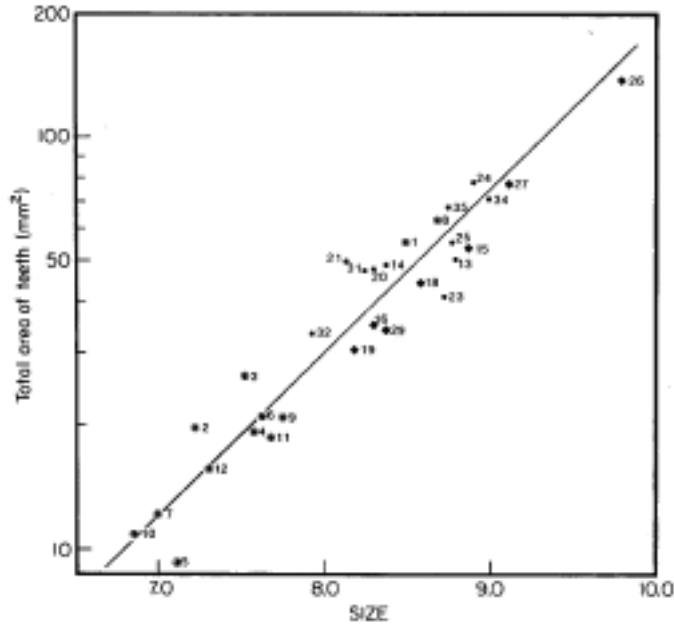**Figure 3**. A bivariate plot of total tooth area versus SIZE with the reduced major ($r = 0.7732$). Symbols are the same as in Fig. 2.
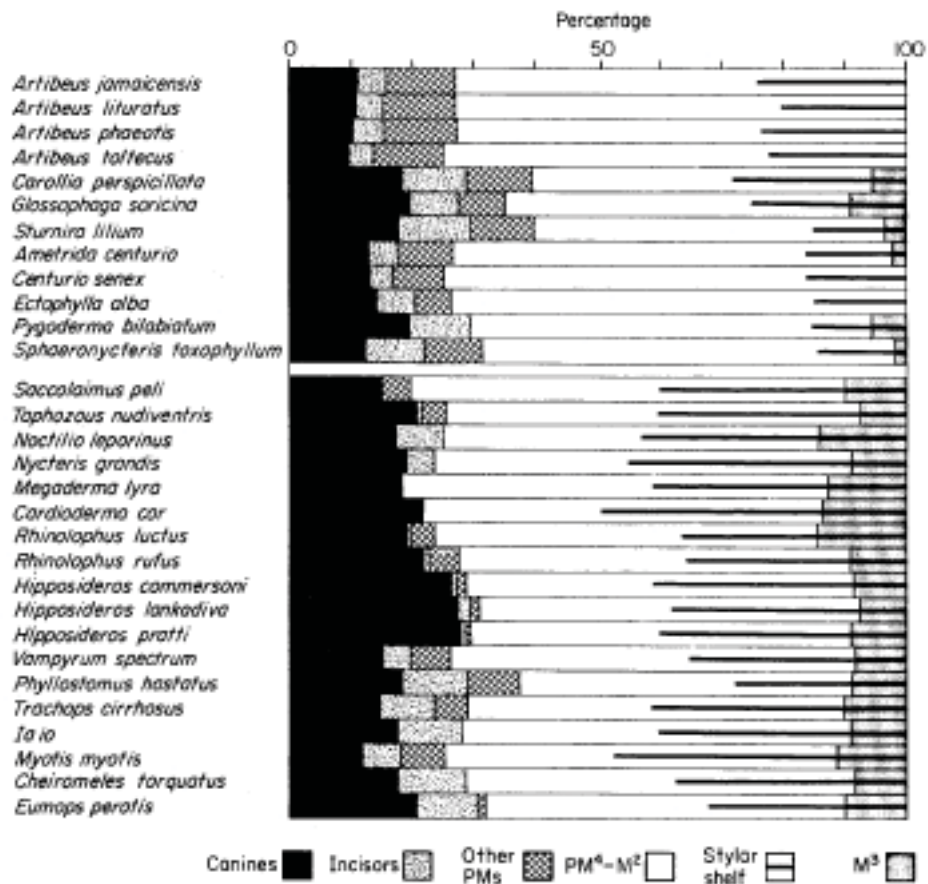

Figure 4. For each species the percentage of total tooth area occupied by each type of tooth is shown.

TABLE 2. Percentage that the different teeth or stylar shelf occupy of total tooth area for each genus

Genus	Canines	Incisors	Other PMs	P⁴–M²	M³	Molar row	Stylar shelf
Artibeus	10.51	4.82	11.16	73.52	0	73.52	22.34
Carollia	17.96	11.10	10.33	54.75	5.86	60.61	28.43
Glossophaga	19.22	8.57	7.13	55.78	9.30	65.08	27.44
Sturnira	17.66	12.00	10.22	56.43	3.69	60.12	15.01
Ametrida	12.63	5.06	8.78	70.98	2.55	73.53	15.82
Centurio	12.87	3.82	8.38	74.93	0	74.93	15.19
Ectophylla	14.08	6.34	5.70	73.88	0	73.88	15.01
Pygoderma	19.41	10.24	0	64.70	5.65	70.35	14.69
Sphaeronycteris	12.24	9.72	9.42	66.56	2.06	68.62	14.08
average	15.18	7.96	7.90	65.76	3.23	68.96	18.67
Saccolaimus	14.77	0	5.09	70.22	9.92	88.22	39.95
Taphozous	20.42	.81	4.25	66.99	7.53	74.52	40.22
Noctilio	17.12	7.69	0	61.31	13.88	75.19	42.77
Nycteris	18.99	4.84	0	67.33	8.84	76.17	44.90
Megaderma	18.03	0	0	69.28	12.67	81.95	41.23
Cardioderma	21.36	0	0	65.06	13.58	78.64	49.18
Rhinolophus	20.13	.98	3.39	62.70	11.81	74.51	34.66
Hipposideros	26.89	2.33	1.15	61.29	8.35	69.64	39.71
Vampyrum	15.10	4.58	6.23	65.98	8.11	74.09	35.41
Phyllostomus	17.60	11.30	7.92	54.38	8.80	63.18	27.88
Trachops	14.31	9.23	5.04	61.13	10.29	71.42	41.34
Ia	17.41	9.37	0	62.01	11.21	71.22	40.49
Myotis	11.57	6.27	7.14	63.62	11.39	75.01	46.66
Cheiromeles	17.38	11.02	0	63.05	8.55	71.60	37.18
Eumops	20.55	9.75	1.05	58.72	9.93	68.65	32.42
average	18.10	5.21	2.75	63.54	10.32	74.26	39.60

