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Form, Function, and Evolution in Skulls and Teeth of Bats

PATRICIA W. FREEMAN

Bats provide a model system for tracking change from the primitive mammalian tooth pattern to patterns indicating the more-derived food habits of carnivory, nectarivory, frugivory, and sanguinivory. Whereas microchiropteran bats show all these transitions, megachiropterans illustrate an alternative pattern concerned only with frugivory and nectarivory. In microchiropterans, it is likely that carnivory, nectarivory, frugivory, and sanguinivory are all derived from a dilambdodont insectivorous tooth pattern. Megachiropterans are troublesome because they appear as nectarivores or frugivores without a clear relationship to ancestral taxa.

The nature of the food item and how teeth respond to that item evolutionarily is an issue I have addressed previously diet by diet (Freeman 1979, 1981a, 1981b, 1984, 1988, 1995). Within the insectivorous family Molossidae, and among insectivorous microchiropteran bats in general, consumers of hard-bodied prey can be distinguished from consumers of soft-bodied prey by their more robust mandibles and crania, larger but fewer teeth, longer canines, and abbreviated third upper molars (M3; Freeman 1979, 1981a, 1981b; Strait 1993a, 1993b). Carnivorous microchiropterans have distinctive large upper molars with lengthened meta-

stalar shelves and elongated skulls with larger brain volumes and external ears than their insectivorous relatives. As in terrestrial mammals, however, there is no clear distinction between insectivorous and carnivorous species (Savage 1977; Freeman 1984). Microchiropteran nectarivores are also on a continuum with insectivores but are characteristically long-snouted with large canines and diminutive post-canine teeth (Freeman 1995). Finally among microchiropterans, frugivores differ from insectivore/carnivores and insectivore/nectarivores by having a substantially different cusp pattern on the molars. The paracone and metacone are pushed labially or buccally to become a simple, raised but sharpened ridge at the perimeter of the dental arcade (Freeman 1988, 1995).

First I examine function of differently shaped skulls and palates of bats in different dietary groups. Among Megachiroptera, frugivores are on a continuum with nectarivores, but there are characteristics of robustness that appear to be good indicators of diet that distinguish the two (Freeman 1995). Megachiropterans have several convergent characteristics in common with microchiropteran nectarivores. I believe this convergence is not only the key to explaining cranial and palatal shape and jaw function in bats but also is

critical to understanding the evolution of nectarivory and frugivory in chiropterans. Associated with the shape of the palate is the way that allocation and emphasis of tooth material on the tooththrow shift between suborders. The relative area that each kind of tooth occupies on the tooththrow is quantified and serves as the basis for my interpretations.

A second goal is to examine function in bat teeth. Here I synthesize my past work on tooth function, particularly with regard to canines and molars, and introduce a novel way to examine function in canines. Function in more complex teeth involves a review of the principal cusps on the upper and lower molars and how cusp patterns have evolved relative to different diets. Specifically, I contrast carnivory in terrestrial mammals and bats, insectivory in insectivorous and nectarivorous species, and frugivory in mega- and microchiropterans. Finally, I suggest that the evolution of dilambdony can be correlated with packaging and digestibility of the food item.

Study Methods

This study is based on 103 species representing 78 genera, 10 families, and two suborders of the order Chiroptera. Among microchiropterans there are 40 insectivorous, 7 carnivorous, 18 nectarivorous, 14 frugivorous, and 2 sanguivorous species. Megachiropteran frugivores and nectarivores are represented by 11 species each (Appendix 9.1). Each species was usually represented by a single adult male skull in perfect or near-perfect condition (i.e., no broken or missing parts), although a perfect adult female skull was preferable to an imperfect male skull. There are no missing data except for naturally missing teeth in the tooththrow, which are treated as missing data and not as zero; including the latter would substantially affect the average of those bats with the tooth present.

Homologies for tooth number are from Andersen (1912). Areal measurements, recalculated for this study, are from camera lucida drawings that were scanned into a Macintosh computer and taken automatically inside (teeth) or outside (palate) high-contrast occlusal outlines. Areas include upper incisors (I); upper canines (C); nonmolariform upper premolars (other PMs); fourth upper premolars (PM4); and first, second, and third upper molars (M1, M2, and M3), where found; the area of the raised stylar shelf (including PM4); and the area of the palate (as modified in Freeman 1988, 1995). Linear measurements are the same as those in Freeman (1995; but see also Freeman 1984, 1988).

This chapter is concerned with large-scale patterns. Details on variation among species can be found in earlier papers. The size character is the same as that used in previous papers (SIZE = sum of the natural logs of condylo-

canine length, zygomatic breadth, and temporal height; Freeman 1984, 1988, 1992, 1995).

Experimental work examining form and function in bat canine teeth involved finite-element modeling and photoelastic analysis. Shapes of cross sections in canine teeth can be edged and nonedged (Freeman 1992), and experiments with models of teeth puncturing a substance can show how these two different types of cross sections initiate different patterns of stress or toothmarks in a substance ("food"; Freeman and Weins, unpublished data). Finite-element modeling is a mathematical description of dimensional or geometric change in a structure when a force is applied to deform the structure to reveal where the most intense stresses should occur (Zienkiewicz and Taylor 1989; Rensberger 1995).

Two-dimensional models were constructed to show stresses occurring in the "food" when penetrated by teeth with 30°, 60°, and 90° angles at their edges and a circular or nonedged tooth. In three dimensions, actual stress analysis tests were performed with a metal cone and a pyramid with an edge of 90°, simulating oversized replicas of teeth (Caputo and Standlee 1987). These oversized "teeth" were loaded into plastic ("food") that had been heated to the point of being liquid and allowed to cool around the loaded forms (called stress-freezing). Cooling freezes the stress-induced patterns permanently in the plastic. The plastic is photoelastic, which means that the birefringent (refractive in two directions) patterns of stress caused by the deformation of the plastic by the different shapes can be observed under polarized light. The visual results of that experiment are presented here. Photoelasticity has been used in dentistry for several years (Guard et al. 1958; Fisher et al. 1975), but only to examine what stresses are being placed on the tooth and not how the tooth is stressing the food.

Results

Cranial and Palatal Form

Shapes of bat skulls, represented by zygomatic breadth divided by condylocanine length, vary between being as wide as they are long to being only a third of the skull length. However, skull width of most species is one-half to three-quarters the length of the skull (Figure 9.1A). Extremes are represented by the microchiropteran family Phyllostomidae, with *Centurio* and other stenodermatines on the wide end and *Musonycteris* and other glossophagines on the narrow end. Four wide-faced insectivorous species, mentioned in earlier studies (Freeman 1984), group together at 0.8 above the majority of species. On the other hand, shapes of palates of bats (breadth across the molars divided by length

