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Canine Teeth of Bats (Microchiroptera): Size, Shape and Role in Crack Propagation

Patricia W. Freeman
University of Nebraska-Lincoln, pfreeman1@unl.edu

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Division of Zoology, University of Nebraska State Museum, Lincoln, Nebraska

ABSTRACT: Upper canines in microchiropteran bats show a variety of cross-sectional shapes. A consistent feature of all species studied here is that the tooth is edged and not simply round or oval. Prominent sharp edges are positioned in several directions but particularly antero-medially toward the incisors and posteriorly toward the premolars. These edges appear to direct the cracks made in food items to the incisors or to the premolars. A continuous cutting edge is apparent in the occlusal view of the palate running from tip of canine to the ectoloph of the molars. Size and shape analysis indicates that larger bats have slender, rather than stouter, canines for their height, a condition that may be attributable to the nature of the prey. Most bats take prey that have little hard substance imbedded within. The compromises in tooth shape may vary between that of a terrestrial predator with short, conical canines for processing endoskeletal prey to that of a small flying predator with long, slender, edged canines for capturing and processing exoskeletal prey. Unicuspid teeth and how they might function in food break-up have been overlooked to the literature; such a study could lead to an understanding of how more complex teeth function.

KEY WORDS: Canines, crack propagation, food textures, functional morphology, microchiroptera, size and shape, teeth

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INTRODUCTION

Canines and incisors have been given little attention in studies on teeth and mastication in mammals. This may be based on the assumption that a simple unicuspid tooth is not complex and therefore not worth further investigation. However, considerable variation occurs in the upper canines in microchiropteran bats such that the cross-sections are not simply round but are triangular and polygonal in shape with at least one, and often two, sharp edges (Fig. 1).
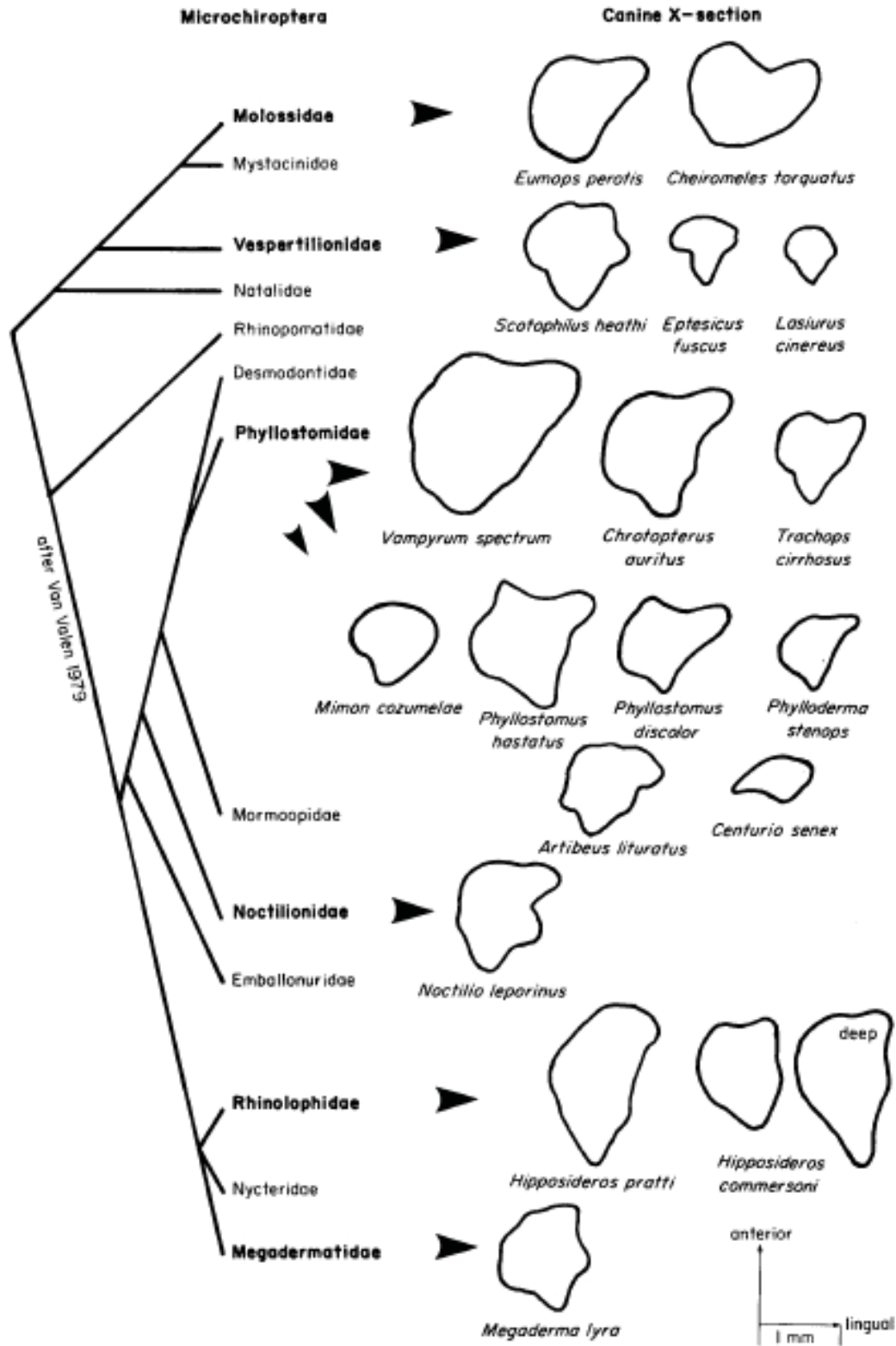
Figure 1. A phylogeny of families of microchiropteran bats with cross-sections of canines of species from the corresponding families. All the sections are oriented the same way, which is the position that they sit in in the toothrow.