DISCUSSION

Stylar shelf

A major feature of the frugivores is that the stylar shelf (also called buccal crown) occupies less area on the molariform row (P⁴–M² or M³) and of total tooth area than in the insectivores and carnivores (Figs 1, 4, 5). The average area for the stylar shelf in the frugivorous species is 18.67% versus 39.60% in animalivorous species (Table 1). Although this has been pointed out as early as 1907 by Miller and again by Slaughter (1970) in describing the morphology of teeth in these phyllostomids, these authors make no mention of how the teeth may actually be functioning. However, these authors and others (Gillette, 1975; Smith, 1976; Van Valen, 1979) agree that the pattern shown in the teeth of frugivorous microchiropterans is derived from that of an insectivorous ancestor. At one extreme is a broad, deeply emarginate stylar shelf with the typical dilambdodont ectoloph of insectivores, and at the other is one where the stylar shelf and ectoloph are one and forms a non-emarginate rim on the labial side of the molar. Paracone and metacone become part of this raised buccal rim, forming a cutting edge, and along with the close fitting and continuous cutting edges of the canines and premolars give the palate the appearance of a cookie cutter. The sharp, labially flattened tips of the teeth rise above the continous border and form a serrated edge. Although this buccal rim skirts nearly the entire palate, it is not as elevated on M². The cookie cutter appearance holds for the ca-
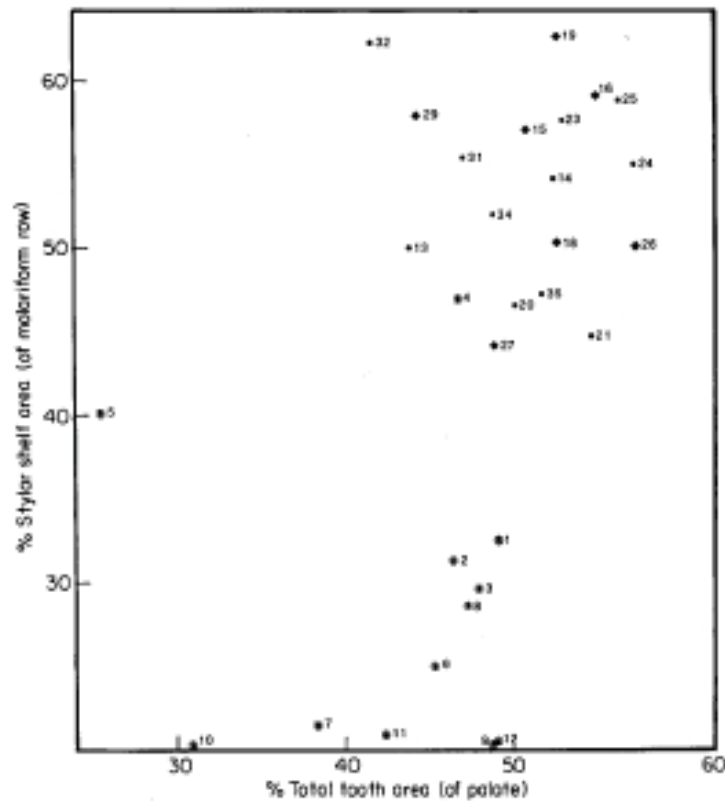
Figure 5. Two different but related areas are illustrated here. One is the percentage area that the stylar shelf occupies of the total molariform row area, and the other is the percentage that total tooth area occupies of the total palatal area. Frugivorous bats with the exception of *Carollia* are clearly separated from animalivorous bats by having smaller stylar shelves or diminutive teeth (*Glossophaga*). Symbols are listed in Fig. 2.

nines and premolars of the lower teeth as well but not for the lower molars. These are low crowned, flattened teeth. This rim configuration is typical in *Artibeus,* perhaps the quintessential frugivore, but is especially pronounced in *Pygoderma, Centurio, Sphaeronycteris, Ametrida.* Gardner (1977) suggested that bats like *Pygoderma, Centurio,* and *Ametrida,* and I would include *Sphaeronycteris* too, may be obligate frugivores. The canine teeth of *Centurio* are not round in cross-section but shaped like a comma with the tail directly aligned with the buccal rim of the molariform row (Freeman, unpublished data). This is a latero-lingual orientation and not an antero-posterior one, and is aligned as part of the rim of the cookie cutter. The five genera mentioned are stenodermine phyllostomids and all have closely fitting teeth with the labial rim around the lower teeth fitting neatly inside the labial rim of the upper teeth. The teeth are even more compressed and the nesting of lower into upper teeth even more tightly fitting in the species with short rostra.