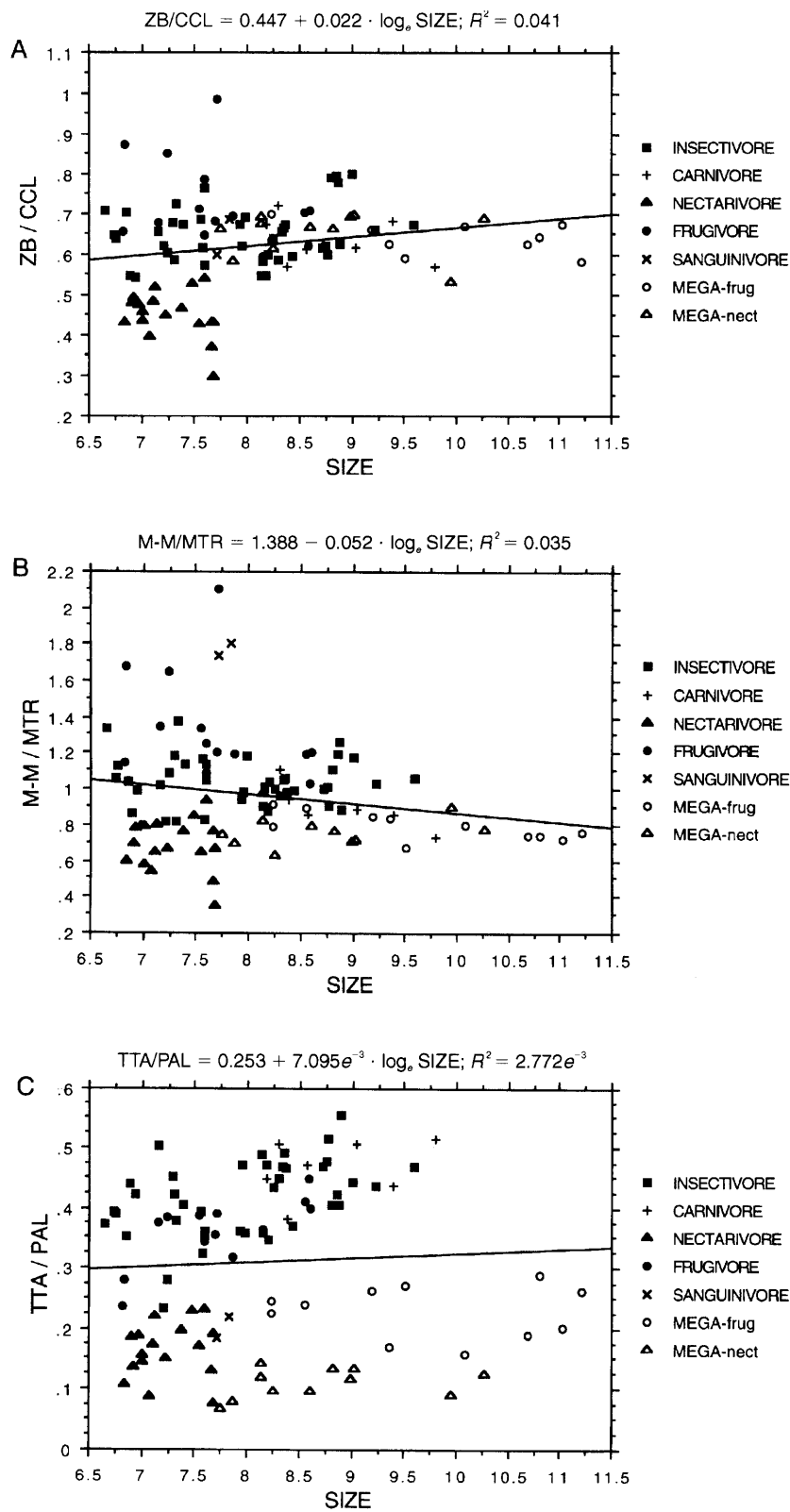


Figure 9.1. Cranial and palatal features that are important in chiropterans. (A) Zygomatic breadth (ZB) divided by condylocanine length (CCL) regressed against SIZE (see *Methods*). (B) Breadth across upper molars (M-M) divided by length of maxillary tooththrow (MTR) regressed against SIZE. (C) Total tooth area (TTA) divided by palatal area (PAL) regressed against SIZE. Open symbols denote megachiropterans; all other symbols denote microchiropterans. Megachiropterans have heads that are relatively as wide as most other chiropterans' heads (A) but have narrower palates (B). Megachiropterans (both frugivores and nectarivores, MEGA-frug and MEGA-nect) and microchiropteran nectarivores have small teeth on large palates, whereas microchiropteran insectivores, carnivores, and frugivores have large teeth on small palates (C). Two microchiropteran frugivores, *Ametrida* and *Ectophylla* (in order away from regression line), and two microchiropteran insectivores, *Lonchorhina* and *Mormoops*, have smaller teeth on larger palates than do others in these two dietary groups.

of maxillary tooththrow) show a substantial downward shift from the line representing skull shape, such that microchiropteran nectarivores, megachiropterans, and several microchiropteran carnivorous species have long, narrow palates (Figure 9.1B). Again, phyllostomids show the greatest variation, but the wide-palated forms include two species of sanguinivores.

Form and Emphasis of Teeth

With few exceptions, the microchiropteran insectivores, carnivores, and frugivores have relatively large teeth on small palates, and microchiropteran nectarivores and megachiropterans have relatively small teeth on large palates (Figure 9.1C). Megachiropteran nectarivores have relatively smaller teeth on the palate than megachiropteran frugivores. These relative proportions are maintained regardless of the size of the bat (as represented here by the composite SIZE character) and presumably body mass (Freeman 1988).

The relative area of the tooththrow occupied by different teeth can be compared across teeth, suborders, and feeding

groups (Figure 9.2A,B). Dietary categories are further subdivided into groups of species sharing the same tooth formula (Figure 9.2C). First and second upper molars in microchiropterans occupy the greatest relative areas (23% and 22%, respectively), followed by canine area (18%) and third upper molars (10%) if present, and other PMs and incisors (6% each). In contrast, canines occupy the greatest amount of area in megachiropteran tooththrows (27%), followed by other PMs, PM4s, and M1s (20% each); second upper molars occupy only 9%, and incisors, a small 4.5%.

Among microchiropterans, insectivorous and carnivorous species are similar in that nearly half the tooththrow is devoted to first and second molars. In insectivores with only PM4 in the upper row (insectivore 2, Figure 9.2C), the incisors, first and second molars, and styler shelves become larger. Carnivorous species have the most variability in teeth present on the tooththrow; premolars, incisors, or both premolars and incisors can be missing. In the latter case, canines and M3s become larger. Carnivorous microchiropterans have, relatively, the largest M1s, M2s, and styler shelves of any bat, and like insectivores with only PM4

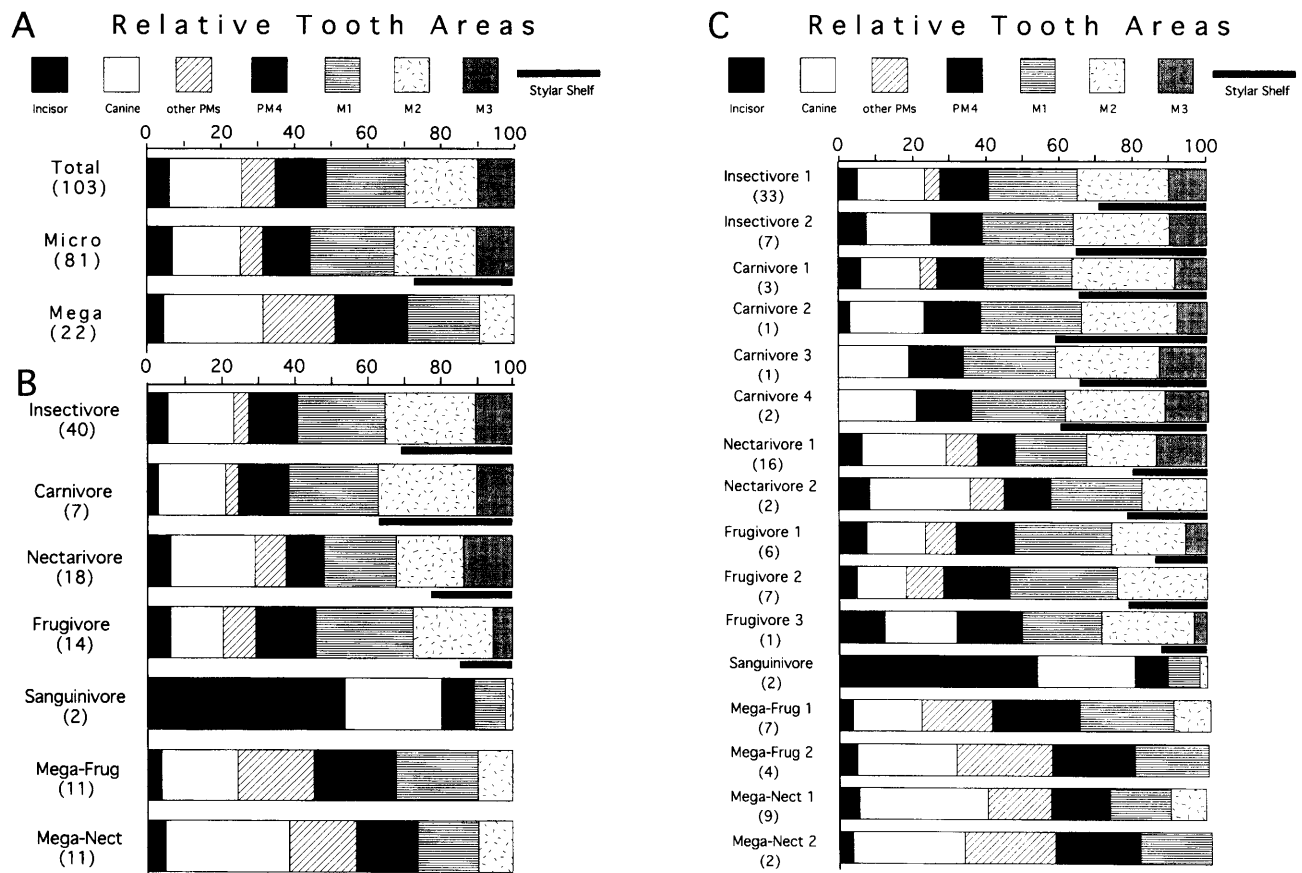


Figure 9.2. Average percentage of total tooth area occupied by different teeth: (A) for all bats and by suborder; (B) by dietary group (see Appendix 9.1); (C) by dietary subgroups (dietary groups subdivided further by tooth formula; see Appendix 9.1).