The proposal made here is that these sharp edges have a specific cutting function. If the canines are thought of as tools that break into a package, the position of these edges relative to the adjacent incisors and premolars take on a unified functional role, a role that may be important for small flying predators.

In mammals canine teeth may function as tools for killing, grasping, opening or dividing prey or in display. In meat-eating mammals, where occlusal events are rapid and precise, canines may function as occlusal guides for postcanine teeth (Mellett, 1985). The first contact of upper and lower canines initiates an autocclusal path which the other teeth and jaw joint must follow without deviation. This mechanical tyranny would not be dictated by neuromuscular coordination. Precise occlusion is a requisite for flying mammalian predators such as bats particularly because of the complex cusp patterns seen in most microchiropterans but also because of the speed with which they must catch and process prey.

The social role of the canines in bats (e.g. defence of harem; Porter, 1978)) is overshadowed by the role of food procurement and manipulation in these mammals whose forelimbs are occupied as wings and not for food-gathering. Many bats capture and consume prey in the air—sometimes with the aid of feet or momentary scooping by the flight membranes (particularly the uropatagium)—but canines and other teeth are responsible for much of the initial procurement of food, whether it is vertebrate, invertebrate or botanical in nature. Although canines function to grasp prey and to kill prey, they must also be intimately involved in the initial break up of food which is processed by the postcanine teeth. This role of crack propagation in canine teeth has gone unmentioned in the literature. Crack propagation by postcanine teeth was introduced in a classic paper by Lucas (1979).

The nature and texture of potential food items are significant to this investigation. Endoskeletal prey present interesting processing problems to a potential predator. Both skin and muscle are soft solids that require edged 'blades' to be cut, while the bone within is a hard brittle solid that requires blunt 'pestle-and-mortar' type dentition to be divided (Lucas, 1979; Lucas & Luke, 1984; Mohsenin, 1977). Where a blade is used on soft material, the blade must pass completely through it because soft solids are too plastic for cracks to propagate beyond the edge of the tooth. Division is only possible with the continued presence of the point or blade (Lucas, 1979). The long, bladed condition of canines of the most derived sabre-toothed cats must have been for slicing through soft tissue unimpeded by bone (Bohlin, 1940; Kurten, 1952; Emerson & Radinsky, 1980; Van Valkenburgh & Ruff, 1987). 'Blades' used on bones would soon be blunted. However, blunt conical canines could be used effectively to divide soft material and still be able to encounter and divide any bone that might be hidden within. The canines of most carnivores then would be a compromise tool for dividing both soft solids, like skin and muscle, on the outside of the prey and the hard, brittle bone on the inside. Instead of a sharp blade that would soon be blunted, the carnivoran canine could be a duller, rounder tooth that could both withstand the hardness of the bone yet still be able to divide soft material. That the tooth is not a perfect tool in large carnivorans was recently observed by Van Valkenburgh (1988a) who has found frequent breakage in these teeth. She has attributed the substantially greater incidence of breakage in hyaenas to the hardness of foods eaten. No such breakage has been seen by the author in bat teeth, even in the largest carnivorous species.