　The lower teeth making up the labial rim act as 'pestles' and shear past the rim of the upper teeth to fit snugly into the trigon basins of the molars and posterior heels of the premolars and canines or the 'mortars'. The bite of these animals on their non-struggling food item has several other aspects. Unlike animalivorous species, which have enlarged lower molars that occlude with the upper teeth from back to front like a pair of scissors, the premolars of these frugivores engage *before* the molars and indicate to me the importance that anterior teeth—
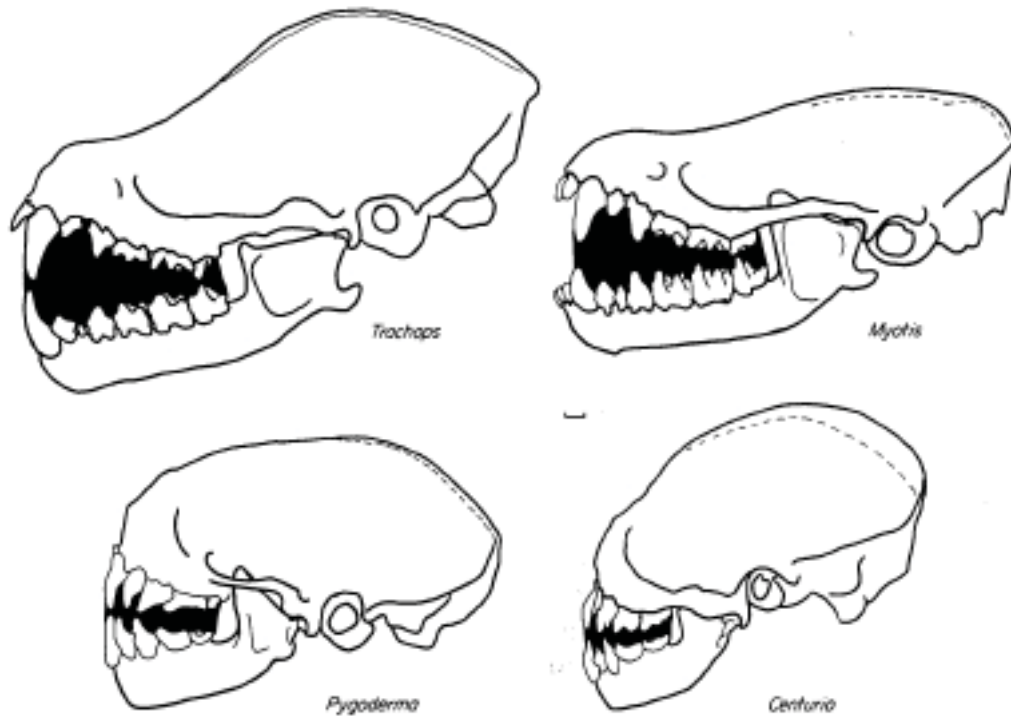
Figure 6. Profile views of two animalivorous bats, *Trachops* and *Myotis*, where the molars occlude from back to front, and two frugivorous bats, *Pygoderma* and *Centurio*, where the premolars occlude before the molars at the posterior end.

incisors, canines, and premolars—play in executing a successful bite through the skin of a fruit (Fig. 6). The bite or grip firmly secures the food item and is the initial deformation of the solid particle (Lucas *et al.,* 1985). Exactly how many teeth in the toothrow are involved in the bite is not clear, but a species like *Centurio* with its very shallow face and wide dental arcade may well have its entire toothrow, at least up to the paracone of the M^1, involved in removing a divot from a fruit. The labial rims of the upper and lower teeth (with the possible exception of the lower molars) would form a continuous cutting edge that could cut through the skin of small and large fruits. These would be the ideal teeth, because of their sharply serrated edge, to slice through a fruit with a moderately tough skin containing a mushy, ripe interior. It would be like cutting a tomato with a sharp serrated knife so that the contents would not be squeezed out when pressure is applied to the tougher outer surface. If much or all of the toothrow is involved in the bite then there must be not only the cutting action of getting the divot out of the fruit but also a certain amount of crushing occurring as the pestles come in contact with the mortars.

   Crushing may not be going on if the animal has just plucked a large fruit and must carry it off to consume it. Species of *Artibeus* particularly the larger ones, carry off huge fruits (figs) and also have large canines whose tips extend beyond the occlusal surface of upper and lower teeth. These teeth would be an advantage in gripping a large fruit deeply and pulling it from the tree. There is a hole in the perimeter of the cookie cutter, that occurs at the incisors where the lower teeth do not occlude with the uppers. In *Artibeus* where the canines are longer there are spaces on either side of the lower canines, but in *Centurio, Sphaeronycteris, Ametrida,*

and *Pygoderma* the canines fit like puzzle pieces and only the distinctive hole formed by the non-occluding incisors remains. Possibly this hole is an outlet for juice that is produced at the time of the bite to escape. It would be difficult for juice, which is an incompressible liquid, to escape from any other place along the closed perimeters of the teeth that are involved in the bite. It has also been suggested that a bat like *Centurio* actually sucks up overripe fruit (Nowak & Paradiso, 1983) and this hole could be the mechanism for that habit as well. Interestingly, while the upper incisors are spatulate or nearly so in these four species, the lower incisors are grooved transversely to the toothrow and resemble little spouts.