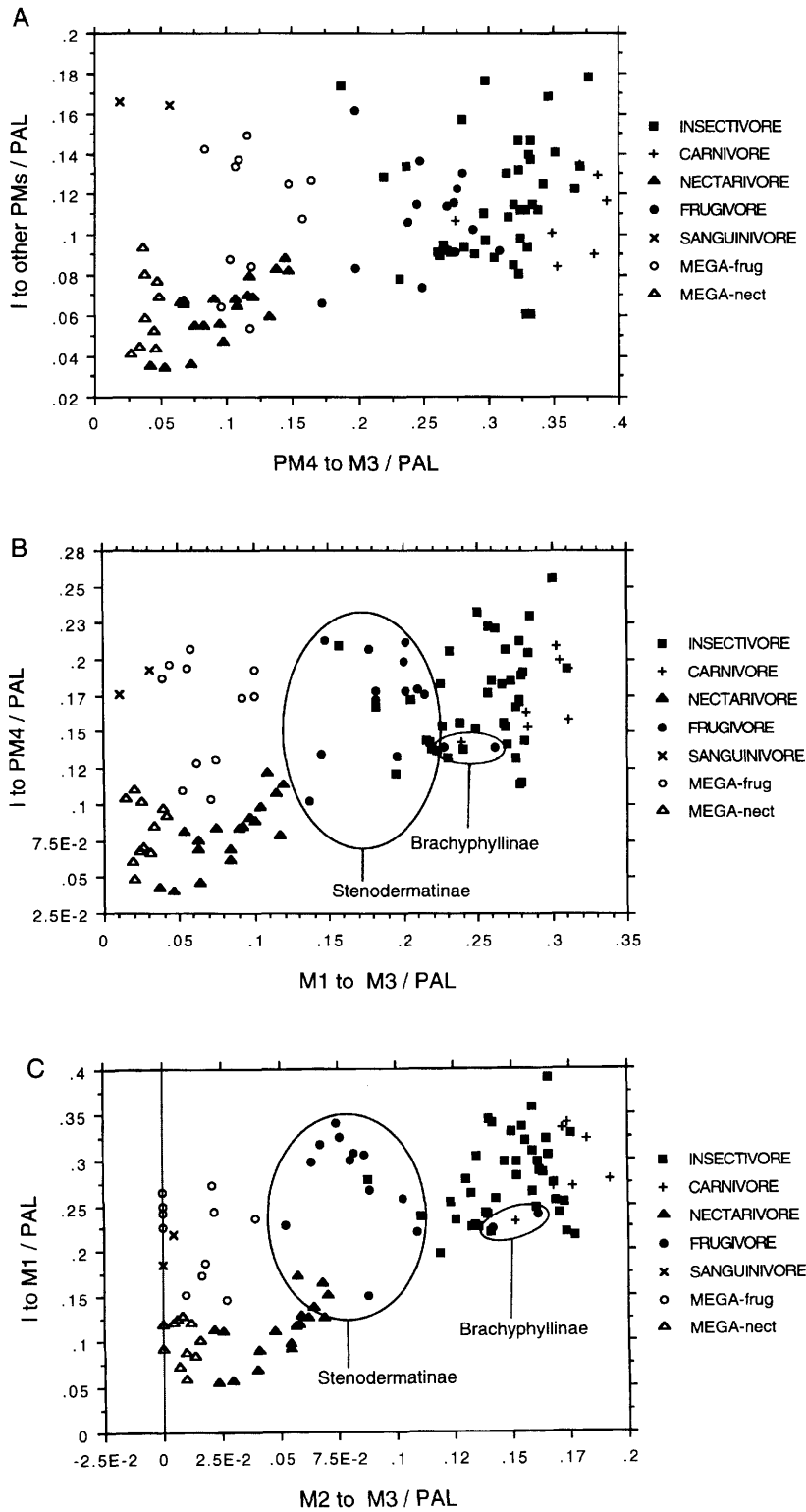


Figure 9.3. The allocation of dental material shifts anteriorly on the palate (PAL) between suborders and among different dietary groups of microchiropterans. Open symbols denote megachiropterans; all other symbols denote microchiropterans. (A) Area that nonmolariform incisors, canines, and other premolar teeth (I to other PMs/PAL) occupy of palatal area (not total tooth area), compared to area occupied by molariform (M) teeth (PM4 to M3/PAL). (B) Area that incisors, canines, other premolars, and PM4 (I to PM4/PAL) occupy of palate, compared to area occupied by molars (M1 to M3/PAL). (C) Area that incisors through the first molar (I to M1/PAL) occupy of palatal area, compared to area occupied by the most-posterior molars (M2 to M3/PAL).

present, have larger M2s than M1s. In fact, the smallest carnivores—*Nycteris*, *Cardioderma*, and *Trachops*—have some of the very largest M2s and stylar shelves (*Nycteris* is carnivore 2 in Figure 9.2C). Regardless of the variation anteriorly, M1 and M2 constitute more than 50% of the total tooth area in carnivorous bats.

The largest tooth on the microchiropteran nectarivore tooththrow, relative to total tooth area, is the canine (23%), followed by the molars, PM4, and other PMs. In addition to large canines, nectarivores differ from insectivores by having larger M3s (13.5%) and smaller PM4s (10%) but other PMs that are larger (8.5%). In nectarivores in which M3 is absent, canines and M1s are larger (27% and 25%, respectively). Stylar shelves are smaller (22%) than in insectivores (32%) and much smaller than in carnivores (37%). In absolute size, teeth in nectarivores are considerably smaller than in other microchiropterans (see Figure 9.1C; Freeman 1995).

Frugivorous microchiropterans have relatively the largest PM4s and M1s and the smallest canines, M3s, and stylar shelves of all microchiropteran dietary groups. In those bats in which M3 is absent, M1 occupies a third of the tooththrow and all the premolars occupy a third. In the one frugivore with PM4 only, incisors and canines are larger (12% and 20%, respectively; *Pygoderma* is frugivore 3, Figure 9.2C). Finally, large incisors (54%) and large canines (27%) dominate tooththrows of blood-feeding microchiropterans at the expense of postcanine teeth (20%; *Desmodus* has no M2, but I did not subdivide this category further).

Megachiropterans have the greatest relative area invested in canines (27%) followed by equal proportions invested in other PMs, PM4, and M1 (20% each); however, these figures obscure the large difference in canine area between megachiropteran frugivores and nectarivores. Among frugivores, canines are smaller (21%) and PM4 and M1 are larger (23% each), whereas megachiropteran nectarivores have larger canine areas (34%) and smaller PM4s and M1s (17% each). Other PMs are larger in megachiropterans than microchiropterans. Megachiropteran frugivores that have lost M2 have larger areas for canines (27%) and for other PMs (26%); nectarivores without M2s have less area for canines (30%) but increased area for other PMs (25%), PM4 (23%), and M1 (19%). However, as in microchiropterans, the absolute size of teeth of megachiropteran nectarivores is smaller than the teeth of megachiropteran frugivores (see Figure 9.1C; Freeman 1995).

Emphasis in tooth material on the palate shifts between suborders and among dietary groups. Megachiropteran palates have relatively larger areas for nonmolar teeth while most microchiropterans have relatively larger areas for molariform teeth (Figure 9.3A). This pattern is true regardless of the size of the bat. Not surprisingly the proportion of

the palate occupied by anterior nonmolariform teeth in megachiropterans is affected by the absence of molars (M3s and M2s) in the tooththrow (Figure 9.3A). The proportion of the palate occupied by all teeth anterior to the molars (I to PM4) further concentrates in the megachiropterans on the horizontal axis and starts to show the difference between microchiropteran frugivores and carnivores (Figure 9.3B). Stenodermatines have small or no M3s (but large M1s) and are different from the two brachyphyllines, which have substantial M3s. Finally, when the tooththrow is divided so that M1 is included in the anterior portion of the palate (Figure 9.3C), stenodermatine frugivores are well separated from all carnivorous microchiropterans and insectivorous bats and brachyphyllines range in between.

Canine teeth have different cross-sectional shapes (Freeman 1992). Finite-element modeling in two dimensions predicts the distribution of stress in a “food” material and indicates where cracks are most likely to form. Stresses around the edged mark are greater than those surrounding the circular mark and are concentrated at the edges (Figure 9.4A). Further, stresses actually increase as the angle at the edge decreases. Initial experimentation in three dimensions at the tooth–food interface with photoelastic techniques verified that the lines or fringes of stress are concentrated at the edges of the edged tooth. In the circular or nonedged tooth, stresses are uniformly distributed (Figure 9.4B).

Discussion

Cranial and Palatal Function

NARROW SKULLS. It is not surprising that bat skulls can be short and wide or long and narrow, but it is of considerable evolutionary interest that the shortest, widest skulls and the longest, narrowest skulls are found in the same family, Phyllostomidae, and not across suborders. However, bats with long, narrow palates include microchiropteran and megachiropteran nectarivores and megachiropteran frugivores. In addition to elongated palates, these bats have in common (1) greater distances from the last lower molar to the jaw joint (Freeman 1995), (2) smaller tooth-to-palate ratios with spaces separating the teeth, (3) fused mandibles, (4) shallower, less well defined glenoid fossae (Freeman 1995), and (5) thegosed upper canines that occupy relatively large areas of the tooththrow.