The trade-off between slicing ability and strength is unnecessary with an exoskeletal food package because there is no hard brittle solid within. Insect exoskeleton or cuticle is a stiff brittle composite (actually laminated like plywood) that, depending on the amount of stiffening agent, chitin, resists crack propagation because different layers of fibres run in different directions. Such a composite is said to have 'fracture toughness' (Wainwright et al., 1976; Hepburn & Joffe, 1976; Vincent, 1980) in the sense that when an insect is being punctured the canine presses onto the elastic cuticular surface deeply before finally breaking through the surface. Cracks in a fracture-tough package, e.g. in a soft solid, would not be able to propagate far beyond the tooth and would also best be divided by an 'edged' tooth. Although the tooth would have to remain in the composite for successful division it could be long, bladed and sharp with impunity because there would be no bone within to blunt it.

Frugivorous food items are more difficult to categorize and the optimal shape for the canine of a bat that eats fruit some or all of the time is not clear. Although cellulose is a composite similar to cuticle (Wainwright et al., 1976; Vincent, 1980, 1982), the variability of plant parts requires a canine that can perform a multitude of functions. The outer surface of the fruit may be tough, hard or soft, there may be an external covering and there may also be a hard seed hidden within. Some fruits may mirror the disadvantages of exo- and endoskeletal prey in having a hard covering and hard material hidden within as well, others may have some or none of these disadvantages. In addition, ripeness of the fruit may affect the parts so that what may be difficult to open one day may be very easy to open the next. The non-struggling nature of the prey may affect the length of canine in frugivores such that they are shorter than those in animalivores (Freeman, 1988).

MATERIALS AND METHODS

Plastic replicas were cast of unworn upper canine teeth and toothrows of adult male specimens for each of 18 species from six microchiropteran families (many of the same species as in Freeman, 1984, 1988) and four canivorans, two of which have skulls within the size range of the bats. Transverse cross-sections were made on the shank of the tooth while in the toothrow at the level of the tip of the tallest adjacent premolar, where that tooth would start to participate in the bite, and parallel to the base of the tooth when viewed laterally (Fig. 2A). The plane of the cut was parallel to both the base and to the occlusal plane of viewing. Ratios are used to describe the cross-sectional features and not absolute values. Casts were made to avoid destruction of the actual tooth for cross-sections. These sections are grouped phylogenetically in Fig. 1.