Two of the bats in this study considered to be at least partially frugivorous, *Glossophaga* and *Carollia,* have the more emarginate styler shelves typical of insectivores. Although the stylar shelf in *Glossophaga* occupies a proportion of the molars similar to that in insectivorous bats, this is a bat that simply has small teeth, the smallest of any bat in this study (Figs 1, 5). Since *Glossophaga* takes a fair amount of nectar and pollen (Gardner, 1977; Bonaccorso, 1979) it has diminutive teeth typical of nectarivores (because the tongue has taken over most of the work of feeding). It also feeds on fruits that are soft and small in one or more dimensions so that they are easy to grasp, harvest and masticate; and the insects in its diet are probably soft-bodied (Bonaccorso, personal communication). *Carollia* also has a more emarginate stylar shelf but has relatively larger teeth and is grouped with the insectivores in Fig. 5. *Ectophylla* has both diminutive teeth and diminutive stylar shelves, but these are in line with other frugivores (Fig. 5). These three genera do not have close fitting postcanine teeth but do have occluding, procumbent incisors. There are probably fewer anterior teeth involved in food procurement because there is no great curvature of bite. Toothrows are either parallel or divergent posteriorly, more like animalivorous bats (Fig. 1). I suspect that some of these characteristics, particularly the spaces between the teeth, teeth that are diminutive in *Glossophaga* and *Ectophylla,* may be functionally characteristic of nectar- and pollen-eating.

Sturnira, a stenodermine, and probably a frugivore, has characteristics that are neither totally similar to the other stenodermines nor like *Carollia* or *Glossophaga* either. The molars do have labial rims but they also have lingual rims so that the teeth have a mortar-like groove running antero-posteriorly. The teeth are close fitting but there is no great curvature of bite. The incisors are also close fitting. The result is that the mortar and pestle arrangement is present but the incisors and canines may be the only teeth involved in the bite.

Allocation of space on the toothrow

A second focus of investigation centres on the amount of space on the palate allocated to the different teeth on the toothrow. Molars bearing a well-developed labial rim and broad horizontal surfaces lingually function, presumably, to crush or mash food items for juice extraction (Lucas, 1979). The amount of tooth area allocated to the molariform row (P^4–M^2) in all the sampled frugivorous bats is greater than that same area in animalivorous bats (65.8 *vs*. 63.5%, respectively, and if just *Artibeus* and the obligate frugivores are averaged it becomes 70 *vs*. 63.5%). The M^1 in *Artibeus* is relatively enormous (almost 40% of' molar row) and it is probable that the reduction and loss of M^3 coincided with its expansion. It is only because

they have an additional tooth, M^3, that animalivorous bats have a greater molariform area (Table 2). Large frugivores, such as *Artibeus jamaicensis* and *A. lituratus* can carry off large heavy fruits (Gardner, 1977; Bonaccorso, 1979), but they have also been observed consuming fruit of *Dipteryx panamensis* with average weight of 22.3 g in the parent tree (Bonaccorso, 1979). Bonaccorso (unpublished data) also reports that these two are the only bats of the six or seven in the dry tropical forest of Costa Rica and of those included in this study that have the strength to harvest the larger fig in that community (*Ficus morazaniana*), weighing between 5 and 8 g and taking between 195 and 450 g of force to pluck from the tree. In contrast, a bat like *Glossophaga* could not harvest anything that took more than 135 g of force. These figures were gathered experimentally and are not by extrapolation.

The first upper molars in *Artibeus* and the obligate frugivores are quite wide bucco-lingually and may be an important area on the toothrow for food processing. Lucas *et al.* (1985, 1986) suggest that increased width of teeth at this point in the toothrow may relate to whether or not a bolus of food forms as the food is being broken down into smaller pieces. Some foods are naturally sticky and when large pieces are broken into small ones the smaller ones stick together to form a bolus. The advantage of bolus formation would be that a greater proportion of small particles would get broken per chew, and the probability of fracture would be especially enhanced in mouths that have bucco-lingually wide central postcanine teeth (Lucas et al., 1985). Here the tongue manipulates the bolus laterally so that the large teeth can break open the smaller particles that make up the bolus. *Artibeus* and *Centurio* have these enlarged central postcanine teeth, M^1s, and along with their tongues, at least for *Artibeus*, squeeze the contents from a fruity bolus (Morrison, 1980; Bonaccorso & Gush, 1987). In a bat like *Sturnira* where the molariform teeth are much more similar in size and not particularly wider than long, the foods more likely taken would be small, chemically sealed food particles that do not cohere into a bolus (*Piper* fruits?). Although both are frugivores, the difference in the nature of the fruits taken may be critically important to the form of the teeth.

I predicted that frugivores may have smaller canines and incisors than insectivores and carnivores because the latter two would need more robust teeth to capture their struggling prey. I measured canine size in two ways. First, lengths of all the canines of frugivores when plotted against size falls either on the reduced major axis or below it, indicating average to small lengths. Second, average area occupied by the canines of all frugivores compared to that area for animalivores is smaller (14 *vs*. 19.2%; Fig. 4). The canines of the stenodermines occupy only 13% of the total tooth area; this area is also less than that occupied by the three carnivorous phyllostomids (15.7%). Because canines are often sexually dimorphic in mammals, I should mention that when the canines of just the male frugivores were used they were smaller than those of the sampled animalivores, which were all male. Within the sampled bats, sexual dimorphism is apparent but in several of these species the females are larger than the males (*Ametrida* and *Pygoderma* are good examples). The lengths of the canines of *Artibeus* are moderately long as are those of *Pygoderma*. We know at least with *Artibeus* that as a canopy frugivore it transports a lot of fruit in its mouth (Bonaccorso, 1979). The small canines in *Centurio*, *Sphaeronycteris* and *Ametrida* may indicate that they do not transport fruit because they cannot get a good grip on the fruit but resort instead to scavenging fallen, overripe fruit as Bonaccorso (1979) suggests or feeding on fruit without transporting it from the parent

plant. The upper canines of *Pygoderma* are large (19% of tooth area) with spacious posterior heels (mortars) and the best developed labial rim of all the frugivores because of its prominent premolars. The lower canines are not large. We know nothing about *Pygoderma* except that it is a likely consumer of pulpy ripe fruit (Myers, 1981) and has been likened to *Centurio*. Possibly because of the large upper canines it may also transport fruit such as *Artibeus* or, at least, eat soft fruit with a tougher than usual skin. The first would allow it to get a good grip for transporting and the second would allow it to bite into fruit that the other obligate frugivores could not.