Possession of a long tongue explains these shared features. With the development of a large, elongated tongue, the palate lengthens, and teeth not only occupy a smaller proportion of palate but also have more space between them. In nectarivores, teeth become absolutely smaller (see Figure 9.1C). Also, teeth appear to have moved anteriorly

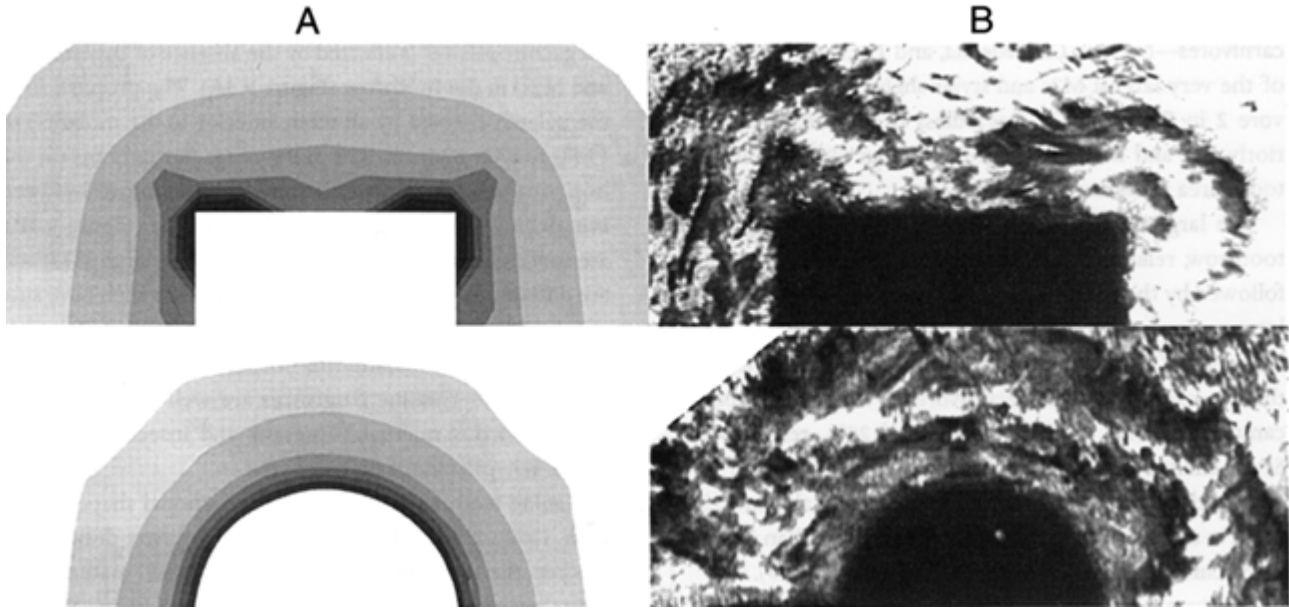


Figure 9.4. Distribution of stresses in a substance that is being penetrated by an edged tooth (top panels) and a nonedged or conical tooth (bottom panels). (A) Two-dimensional constructs simulated with finite-element modeling. In this schematic, the darker the area, the greater the concentration of stress (and the greater the likelihood of cracks forming there). (B) Verification of models using photoelastic stress analysis, a three-dimensional experiment (see *Methods*). Concentrations of stress are visible at the corners of the edged tooth; a more uniformly distributed pattern of fringes (lines of stress) can be seen around the nonedged tooth.

with elongation of the palate, resulting in the last lower molar being farther from the jaw joint than in microchiropteran insectivores, carnivores, and frugivores (Freeman 1995). Greater distance to last lower molar from the jaw joint might suggest bite strength is weak, but this is not realistic for large megachiropteran frugivores that are powerful and can crack open cocoa pods (Hill and Smith 1984). The megachiropteran palate is narrow and elongated but the skull is not (see Figure 9.1A,B). The ratio of zygomatic width to length of skull for megachiropterans is similar to that in most other bats, which suggests muscular strength is similar as well. Moreover, the origin of the masseter at the anterior base of the zygoma in megachiropteran frugivores is farther forward on the maxilla than in megachiropteran nectarivores and overlaps the last upper molar. This arrangement results in a greater mechanical advantage of the masseter (Freeman 1979, 1995). Bite force on the tooth-row may be greatest at the anterior root of the zygoma because the buttressing can absorb much of the force (Crompton and Hiimäe 1969; Werdelin 1989).

Although frugivorous megachiropterans have larger teeth than their more nectarivorous relatives, the teeth of both sit on elongated palates (see Figure 9.1C). Intertooth space is greatest in the most elongated jaws, which may be useful in determining degree of nectarivory (Freeman 1995). For example, among microchiropteran nectarivores *Musonycteris*, *Choeronycteris*, and *Choeroniscus* have the greatest space between teeth, and all three species have lost

lower incisors. This loss reflects the most derived result of the protrusion and retraction of the working nectarivorous tongue (this is discussed later). Among megachiropterans, nectarivorous species have greater intertooth space and more frugivorous species have less (Freeman 1995).

Fusion of the mandibular symphysis occurs in frugivorous and nectarivorous species of both suborders and may stabilize or strengthen the anterior end of the jaws (Beecher 1979; Freeman 1988, 1995). Short-faced frugivorous phyllostomids even have chins, which reflects the strengthening of the jaws to resist vertical forces at the front of particularly short, wide jaws. Symphyseal fusion in bats with elongated jaws reflects the reinforcement needed to stabilize the mandible as the long tongue protrudes well beyond the anterior margin of the jaw for nectar-feeding. Some nectarivores have developed a sagittal, bladeliike, bony reinforcement at the symphysis.

Terrestrial carnivores that must have precise occlusion of cusps on upper and lower teeth to slice meat have an unfused symphysis (Scapino 1965) associated with a snug-fitting, tapered cylindrical condyle that limits the degrees of freedom of movement of the jaw. In early creodonts the condyle was loose fitting and the symphysis was long and very well fused. Microadjustment at occlusion in these animals was thought to be accomplished by swinging the mandible sideways so that the transverse ridges on the molars guide the occlusion of the carnassial teeth (Savage 1977).

Microchiropteran insectivores and carnivores also have unfused mandibles. Their close-fitting dilambdodont teeth must fit precisely during each chewing cycle to be effective and not malocclude. Microadjustment of the teeth can be made anteriorly at the unfused symphysis and to some extent at the glenoid. Although not so tight fitting as that in terrestrial carnivores, the glenoid fossa in these bats is a well-defined platform with a well-developed postglenoid process (Freeman 1979, 1995).

Microchiropteran nectarivores and megachiropterans all have looser-fitting glenoid articulations than insectivorous and carnivorous microchiropterans (Freeman 1995) but have fused symphyses. The glenoid fossae are shallower with less distinct articular platforms and poorly developed postglenoid processes. With fusion of the symphysis, teeth either do not need to occlude precisely or, if they do, can adjust at the rear of the jaw in a looser-fitting articulation. Although small, teeth of microchiropteran nectarivores have discernible but not deeply emarginate dilambdodont cusps. As shown next, these small teeth still register with each other at the talonid–protocone contact. Several of these bats have a ventral extension of the jugal (the posterior root of the zygoma) that may limit lateral movement of the condyle, but all have narrow condyles and reduced postglenoid processes (Freeman 1995). The ventral extension may aid the registration of dilambdodont teeth in jaws with a fused symphysis.

Microchiropteran frugivores have a fused mandible as well as a well-defined glenoid articular platform with a well-developed postglenoid process. Here the dilambdodont pattern and precisely fitting transverse cusps are diminished to a raised rim, and only vertical registration is necessary for the lower dental arcade to nest inside the perimeter of the upper teeth.

Megachiropteran frugivores, which use long tongues to eat both fruit and nectar, also have fused symphyses. Indeed large, pointed tongues of “enormous protruding capacity” are a hallmark of feeding in megachiropteran frugivores (Greet and De Vree 1984). For example, to eat bananas the tongue moves forward to mash the bolus against the dorsal palatal ridges. The tongue does not stop at the margin of the mouth but protrudes beyond the mouth to curl forward over the nose. The tongue protrudes less and less with harder foods like apples. Megachiropterans have simple-basined teeth surrounded by low edges that hardly touch at occlusion. Indeed, without touching and interlocking, homologous cusps cannot be discerned (Koopman and MacIntyre 1980). Fused mandibles may limit the ability of the jaws to register the teeth precisely or at all at occlusion. If registration of teeth is inversely related to fusion at the mandible, and, if fusion evolved first because having fused mandibles meant better support of a long tongue, then

teeth in megachiropterans cannot be expected to interlock very well or at all nor could discernible cusps be expected.

WIDE SKULLS. Bats can also have wide skulls and palates (see Figure 9.1A,B). Wide skulls in microchiropteran insectivorous bats are robust with enlarged cranial crests, teeth closer to the fulcrum of the jaw joint, increased muscle mass for the more anteriorly placed masseter, and usually lengthened canines (Freeman 1984). Wider-skulled insectivores eat harder-shelled insect prey (Freeman 1981a; Strait 1993a, 1993b). However, wide skulls in microchiropteran frugivores are not necessarily robust, and the very widest, such as *Centurio*, is paedomorphic and fragile. The widest stenodermatines also have wide palates that allow more teeth to be involved with the bite, a bite which should have good mechanical advantage given the close proximity of the teeth to the jaw joint (Greaves 1985). Canines in these most extreme frugivores are small, and the cheekteeth close on food from front to back rather than from back to front as in insectivores and carnivores (Freeman 1988). In these frugivores, wide faces would be well adapted for taking plugs out of fruit and being able to secure a wide grip on fruits for transporting. Morrison (1980) observed feeding in *Artibeus* and found that this stenodermatine consumed fruit in small bites. After chewing, each bolus was then pressed against the ridges of the palate with the tongue, the juice swallowed, and dry pellets spat out. There was no discussion of the tongue extending beyond the mouth during feeding, and although it can be extended to drink (C. J. Phillips, personal communication), the tongue is not thought to be specialized for protrusible feeding (T. A. Griffiths, personal communication). These observations lead me to believe that tongues are not elongated in phyllostomid frugivores.

Dental Function

CANINES. Calculating the percentages of the tooththrow that are occupied by particular teeth is a first attempt in determining the functional emphasis of a tooth. However, area indicates little about how shanks of canines and stylar shelf patterns on molars may function at the tooth–food interface. Canine teeth occupy a substantial proportion of the tooththrow and have the primary function in gathering and subduing prey (Freeman 1992). I have speculated that the cross-sectional shape of insectivorous bats involved the flattening of at least one side of the tooth to form a knifelike flange that would allow the tooth to more easily pierce the exoskeleton of insect prey (Freeman 1979). In truth, canines of bats are quite diverse and cross-sectional shapes can be triangular or polygonal, with the vertices of the triangle or polygon representing edges that extend longitudinally from

tip to cingulum. A reasonable assumption is that there should be differences in how cracks are propagated in the substance being penetrated on the basis of the shape of the tooth (Freeman 1992).

In recent experiments, Freeman and Weins (1997) punctured apples with casts of bat teeth to determine what sharpnesses and forces occurred at the tips of teeth. Not surprisingly, sharper tips required less force to penetrate the surface than blunter tips. More complex, however, was the investigation of how the shank of the tooth might interact with a food item. Both finite-element models and experimentation with photoelastic materials support the notion that longitudinal edges on canines would be beneficial in initiating cracks in foods (see Figure 9.4A,B). Because energy increases (indicated by higher concentration of stress) at the edges of canines, cutting through prey would be optimized much like the edge of a surgical needle, which is triangular in cross section.

The alternative shape, with a round cross section, would mean the tooth must press deeper into the prey to finally break through the surface by force. Given the elasticity of surfaces of endo- and exoskeletal prey and fruits, the latter penetration would be less efficient. Freeman (1992) identified and quantified as sharp at least one or both of two edges on bat canines, one directed toward the incisors and one directed toward the ectoloph of the postcanine teeth. Edges on canine teeth may be especially beneficial to predators and harvesters whose forelimbs are modified for flight and must eat or gather (many) items while flying. Single and multiple edges are found on all canine teeth of these bats (Freeman and Hayward, unpublished data). The relationship between the pattern of sharp and blunt edges and diet is under study.

A final feature shared by megachiropterans and microchiropteran nectarivores is that the anterior surface of the upper canines is worn by the lower canines. This phenomenon is especially noticeable in nectarivores. Tooth-on-tooth wearing and self-sharpening has been called thegosis (Every 1970) or simply attrition (Butler 1972; Osborn and Lumsden 1978). In nectarivores, the lower canines are splayed laterally during jaw closure (when viewed frontally; Figure 7 in Freeman 1995) so that they engage both upper canines well before occlusion of the cheekteeth. I believe that wear occurs because both lower canines can brace themselves simultaneously against both upper canines with the posterior pull of the jaw muscles. A bracing function would help support the lower jaw while the long tongue is being extended well beyond the anterior margin of the jaw to retrieve nectar from horizontally oriented flowers (Freeman 1995). Rapid protrusion and retraction and the mass of the tongue needed to gather nectar would create large depressive loads at the front end of the lower jaw.

The extent of wear varies in microchiropteran nectarivores from just a small patch of wear at the cingulum of the upper canine in species that have lost lower incisors to an entirely worn anterior face of the upper canine in species that retain the lower incisors (Freeman 1995). Loss of incisors occurs in the most derived nectarivores, presumably to allow an unhindered path for protrusion and retraction of the tongue during feeding. Although feeding in these extreme nectarivores could be done without opening the jaws widely or at all, the lower canines still brace at the upper cingulum as evidenced by the small but quite distinct patch of wear. In those nectarivores with lower incisors present, the entire face of the upper canine is worn because the jaws have to open wide enough to allow the tongue to move but also to avoid the lower teeth.

Longitudinal edges of canines in nectarivores (but not those in insectivores, carnivores, or frugivores) are sharpened by wear, which can affect cross-sectional shape (Freeman and Hayward, unpublished data) and may also serve some function during feeding, perhaps that of cutting into flower parts for nectar. With the additional features of relatively large canines and fusion of the mandibular symphysis, megachiropteran and microchiropteran nectarivores and megachiropteran frugivores are able to effectively support large, protrusible tongues.

Artibeus shows slight wear on the distal half of the anterolingual slope of the upper canine, which is typical of many insectivorous and carnivorous microchiropterans, and occurs when one or the other lower canine engages one or the other upper canine just before occlusion. The cross-sectional shape of these microchiropterans is not affected by wear (Freeman 1992). Further, lower canines are vertically aligned and not splayed laterally so that simultaneous contact among all four canines before occlusion of the cheek teeth is rare, if not impossible.

MOLARIFORM TEETH. The interlocking of upper and lower teeth at occlusion is straightforward: Each lower molar occludes with two upper teeth, which is where PM4 participates and why PM4 is a functional part of the molariform row (Figure 9.5; top drawing for each bat). Understanding how the high-cusped, dilambdodont molars occlude, however, is critical to understanding not only function but also evolutionary changes in cusp patterns.

The two principal cusps on the upper molar are the anterior paracone followed by the more posterior metacone (Figure 9.6). Each has two crests radiating labially or buccally from it to give the characteristic W-shape stylar shelf or ectoloph (Butler 1941). Lingual to the paracone and across a valley is the protocone. The little diamond-shaped valley formed by the protocone and the bases of the para-

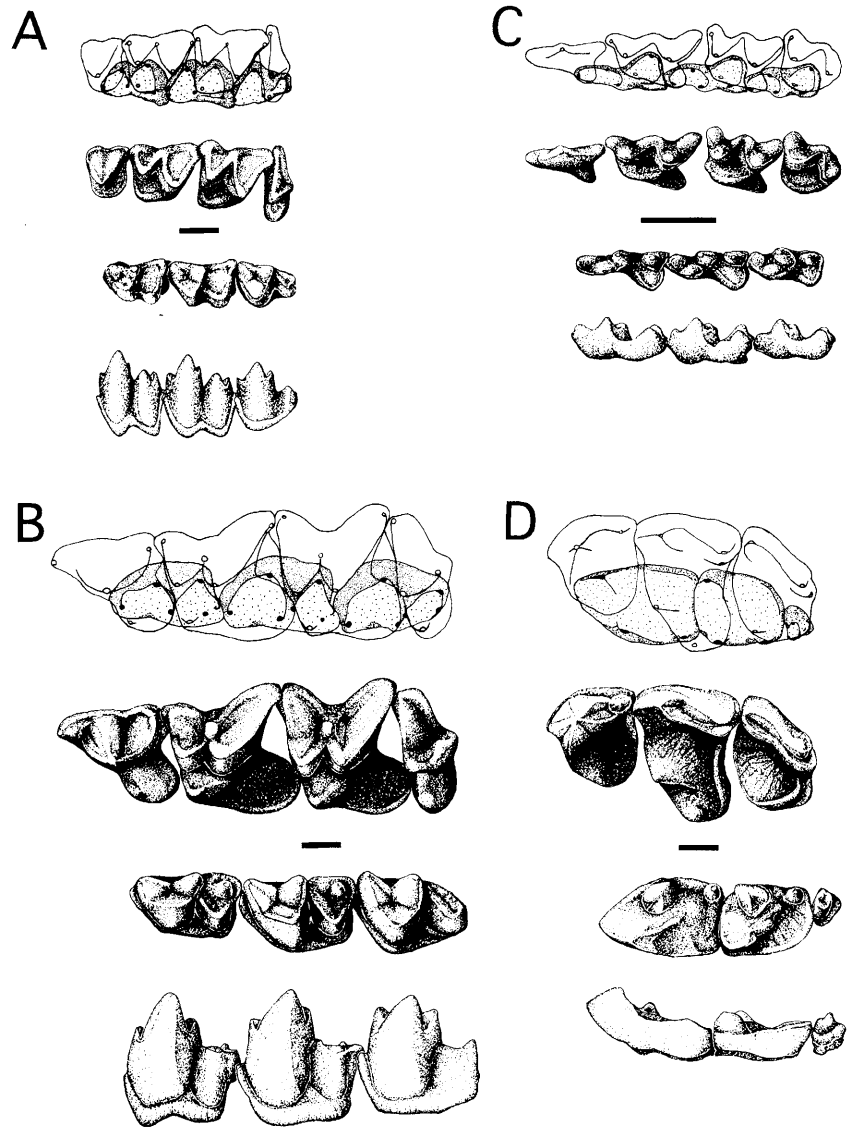


Figure 9.5. Left upper and lower molariform teeth of microchiropterans: (A) an insectivore, *Antrozous pallidus*; (B) a carnivore, *Macroderma gigas*; (C) a nectarivore, *Monophyllus redmani*; (D) a frugivore, *Artibeus jamaicensis*. Each example shows the interlocking of upper teeth and lower (stippled) teeth at occlusion, occlusal views of upper and lower teeth, and lateral view of lower teeth. Contact of the trigonid and talonid is shown by lighter stippling. The talonid is narrowest compared to the trigonid in carnivores and widest in nectarivores. Canines would be to the left, and the scale bar, which equals 1 mm, is placed lingual to the occlusal views. Names of cusps appear in Figure 9.6.

cone and metacone is the protoconal or trigon basin, and it is this basin that receives the talonid of the lower tooth. Posterior or distal to the protoconal basin is the hypocone and hypoconal basin, both of which are variable in appearance. The hypoconal basin is enormous in *Macroderma* (Figure 9.5B) and other carnivorous bats, but the actual hypocone is cryptic.