A fair percentage of the toothrow is allocated to the anterior teeth—canines, incisors and non-molariform premolars—in the frugivores (Fig. 4). *Carollia*, *Sturnira* and *Glossophaga* have between 35 and 40% invested in this area, while the frugivores as a whole have 31%. Animalivorous bats have 26% allocated to these teeth. Maier (1984) suggests "that anterior teeth are more directly correlated with the gross structure of food and they may more directly reflect ecological adaptations of a species". If true, a bat like Centurio interfaces with the environment with nearly all of its teeth.

In contrast, the animalivorous bats (omitting *Phyllostomus hastatus* momentarily) have variable appearance of ancisors and non-molariform premolars. Some have very large canine (*Hipposideros pratti* has canines occupying 28%, almost a third, of total tooth area; Fig. 4). All of the animalivorous bats have M^3s, the smallest occupying 8% of tooth area-perhaps not surprisingly by a Hipposideros-and the largest occupying as much as 14.5% (*Rhinolophus luctus*). There is a tendency for less allocation to either non-molariform teeth or incisors or both. Canines and M^3s are both well represented.

The molariform row of many of the animalivorous bats including several carnivorous species are large relative to the area of the palate. These are the same species whose total tooth area occupies over 50% of the palate in Fig. 5. The largeness of the molars may have something to do with the size of the mouthful of food taken in to be processed. Lucas et al. (1985) define a mouthful as the proportion of the volume of intra-oral space, the space within the dental arcade that is occupied by food. These authors think that considering tooth size relative to mouth size is a more reasonable consideration when examining rate of the masticatory process and the metabolic demands of the whole animal than is whole body size. What this may mean to an animalivorous bat is unknown but it is intriguing that these carnivorous bats have not only some of the closest set toothrows but also some of the largest teeth relative to mouth size of any bat here. Terrestrial carnivores bite off and swallow food particles of large size (Savage, 1977). These aerial carnivores may also take large bites although what they swallow is finely fragmented (Bonaccorsa, personal communication). Lucas & Luke (1984) suggest that the size of the dentition is primary in determining food particle size. Interestingly, fruit bats, at least as characterized by *Artibeus jamaicensis*, take small bites from the fruits they eat (Morrison, 1980).

Glossophaga is partly nectarivorous and has small teeth, and although it has the smallest canines absolutely, relative to the rest of its diminutive toothrow the canines occupy almost 20%. Areal proportions of the other teeth are like those in *Carollia, Sturnira* and *Phyllostomus hastatus,* but are unlike the rest of the bats in the study, frugivorous and animalivorous

bats alike. These four represent four different subfamilies of Phyllostomidae (Anderson & Jones, 1984). *Carollia* and *Sturnira* have proportionally smaller M³s. I think these four must be more generalized in food habits, indicating broad feeding niches, and there is evidence from the field, primarily the well-studied dry tropical forest of Costa Rica and moister forest of Barro Colorado Island in Panama, supporting this claim.

Certainly data suggest omnivory is typical of *P. hastatus* (Gardner, 1977), which, although it eats vertebrate prey, also eats a myriad of other foods including insects, fruit, pollen, nectar and flower parts. Howell & Burch (1974) noted that individuals that they captured and analysed for diet had mixed materials in their faecal matter indicating that both fruit and insects were being taken in a single foraging bout. Other species they examined showed a single food item per individual although the total sample for the species contained both plant and insects. The molars of *P. hastatus* are strongly dilambdodont and more similar to insectivores than to carnivores (Freeman, 1984) and it is a large powerful bat. The dilambdodont teeth would be good cutting teeth for most food items including large fruits, insects, or vertebrate prey. It is possible that the areal proportions allocated to the different teeth in *Phyllostomus* are proportions typical of omnivores where there is no predominance of food type, but where a good proportion of all the different kinds of teeth are required to handle a variety of different food items. *Glossophaga, Carollia* and *Sturnira* have similar proportions.

Bonaccorso (1979) placed *Glossophaga soricina* into a nectar-pollen-fruit-insect omnivore guild and stated that it took mostly pollen and fruit but some insects. Fleming, Hooper & Wilson (1972) and La Val & Fitch (1977) also categorized it as an omnivore. Heithaus, Fleming & Opler (1975) stated that is was primarily nectarivorous and, unlike the other bats in this community, had pollen loads in the wet season as well as in the dry season. Howell & Burch (1974) found that it ate only lepidopterans when it ate insects and that it switched from mixed insect-plant diet to a more strictly plant diet in the rainy season. They also stated, and I agree, that this diet seemed reasonable for a less specialized member of the subfamily Glossophaginae with a greater ectoloph on its teeth than other glossophagines (and very derived nectarivores). That *G. soricina* is capable of eating insects cannot be denied because insects are a favourite food of these bats in captivity (Ayala & D'Allessandro, 1973). Here the bats captured and chewed them for a short time and spat out the exoskeletal remains. The soft parts of the remains were missing.