In some insectivores, there is neither hypocone nor hypoconal basin (Figure 9.5A). The nectarivore *Monophyllus* (Figure 9.5C) has a well-distinguished hypoconal area, but the most distinct hypocone is seen on M1 in the frugivore *Artibeus* (Figure 9.5D), which is lingual to the protocone and sits on a well-developed ledge. These features are clear on M1 and M2, but M3, if present, can be abbreviated from the back forward. The endpoint of the posterior arm of the W, the metastyle, is lost and the posteriormost arm or crest, the metacrista, is reduced. Microchiropteran nectarivores have

the most complete M3s, but metastyles are missing. The resulting shape is a backward N (Figure 9.5C). Further loss of the metacone and the anterior arm leading from it, the premetacrista, gives the tooth a V-shape (Figure 9.5B). The endpoint of the posterior arm of the V, the mesostyle, is lost in the most abbreviated M3s; the posterior crest leading from the paracone to the mesostyle, the postparacrista, can be much shorter than the anterior paracrista (Figure 9.5A).

The relative areas of the molariform teeth that the stylar shelves occupy compared to the relative areas of palates that teeth occupy are distinctive for microchiropterans with different diets. Generally, insectivores and carnivores have large teeth with large stylar shelves, frugivores have large teeth with the smallest stylar shelves, and nectarivores have small teeth with small to moderate stylar shelves (Figure 9.7).

The lower molars are composed of the familiar triangle of three cusps, the trigonid, with the large, buccal

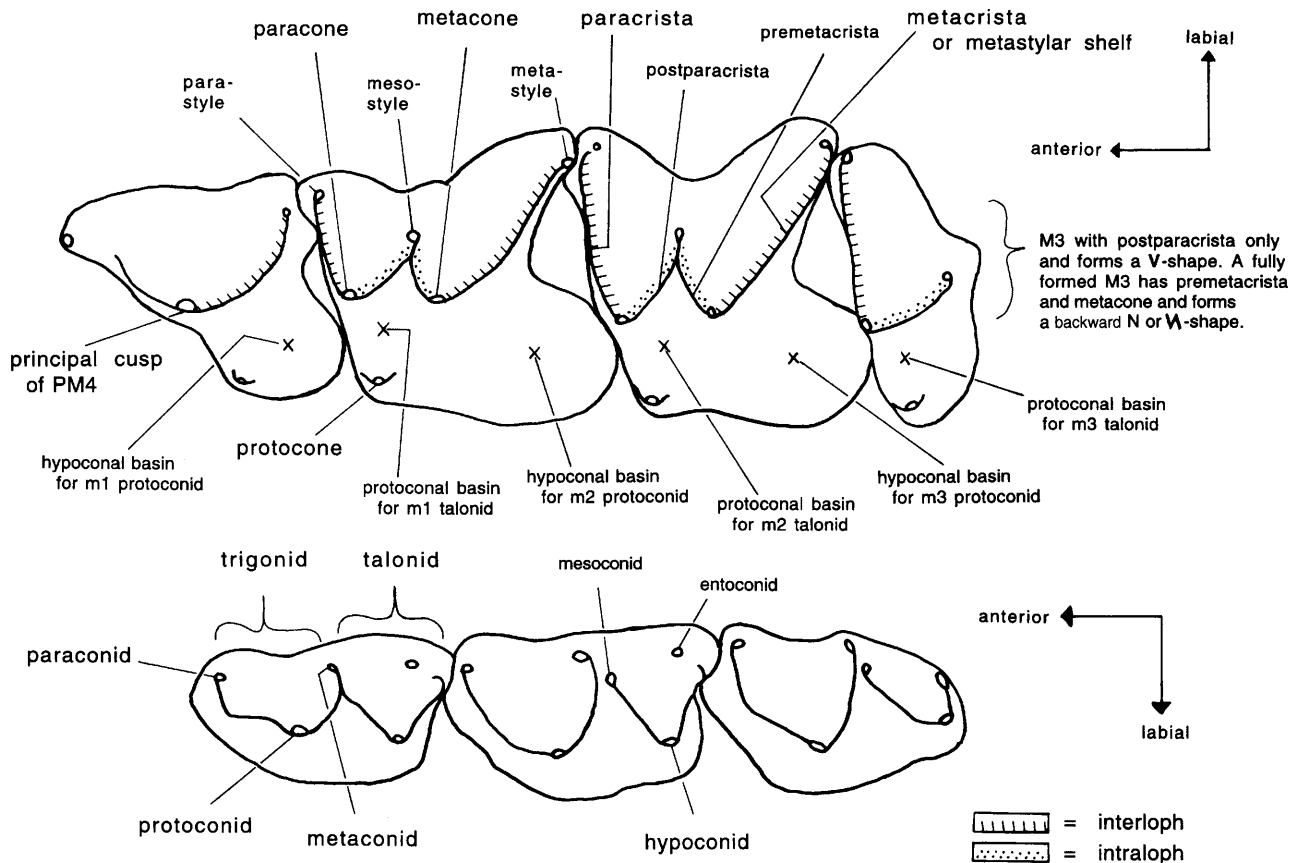


Figure 9.6. An enlarged occlusal diagram of the left upper and lower tooththrows of *Macroderma gigas*, with principle cusps, basins, and cristae—including interlophs and intralophs—identified. The abbreviated cusp pattern of M3 is a more derived condition for microchiropterans. A more primitive configuration occurs in *Monophyllus* (Figure 9.5C).

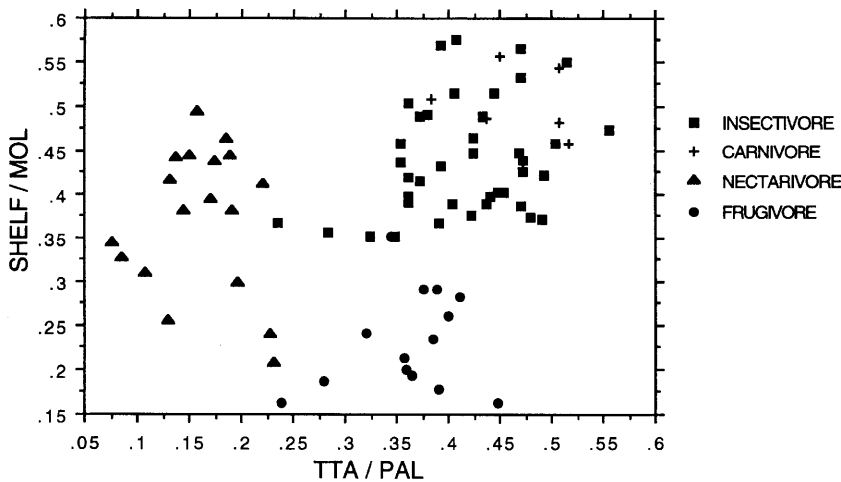


Figure 9.7. Summary of area that the stylar shelf (SHELF) occupies of molariform row (MOL, PM4 plus molars) versus the area that total tooth area (TTA) occupies of the palate (PAL) in microchiropterans. These ratios have been effective in separating insectivores and carnivores, which have the largest teeth and largest stylar shelves, from frugivores, both of which have large teeth but small stylar shelves, and nectarivores, which have small teeth and small to moderate stylar shelves. New to this study are several species that make the separation of groups less distinct. Among insectivores, *Mormoops* has the smallest teeth, and *Lonchorhina* the next smallest. Among frugivores, *Ectophylla* has the smallest teeth, then *Ametrida* and *Chiroderma*; *Uroderma* has the largest stylar shelf. *Phyllonycteris* and *Erophylla* have the largest teeth and the smallest stylar shelves among nectarivores.

protoconid flanked anterolingually by the paraconid and posterolingually by the metaconid (see Figure 9.6). Posterior to the trigonid is the heel of the molar or the talonid, where usually two cusps are present, the labial hypoconid and the lingual entoconid. As with M3, m3 (the third lower molar) is often abbreviated, and hypoconid and entoconid are not always distinguishable.

In general, the principal cusp on PM4 forms the anterior cutting crest of the interloph (the two-arm section of the ectoloph that is shared between upper teeth; Freeman 1984) (see Figure 9.6) with M1 to receive the trigonid of the lower molar. The protoconid itself fits into the deep valley bordered by the interloph to occlude against the lingual basin of PM4. This lingual basin is greatly expanded in *Macroderma* (Figure 9.5B) and corresponds to the hypoconal basins of M1 and M2. Functionally, these three deeply expanded basins receive the enlarged protoconids of lower molars in carnivorous bats. Posteriorly, the protoconal basin of the next posterior molar receives the talonid of the lower tooth. The first lower molar straddles the posterolingual basin of PM4 and the anterior protoconal basin of M1 (see overlying teeth, Figure 9.5).

Talonids and protoconal basins move across each other in lock-and-key fashion and appear to carry out the primary chopping and crushing action of the “pinking shears” teeth in insectivorous species. Indeed, it is this talonid–protoconal basin contact that is not only retained but even expanded in nectarivores, which have diminutive and widely spaced teeth. In insectivorous bats, the talonid is usually bigger than the trigonid and fits neatly into the deeply emarginated intraloph (that part of the ectoloph formed by the paracone, mesostyle, and metacone of the same upper tooth; Freeman 1984) (see Figure 9.6). Here the mesostyle, the middle peak of the W-shape, nearly reaches the buccal margin of the tooth. In carnivorous bats the mesostyle is more lingual, the intraloph is reduced, and the metastylar shelf (also called the metacrista) is elongated and aligned more anteroposteriorly. Talonids are narrower than the trigonids on lower molars of carnivorous bats.