Carollia perspicillata is considered a ground story frugivore by Bonaccorso (1979) where it is a food generalist taking mostly *Piper* fruit but insects too. Heithaus *et al.* (1975) stated that this bat was primarily a frugivore but utilized nectar in the dry season. Thirteen percent of 272 bats had eaten insects. Fleming *et al.* (1972) put *C. perspicillata* in a fruit-insect category while La Val & Fitch (1977) put it into a plant-fruit category. Howell & Burch (1974) intimated that *Carollia* is a *Piper* specialist and that *C. perspicillata* while it took other things including insects relied heavily on *Piper*. Like *Glossophaga soricina,* this bat will take insects in captivity, chew the body briefly for the soft parts and spit out the exoskeletal remains (Ayala & D'Allesandro, 1973). Sazima (1976) mentions that this bat exploits the nectar-feeding niche and is often confused with *G. soricina.*

Sturnira like most other stenodermine frugivores has about 15% of its molariform area allocated to the stylar shelf. *Glossophaga, Carollia* and *Phyllostomus* have up to 28%. Space proportions allocated to the different teeth however are similar to those three genera. Predominance of fruit in the diet of *Sturnira* supports frugivory, although Heithaus *et al.* (1975) mentioned that there is a strong dietary shift from fruit in the wet season to nectar in the dry season. As suggested earlier it simply may be taking different kinds of fruits, possibly small non-cohering ones.

I think there is ample evidence to support the notion that *Glossophaga* is a nectarivore with omnivorous tendencies, that *Carollia* is a frugivore with omnivorous tendencies, and that the frugivorous *Sturnira* has tendencies toward nectarivory. These space allocations for the different teeth in these species, like in *Phyllostomus hastatus,* are proportions that may result from eating a more generalized, omnivorous diet. All but *Sturnira* also have more dilambdodont teeth.

Few food data are available for *Ectophylla,* a small stenodermine bat. Gardner (1977) presumes fruit although insects have been suggested too. I suspect from the lack of robusticity of the teeth and skull and its small size that *Ectophylla* may take soft (ripe) fruits. Unlike the other frugivores here the large tooth in the molar row is the M^2 not the M^1. This large hind tooth has little emargination of the ectoloph and a large trigon basin that is typical of frugivorous species. However the spaces between the premolars and molars are reminiscent of a nectarivore.

Skull shape

Fruit bats have wide palates and some of them, particularly *Centurio, Sphaeronycteris, Ametrida,* and *Pygoderma,* have especially wide faces. The zygomatic breath of these last four range between 80 and 98% of condylocanine length. The skull of *Centurio* is almost as wide as it is long.

In an earlier study (Freeman, 1984), I proposed that wide-faced bats with robust skulls were durophagus, that is, capable of eating hard foods. The widest-faced bats had a ZYG/CCL ratio around 80%, and clearly by this criterion *Centurio* and its three consubfamilials with a ratio of 80–98% should be durophagus. The assumption being that with a wide face and short skull the teeth are brought closer to the fulcrum of the jaw lever and the strength would be greater. Also since the prey item is stationary, long jaws, which are thought to be important for capturing swift prey (Lundelius, 1956; Lederer, 1980), are not as necessary. Indeed, in a simple plot of greatest width across molars versus maxillary toothrow, all the frugivores with the exception of *Glossophaga* lie above a line representing equal widths and lengths of the palate. All the carnivores except *Nycteris grandis* and *Phyllostomus hastatus* (which may be better classified as an omnivore) lie below this line (Fig. 2). The frugivores have wider palates and the carnivores have narrower palates. Taking a plug out of a large fruit seems to require breadth rather than length. Also, having a wide bite may be important for transporting large fruits—rather like palming a basketball or carrying off an apple with one large bite.

Although the widest-faced bats here are *Centurio, Ametrida* and *Sphaeronycteris,* they do not have particularly robust skulls (as indicated by their small masseter volumes and masseter moment arms, Table 1). These fruit-eating bats with broad mouths may not need to be robust if they are indeed scooping out mushy, ripe fruit by way of one small bite after another.

In primates there is a gradation from a long narrow rostrum with a V-shaped dental arcade and unfused mandibulae to a short wide rostrum, broad U-shaped arcade and fused mandibulae. The characteristics follow the change in diet from insectivorous to carnivorous, herbivorous, and omnivorous (Hershkovitz, 1977). Beecher (1977, 1979) examined the morphology of the mandibular symphysis and the stresses put on it during chewing in primates and several other orders of mammals and concluded that calcification and ossification of the symphysis increased as tougher foods were introduced and maintained in the diet. He used the examples of leaves and bone-crushing.

A similar gradation can be seen in the fruit bats of this study. *Carollia* with an unfused symphysis and *Glossophaga* with a fused symphysis are at one extreme with V-shaped arcade (Fig. 1). Both have long jaws for their size but those of *Glossophaga* are longer, a feature possibly attributable to its nectar- and pollen-eating habit. At the other extreme is *Centurio* with *Ametrida* and *Sphaeronycteris* close behind. The outline of the palate of *Centurio* is more arcuate than in any of the primates including man (130° *vs.* 60°, Fig. 1). The mandibular symphyses are fused in all the fruit bats except for *Carollia.* It was surprising to find that the symphysis of *Glossophaga* (and other more derived Glossophagines) was fused. Either nectarivory requires the stability of fused mandibles or simply does not require moveable dentaries or fused mandibles are just a hold over from more robust ancestors. All three of the really wide-mouthed bats and *Pygoderma* have chins. Chins in primates are said to counteract the stress at the anterior palate, and that feature along with the U-shaped dental arcade in apes is well suited for very high verticle biting forces (Wolfe, 1984). This is further evidence for the importance of the anterior teeth in the obligate frugivores and the role these teeth with their cutting labial edges play in biting.

Food categories

The traditional way to categorize foods and the way that I have used thus far in this paper has been related to the species eaten (frugivores, insectivores, carnivores, etc.). These categories have been subcategorized so that consumers of plant matter are eaters of just the flowers, or just the leaves and so on (Van Roosmalen, 1984; Kay & Covert, 1984). Lucas (1979) and Lucas & Luke (1984) present excellent reasons to categorize foods based on their physical properties or texture, and suggest that only by understanding these properties and how food breaks up can we understand dental design. Following this logic those authors divide foods of primates into three categories: (1) hard, brittle foods such as seeds, unripe fruit, nuts, bone, and possibly root storage organs, and insects; (2) juicy foods such as ripe juicy fruits and possibly insects; and (3) tough and/or soft foods such as insects, animal soft tissues, leaves, grasses. My own work with bats (Freeman, 1979, 1981, 1984) has intimated the use of hard

and soft texture categories. Fortunately because there are many similarities between primate and bat diets, many of the food items and their textures would apply to bats as well. Although it may be more difficult to know not only the kind of fruit or insects eaten by a bat but also how ripe or how hard that item was at consumption, it is clear these are important parameters to be gathering about foods for the interpretation of tooth patterns. External food properties such as size and shape of food particles, total volume present in the mouth; and internal properties such as deformability, strength and fracture toughness are all important mechanical and textural features that will influence tooth design and skull shape (Lucas et al., 1986).

Hardness and softness of insects, not necessarily those eaten by bats, have been quantified or qualified by several authors (Krzelj & Jeuniaux, 1966, Neville, 1975; Hepburn & Joffe, 1976; Freeman, 1981) but little has been done for fruits. Even the simplest measurements such as weight and diameter as Wheelwright, Haber, Murray & Guindon (1984) have recorded for birds would be helpful.

The term durophagus has been used to describe animals that eat hard brittle foods (Hildebrand, 1982; Freeman, 1984). To this I propose adding the terms jusophagus for consumers of juicy foods and elasticophagus for animals that eat tough, chewy foods. Lucas & Luke (1984) suggest that primates, characterized by pestle and mortar dentitions, would be able to eat not only juicy foods but would often use the same equipment to eat hard, brittle foods like unripe fruits and nuts. Such primates would be both jusophagus and durophagus.

Blades are the primary equipment necessary for processing tough foods, foods that are chewy and difficult to break open. Insect exoskeleton or cuticle is a stiff brittle composite (like plywood) that, depending on the amount of sclerotization, resists crack propagation because different layers of fibres run in different directions. A composite like this is said to have "fracture toughness" (Hepburn & Joffe, 1976; Wainwright, Biggs, Currey & Gosline, 1976; Vincent, 1980). Only with sharp, bladed teeth are cracks made and maintained (driven) in tough foods. This is the reason for the dilambdodont, pinking shear pattern found in the teeth of insectivorous mammals. Here there are four pairs of small carnassials per molar (Freeman, 1981). Like unripe and ripe fruits, though, there are soft and hard insects, and a bat could be both elasticophagus and durophagus. Durophagy, if it is the predominant food habit, should be associated with robust rather than sharp teeth because hard, brittle items would rapidly dull a sharp blade. For example, hyaenas consume bone and use their massive, conical premolars to crush hard, brittle solids (Savage, 1977; Van Valkenburgh & Ruff, 1987). Among the sampled bats, there are several with short, stout premolars that may be used in consuming the bones of admittedly much smaller bony prey or the hard parts of insect prey. Premolars of the obligate frugivores are sharp edged labially, but those of the animalivorous bat, *Vampyrum* (perhaps an obligate carnivore; Vehrencamp, Stiles & Bradbury, 1977) are short, stout, wide-based premolars that are not particularly sharp. There are very likely hard, brittle foods (bones) in the diet of *Vampyrum*, but another animalivorous bat, *Otomops martiensseni,* and one suspected of eating soft, large insects, also has a "rather blunt, nonshearing PM³" (Freeman, 1979). Perhaps there are hard items in the diet of *Otomops* that would require teeth such as these but presently there are few data as to what is in its diet. Interestingly, *Otomops* and *Vampyrum* have both long jaws and short, blunt premolars. Another animalivore, *Scotophilus gigas*, and thought by me to be durophagus because of its wide face and robust skull (Free-

man, 1984), has particularly blunt cusps on its dilambdodont teeth. Unfortunately there is no food habit data for this bat to support the view that blunt teeth might be typical of a durophagus diet.

CONCLUSION

Evolutionarily, I think there has been a move from elasticophagy (eaters of tough foods) to jusophagy (eaters of soft, juicy foods) in bats that have specialized in eating fruits. The occlusal surfaces of the molars have changed such that the paracone and metacone occupy only the labial border of the tooth and form a raised edge surrounding an interior depression. This is a change from a dilambdodont cusp pattern, or pinking shear pattern, that bears four transverse cutting edges per molar (and more molars) and interdigitates with the lower cusps to a non-emarginate cusp pattern, or cookie cutter pattern, that bears a single labial edge and shears past the comparable labial edge of the lower teeth. Omnivorous bats in this study tend to retain the more dilambdodont pattern, and, although their teeth may be smaller, all the different kinds of teeth including the incisors and non-molariform premolars have a more equal representation on the toothrow. These features would allow a wider flexibility in the foods these bats are able to consume.

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APPENDIX 1. SPECIES MEASURED

FRUGIVORES
1. *Artibeus jamaicensis*
2. *Artibeus phaeotis*
3. *Artibeus toltecus*
4. *Carollia perspicillata*
5. *Glossophaga soricina*
6. *Sturnira lilium*
7. *Ametrida centurio*
8. *Artibeus lituratus*
9. *Centurio senex*
10. *Extophylla alba*
11. *Pygoderma bilabiatum*
12. *Sphaeronycteris toxophyllum*

ANIMALIVORES
13. *Saccolaimus peli*
14. *Taphozous nudiventris*
15. *Noctilio leporinus*
16. *Nycteris grandis*
17. **Macroderma gigas*
18. *Megaderma lyra*
19. *Cardioderma cor*
20. *Rhinolophus luctus*
21. *Rhinolophus rufus*

22. **Hipposideros commersoni gigas*
23. *Hipposideros commersoni commersoni*
24. *Hipposideros lankadiva*
25. *Hipposideros pratti*
26. *Vampyrum spectrum*
27. *Phyllostomus hastatus*
28. **Chrotopterus auritus*
29. *Trachops cirrhosus*
30. **Scotophilus gigas*
31. *Ia io*
32. *Myotis myotis*
33. **Nyctalus lasiopterus*
34. *Cheiromeles torquatus*
35. *Eumops perotis*
36. **Eumops underwoodi*
37. **Otomops martiensseni*
38. **Peropteryx kappleri*
39. **Rhinolophus blasii*
40. **Hipposideros caffer*
41. **Macrotus californicus*
42. **Lasiurus borealis*
43. ** Myotis velifer*
44. ** Tadarida brasiliensis*
45. **Molossus molossus*

*Species not included in certain areal comparisons.