The overall difference between insectivorous and carnivorous bat teeth lies in the shift of emphasis from the hypoconid in the former to the protoconid in the latter or from the talonid to the trigonid. The transverse movement of occluding teeth is kept stable and precisely guided by the transverse alignment of the transverse anterior cristae, from paracone to parastyle and from protocone to parastyle (the anterior edge of the tooth) of the upper molars and the protoconid–metaconid cutting crest of the lower teeth.

CARNIVORY. Elongation of the metastylar shelf and anteroposterior alignment on upper molars are typical in the evo-

lution of terrestrial carnivore teeth (particularly creodonts) (Osborn 1907; Butler 1946). In the lower molars of those carnivores the trigonid starts to straighten out; that is, the paraconid and metaconid move to a plane in line with the protoconid, the metaconid disappears, the cutting crest between the paraconid and protoconid becomes a blade, and the talonid gets smaller and smaller until it disappears. As the tooth simplifies with the reduction of the protocone and metaconid, the transverse occlusal guides are lost and replaced by a more longitudinal, sagittal jaw action but one that is just as much in need of precision. This is why the tapered, cylindrical condyle fits tightly into a glenoid fossa with prominent pre- and postglenoid processes. The tight fit allows only slight lateral movement, so that microadjustment of the carnassial blades is possible only at the unfused symphysis at the anterior end of the mandibles (Scapino 1965; Savage 1977). The greatest modification of cusps occurs at the carnassial pair, which in modern carnivores is PM4–m1. The trigonid on m1 of carnivorous bats has begun to form the in-line cusp pattern in *Vampyrum*, where the paraconid–protoconid blade is quite prominent and the metaconid is reduced to a diminutive bump on the posterior crest of the protoconid. Talonids are generally smaller than the trigonids in carnivorous bats (see Figure 9.5B).

In carnivorous bats, as the metastylar shelf (and interloph) lengthens the metastyle moves linguallly to shorten the intraloph. Both these modifications together simplify the complex dilambdodont pattern, which is not unlike what happens at the carnassial pair in terrestrial creodonts (particularly the series represented by *Sinopa*, *Pterodon*, and *Hyaenodon* in Hyaenodontinae, but also seen in Limnocyoninae and Machaeroidinae; Butler 1946). Here the metastyle moves linguallly and the intraloph becomes shorter. The paracone and metacone move closer and closer together until no space is left between them (the intraloph disappears). Simultaneously, the protocone diminishes completely to leave only a paracone–metacone blade for the upper carnassial.

The tooththrow in carnivorous bats simplifies into three large pestle-and-mortar systems and two smaller ones. Enlarged protoconids (pestles) in carnivorous bats would be good for deep penetration of endoskeletal foods and the large hypoconal basins (mortars) good for crushing bones of small mammals and birds. The basins may also shield the gums from pieces of bone, chitin, or other hard parts. Remains of prey including bones and teeth are finely chewed up by *Macroderma* (Douglas 1967). *Vampyrum* also eats bones (Peterson and Kirmse 1969; McCarthy 1987), and in captivity was observed to eat rodents and bats head first, teeth and all, but leaving a cape of skin along with the hindfeet and tail (J. S. Altenbach, personal communication). *Chrotopterus* ate

all but the rostrum, wings, legs, and associated patagia of bats (McCarthy 1987). Patterns of molar microwear may correlate with the extent to which carnivorous bats masticate bony material (Strait 1993b), but more experimental data are needed. Strait did not find as much evidence of hard-item ingestion in *Vampyrum* as she did in *Macroderma* when she examined microwear at the hypoconid–protocone contact. She did not examine wear on the protoconids that contact the expanded hypoconal basin, which is likely the critical crushing area in carnivorous bats.

NECTARIVORY. Although diminutive and not as high-crowned or emarginate as insectivores, the molars of nectarivores are still working teeth. Occlusion is particularly apparent between the wide talonid and the upper protoconal basin (see Figure 9.5C). The wear from this occlusion is obvious in even the most extreme nectarivores such as *Musonycteris*. Anterior to the talonid, the three cusps of the narrow trigonid are prominent, but the paraconid and protoconid form a small, in-line cutting crest and the especially prominent metaconid sits lingually to the protoconid. In a representative nectarivore, *Monophyllus redmani* (Figure 9.5C), there is a small upper hypoconal area against which this small cutting crest occludes. However, in nectarivores with spaces separating teeth, the crest falls between teeth, occluding longitudinally against the upper gum only, and is likely capable of processing only the softest items.

FRUGIVORY. Teeth of frugivorous bats are completely different from those of their insectivorous relatives. Paracone and metacone have moved to the labial or buccal edge of the upper molars to form a raised rim and occupy the least area of all microchiropterans (Figure 9.5D). As a result, the stylar shelf is a wavy edge only vaguely reminiscent of the W-shape. The lingualmost face of this raised edge may not be homologous with that in insectivores, but may also include the metaconule (Slaughter 1970)—which would make my estimates of area of stylar shelves overestimates. However, the posterior crest on the primary cusps (paracones?) of the upper canine and premolar has a tendency to split to form two sharp edges. This phenomenon could also affect development of paraconids on molars and may determine what exactly comprises the homologous ectoloph (see paraconid on M1, Figure 9.5D; also see Freeman 1988).

Occlusion in frugivores is not an interlocking affair dependent on transverse crests. The upper ectoloph has simplified from a complex zigzag pattern to a single continuous, cutting edge (a cookie cutter) so that the dental arcade of lower teeth fits inside its perimeter. The outside or buccal edge of the lower molars acts as a pestle that nestles into

the wide continuous mortar created by the lingual basin of PM4 and protoconal basins of M1 and M2 and has little side-to-side movement (see Figure 9.5D). The lingual parts of the teeth are broad crushing areas with small upper and lower lingual cusps adding rugosity to the surface. These small cusps fit together as loose mortars and pestles that would help crush rather than chop foods, but there is little contact between teeth lingually. When viewed laterally the dental arcade of the upper teeth, which are close-fitting teeth, is sharp and serrated.

Evolution

MEGACHIROPTERAN ANCESTOR. Traditionally nectarivores are thought to be derived from frugivorous megachiropterans. However, I believe all megachiropterans evolved from a long-tongued ancestor, which could easily have been a nectarivore. Both nectarivores and frugivores have narrow, elongated palates with space between relatively simple, noncomplex teeth that do not register, fused mandibles, shallower, less distinct jaw joints, and thegosed upper canines. This suite of characteristics argues for a tongue-feeding ancestor that may have been either a nectarivore or a tongue-feeding frugivore or both. If this were the case, frugivorous megachiropterans became more robust with bigger teeth. Many of them reached large body masses and some of them became short-snouted (intertooth space is nonexistent in *Cynopterus* and small in *Dobsonia* and *Nyctimene*). Recent DNA evidence suggesting that nectarivorous megachiropterans are polyphyletic does not negate this possibility (Kirsch and Lapointe 1997). These authors show that more obligate nectarivores could have arisen several times from a long-tongued ancestor. Megachiropteran nectarivory and frugivory are based on a similar feeding mechanism and represent a continuum along a nectarivory–frugivory gradient.

TWO KINDS OF FRUGIVORY. Frugivory in bats has evolved twice but has been achieved in fundamentally different ways. Microchiropteran frugivores differ from their nectarivorous confamilials in their short, wide palates and non-dilambdodont, close-fitting teeth. Microchiropteran nectarivory and frugivory are not on the same continuum but represent two entirely different feeding mechanisms.

Microchiropteran and megachiropteran frugivores both mash fruit against their ridged palates with their tongues and have teeth with less discernible cusps, but they use different equipment and execution. Microchiropteran bats possess short, nonprotrusible tongues and use short, wide faces and a tooththrow of serrated edges to cut into fruits with

small bites. Perhaps the anecdote of why the wrinkled-face bat *Centurio* has wrinkles is true: It probably does have to bury its wide scoop-face right into a fruit to eat, and juice may well run down the wrinkles to the mouth in the absence of a big tongue. These stories also liken the nakedness of *Centurio*'s face to the baldness of the heads of vultures (Findley 1993).

In contrast, megachiropteran frugivore jaws are usually long, allowing bigger gapes and bigger bites. Processing is by teeth with blunt labial cusps and by a long, protusible tongue that reduces fruit on the ridged palate as it moves forward past the food to extend out of the mouth. Further, chewing is orthal or more vertical than chewing in a microchiropteran insectivore, which has a more lateral component to the chewing cycle (Greet and De Vree 1984). Large bites could be a function of longer jaws, teeth more anterior on the toothrow, and larger gapes (Savage 1977). The result is that tongue-feeding frugivory has evolved in megachiropterans and cookie-cutter frugivory has evolved in microchiropterans.

Modifying cookie-cutter frugivory to sanguinivory does not seem evolutionarily difficult but is not totally without obstacles. The raised stylar shelf of an ancestral frugivore could become the edge that is the cheekteeth in blood-feeders, and the shift of emphasis to the incisors at the anterior end of the palate continues the shift to the more anterior teeth seen in stenodermatine frugivores. *Pygoderma* (see Figure 9.2C) has greater incisor and canine area than consubfamilials. Sanguinivores also have relatively wide palates like stenodermatines (see Figure 9.1B), and occlusion is the ultimate in two cookie-cutter edges that shear past one another vertically without side-to-side movement. However, if derivation from stenodermatine frugivory were the case, the lingual areas of the teeth must have diminished and disappeared entirely, which would not be unlikely if the tongue were significantly larger. The anterior surfaces of the upper canines are heavily worn on the entire anterior surface and probably support a tongue that protrudes enough to lap. As in stenodermatines, the mandibles are fused completely in *Diphylla*. Fusion is less complete in *Desmodus*, which is problematical.

DILAMBODONTY AND DIGESTIBILITY. Finally, dilambdodonty in microchiropteran bat teeth is likely to be correlated with digestibility of prey such that deeply emarginate teeth process the foods most difficult to digest. Chopping up insect prey into fine pieces may be as critical to the digestibility of insects in bats as it is for primates (Kay and Sheine 1979). The complex pinking-shears pattern allows insectivorous bats to take advantage of an abundant insect resource. How-

ever, the principal trend in the evolution of molar teeth in bats, as in terrestrial carnivores, is one of simplification, or a decrease in dilambdodonty. Bats evolved to larger sizes to take advantage of larger insects, but they also became large enough to take small vertebrates as well. Endoskeletal prey items are probably easier packages to break into and digest, especially with relatively large teeth. These teeth however would not need to be as deeply emarginate to chop and prepare food for digestion. The less-emarginate pattern in carnivorous species with their elongated interlophs, shortened intralophs, and correspondingly large protoconids seems well suited for processing meat on the bones of small prey and the bones themselves.

Teeth of nectarivorous bats have simplified by becoming diminutive and having a dilambdodont pattern that is shallower and not as high cusped. Nectar, pollen and whatever soft foods (insects? flowers?) nectarivores might be taking are surely more digestible than a diet restricted to insects. Although the enlarged tongue gathers much of the food, the talonids and protocones still have a crushing function and M3s can be fully formed. Dilambdodonty is reduced to form a dental arcade with a continuous, raised and sharpened edge in frugivores, a good design for cutting through the skin of fruit. A mouthful of the fruit's contents is crushed between broad horizontal surfaces of the teeth lingual to the rim and mashed by the tongue against the roof of the mouth to release the easily digested juice. Finally, blood-feeding bats need only vertical edges to cut through the skin of endoskeletal foods to release the liquid from within. Horizontal surfaces on the teeth and their crushing function disappear completely, and the protrusible tongue with its lapping function takes a more central role.

Conclusions

Megachiropteran frugivores, megachiropteran nectarivores, and microchiropteran nectarivores have in common craniodental characteristics that are correlated with having a long tongue. A long tongue in megachiropterans can explain why teeth do not interlock and why homologous cusp patterns cannot be discerned. It also means that megachiropterans evolved from a long-tongued ancestor that could have been a nectarivore or a tongue-feeding frugivore or both. Further, frugivory has been achieved in two different ways in bats: tongue-feeding frugivory in megachiropterans and cookie-cutter frugivory in microchiropterans. Among microchiropterans, nectarivores have functional although diminutive postcanine teeth, proportionally large-sized canines that may brace the long jaw during feeding, and molars which still function at the talonid-protococone contact.

Carnivores, in contrast, emphasize the trigonid–hypocone contact. Here, the protoconids act as large pestles that fit into deep and expanded mortars, which are the hypoconal basins and are probably useful for crushing bones of small vertebrates. Carnivores and insectivores have more dental material at the rear of the toothrow while all other bats emphasize dental material at the front

of the toothrow. Not only is there a shift in allocation of dental material between suborders, there is also a shift among microchiropterans. Canine teeth in bats have edges that are nonrandomly oriented, which may aid in cutting into foods efficiently. Indeed, elaborate canines may be a necessity for aerial mammalian predation and harvesting in general.

Appendix 9.1. Species Examined and Their Categories

Numbers to the left of the species' names refer to categories in Figure 9.2C (e.g., Insectivore 1, Insectivore 2). An asterisk indicates that the species is new to this study.

Microchiropteran Insectivores	1 <i>Mormoops megalophylla*</i>	1 <i>Ametrida centurio</i>
1 <i>Saccolaimus peli</i>	1 <i>Pteronotus parnellii*</i>	2 <i>Centurio senex</i>
1 <i>Taphozous nudiventris</i>		2 <i>Ectophylla alba</i>
1 <i>Peropteryx kappleri</i>	Microchiropteran Carnivores	3 <i>Pygoderma bilabiatum</i>
1 <i>Rhinolophus luctus</i>	4 <i>Macroderma gigas</i>	1 <i>Sphaeronycteris toxophyllum</i>
1 <i>Rhinolophus rufus</i>	3 <i>Megaderma lyra</i>	1 <i>Sturnira lilium</i>
1 <i>Rhinolophus blasii</i>	4 <i>Cardioderma cor</i>	1 <i>Brachyphylla nana</i>
1 <i>Hipposideros commersoni gigas</i>	2 <i>Nycteris grandis</i>	1 <i>Brachyphylla cavernarum</i>
1 <i>Hipposideros commersoni commersoni</i>	1 <i>Vampyrum spectrum</i>	
1 <i>Hipposideros lankadiva</i>	1 <i>Chrotopterus auritus</i>	Microchiropteran Sanguinivores
1 <i>Hipposideros pratti</i>	1 <i>Trachops cirrhosus</i>	<i>Diphylla ecaudata*</i>
1 <i>Hipposideros ruber</i>		<i>Desmodus rotundus*</i>
2 <i>Scotophilus nigrita gigas</i>	Microchiropteran Nectarivores	
1 <i>Ia io</i>	1 <i>Phyllonycteris poeyi</i>	Megachiropteran Frugivores
1 <i>Myotis myotis</i>	1 <i>Erophylla sezekorni</i>	1 <i>Eidolon helvum*</i>
1 <i>Myotis velifer</i>	1 <i>Glossophaga soricina</i>	1 <i>Rousettus angolensis*</i>
1 <i>Nyctalus lasiopterus</i>	1 <i>Glossophaga longirostris</i>	1 <i>Pteropus poliocephalus*</i>
2 <i>Antrozous pallidus*</i>	1 <i>Monophyllus plethodon</i>	1 <i>Pteropus vampyrus*</i>
2 <i>Eptesicus serotinus*</i>	1 <i>Monophyllus redmani</i>	1 <i>Acerodon jubatus</i>
2 <i>Otonycteris hemprichi*</i>	2 <i>Lichonycteris obscura</i>	1 <i>Dobsonia moluccensis</i>
1 <i>Lasiurus cinereus*</i>	2 <i>Leptonycteris curasoae</i>	1 <i>Harpionycteris whiteheadi</i>
1 <i>Lasiurus borealis</i>	1 <i>Anoura caudifer</i>	2 <i>Cynopterus brachyotis*</i>
2 <i>Cheiromeles torquatus</i>	1 <i>Anoura geoffroyi</i>	2 <i>Paranyctimene raptor*</i>
1 <i>Eumops perotis</i>	1 <i>Hylonycteris underwoodi</i>	2 <i>Nyctimene draconilla</i>
1 <i>Eumops underwoodi</i>	1 <i>Choeroniciscus godmani</i>	2 <i>Nyctimene major</i>
1 <i>Otomops martiensseni</i>	1 <i>Choeroniciscus intermedius</i>	
1 <i>Tadarida brasiliensis</i>	1 <i>Choeronycteris mexicana</i>	Megachiropteran Nectarivores
2 <i>Molossus molossus</i>	1 <i>Musonycteris harrisoni</i>	1 <i>Pteropus scapulatus</i>
2 <i>Noctilio leporinus</i>	1 <i>Lonchophylla thomasi</i>	2 <i>Epomops buettikoferi</i>
1 <i>Macrotus californicus*</i>	1 <i>Lonchophylla handleyi</i>	2 <i>Scotonycteris zenkeri</i>
1 <i>Lonchorhina aurita*</i>	1 <i>Lionycteris spurrelli</i>	1 <i>Eonycteris spelaea</i>
1 <i>Micronycteris megalotis*</i>		1 <i>Eonycteris major</i>
1 <i>Mimon bennettii*</i>	Microchiropteran Frugivores	1 <i>Megaloglossus woermanni</i>
1 <i>Phylloderma stenops*</i>	2 <i>Artibeus jamaicensis</i>	1 <i>Macroglossus minimus</i>
1 <i>Phyllostomus hastatus</i>	2 <i>Artibeus lituratus</i>	1 <i>Macroglossus sobrinus</i>
1 <i>Phyllostomus elongatus*</i>	2 <i>Artibeus phacotis</i>	1 <i>Syconycteris australis</i>
1 <i>Phyllostomus discolor*</i>	2 <i>Artibeus toltecus</i>	1 <i>Melonycteris melanops</i>
1 <i>Tonatia silvicola*</i>	1 <i>Chiroderma villosum*</i>	1 <i>Notopteris macdonaldi</i>
1 <i>Carollia perspicillata</i>	1 <i>Uroderma bilobatum*</i>	

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