APPENDIX 2. MEASUREMENTS

1. Condylocanine length (CCL)—from occipital condyle to anterior edge of canine.
2. Maxillary toothrow (MTR)—length from posterior edge of last molar on toothrow to anterior edge of canine (not alveolar length). Also used as length of palate.
3. Zygomatic breadth (ZYG)—greatest width across zygomata.
4. Width across canines (C–C WID)—greatest width across canines at the cingula.
5. Width across palate (M–M WID)—greatest width across the molars. This width is not always at the same place on the toothrow.
6. Upper canine length (UP CANIN)—greatest length from dorsal rim of cingulum to ventral tip of unworn tooth.

7. Temporal depth (TEMP D)—derived by subtracting the width at the postorbital constriction from the zygomatic breadth.
8. Temporal length (TEMP L)—greatest length from the posteriormost edge of either the lambdoidal or sagittal crest to the anteriormost muscle scars at the eminence posterior to the eye. This point is homologous to a postorbital process and the scars can usually be located under a scope with good light.
9. Temporal height (TEMP HT)—from basicranium to the top of the sagittal crest. This is actually height of the braincase and is a more reliable measurement for these bats than that taken earlier (Freeman, 1984). Although a slightly smaller measurement, it does not significantly affect comparison with the bats in that earlier study.
10. Masseter origin (MASS O)—also length of the masseter, from the postglenoid process to the anteriormost extent of muscle scar on the ventral surface of the anterior junction of the zygoma with the maxilla (scars can be seen with scope).
11. Masseter depth (MASS D)—derived from subtracting the width between the lingual mandibular foramina at the base of the coronoids from the zygomatic breadth.
12. Length of molariform row (P–M ROW)—from anterior edge of P^4 to posterior edge of last molar in toothrow.
13. Lower canine length (LO CANIN)—greatest length from ventral rim of cingulum to tip of unworn tooth.
14. Dentary length (DL)—from midpoint of mandibular condyle to anterior edge of dentary. Also the moment arm of resistance when biting with the front teeth.
15. Condyle to M_1 length (COND M1)—from midpoint of mandibular condyle to tip of protoconid of M_1.
16. Condyle to M_3 length (COND M3)—from midpoint of mandibular condyle to posteriormost edge of M_3.
17. Moment arm of the temporal (MAT)—from ventral midpoint of mandibular condyle to the tip of the coronoid process.
18. Moment arm of the masseter (MAM)—from dorsal midpoint of mandibular condyle to ventral border of angular process. Also the height of the masseter.
19. Coronoid height (CORO HT)—greatest   length from tip of coronoid to indentation in the ventral border of dentary.
20. Dentary thickness (DENTTHIC)—the lateral width of the dentary taken at the first root of M_1 to the ventral border of the dentary. Although this is not the homologous point on the dentary as in the animalivores (base of protoconid or first root of M_2), it does appear to be the same functional point, i.e. about the midpoint of the dentary.
21. Dentary depth (DENT D)—the depth through the dentary at the first root of M_1.
22. Condyle length (COND L)—the greatest length of the mandibular condyle,
23. Condyle height (COND HT)—the height of the mandibular condyle above the lower toothrow. Taken in lateral view from a line (cross hair in scope) through the valleys between protoconids and hypoconids of molars (1 and 2 in frugivores, 1 and 3 in animalivores) to the superior edge of the condyle.
24. Area of palate (PALATE)—taken with polar planimeter from drawing encompassing the area from a line drawn across the anterior edge of the posterior emarginations of the palate and including the outermost perimeter of the teeth. In those bats where there is a deep anterior palatal emargination or fragile or non-existent premaxillae, the anterior border is made across the anteriormost margins of the maxillae between the canines.
25. Area of canines and incisors (C–I AREA)—taken with polar planimeter from drawing of area occupied by canines and incisors. Care was taken to mount the palate so that the occlusal surface of the molars was equally in focus when drawn. More procumbent incisors will occupy more area than non-procumbent ones.
26. Area of molariform row (P–M AREA)—taken with polar planimeter from drawing of occlusal area occupied by P^4 and all of the upper molars.
27. Stylar shelf area (SS AREA)—taken with polar planimeter from drawing of the occlusal stylar shelf of the molariform row. This is the raised shelf bordered by the ectoloph on the lingual side.
28. Dentary area (DENTAREA)—the product of dentary thickness and dentary depth and represents the area of the cross-section of the dentary near the midpoint of its length.
29. Temporal volume (TEMP VOL)—the product of temporal fossa length, width, and height and estimates the temporal muscle volume.
30. Masseter volume (MASS VOL)—the product of masseter origin (length), depth, and height (moment arm of the masseter) and estimates the masseter muscle volume.
31. Total tooth area (TT AREA)—taken with polar planimeter from drawing of occlusal area of all teeth (including all premolars).
32. SIZE—the sum of the natural logs of condylocanine length, zygomatic breadth, and temporal height. It is this composite character against which all other measurements are compared using reduced major axes.