Bats for this study were chosen to reflect size and phylogenetic diversity as well as the diversity that may be attributed to different food habits. Insectivorous molossids included the large Eumops perotis and Cheiromeles torquatus and also morphological extremes considered to be soft and hard item specialists, respectively (Freeman, 1979, 198 1 b) . The diverse range of phyllostomids included carnivorous (*Vampyrum spectrum*, *Chrotopterus auritus, Trachops cirrhosus*), insectivorous (*Mimon cosumelae, Phyllostomus discolor*), omnivorous (*Phyllostomus hastatus*) and dietarily unknown (*Phylloderma stenops*) phyllostomines; and frugivorous stenodermines (*Artibeus lituratus, Centurio senex*). *Noctilio leporinus* is a piscivore, *Mega-*
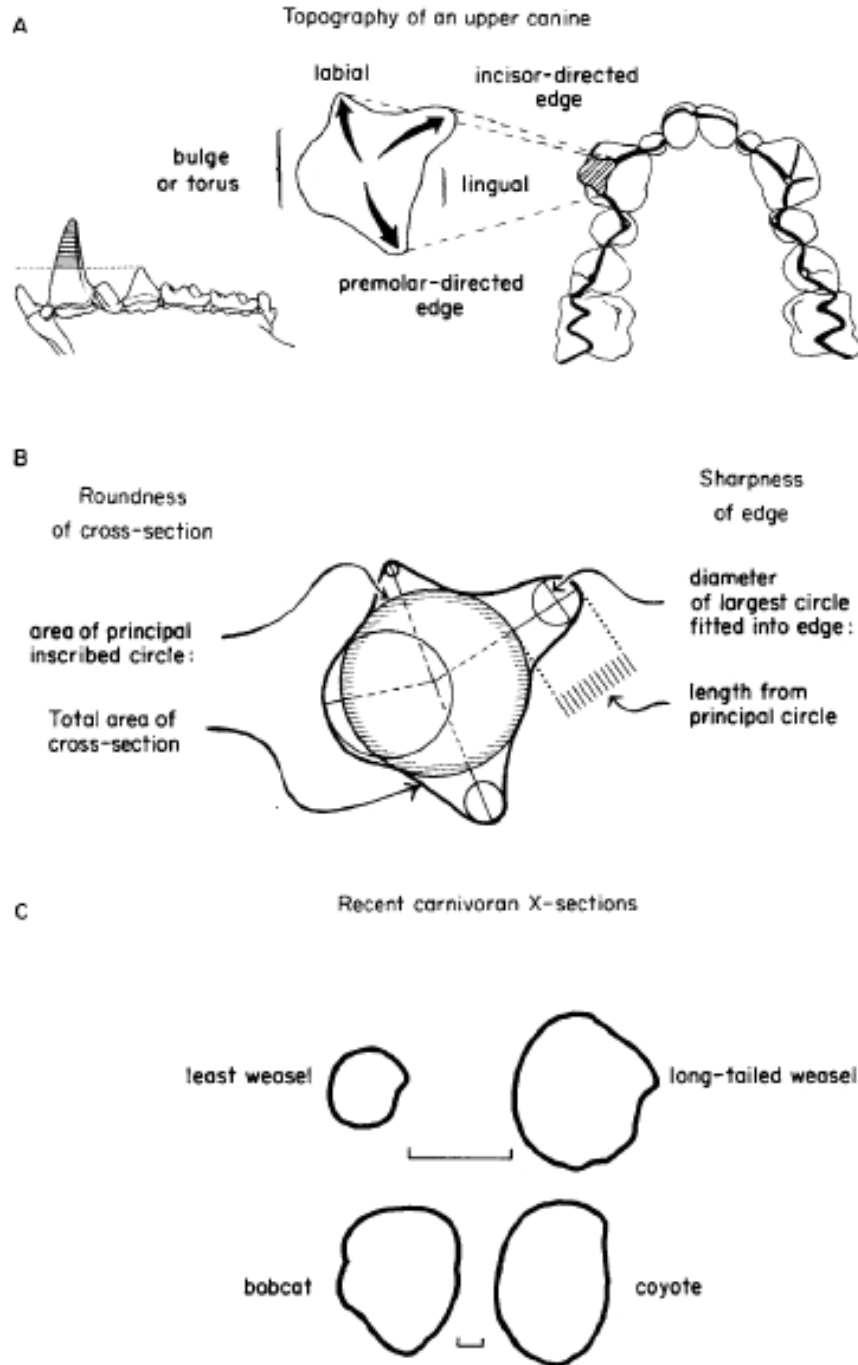
Figure 2. A) Topography of an upper right canine with all possible edges marked with terminology used in this study. The heavy, dark line of the palatal view of *Phyllostomus hastatus* traces the path formed by the crests of the incisors, the edges and tips of the canines, the precristae and postcristae of the premolars, and the ectoloph of the molars. The edges on the canines are positioned such that there is a continuous edge proceeding anteriorly toward the incisors and one proceeding posteriorly toward the molars. A lateral view illustrates the approximate level of the cross-section. All cross- sections are taken with the tooth sitting in the toothrow. B) The derivation of the values for the ratios of roundness of cross-section and sharpness of an edge are shown. An edge with a value < 1.0 is considered sharp, while one > 1.0 considered blunt (details are in Materials and Methods). C) Cross-sections of four Recent carnivorans. The weasels are within the same size range as the range of bats in this sample. Scale here and in all figures represents 1 mm.

derma lyra is a carnivore, and the remainder are insectivores of varying sizes. A complete list of species with abbreviations is in Table 1.

Plastic-resin casts of the teeth were produced following current methodology from vertebrate palaeontology. Casts were made with the following materials: (1) molds: General Electric RTV 700 Silastic with Beta 1 catalyst, a silicon rubber; (2) casts: standard casting epoxy-resin of medium hardness, TAPOX 4:1 formula. The cast teeth were carefully filed down to the appropriate level to produce the cross-section (Fig. 2).

Measurements included a composite size character (SIZE = sum of the natural logs of condylocanine length, zygomatic breadth and temporal height), height of canine from cingulum to tip, roundness of canine and sharpness of each edge on the canine; roundness and sharpness are ratios. Roundness is the percentage that the principal inscribed circle occupies of the total cross-sectional area (Fig. 2B). Sharpness of an edge is the ratio of width over length; if the ratio is < 1.0 the edge is considered sharp; if > 1.0, it is blunt. Length of the edge is measured from the perimeter of the inscribed circle to the outermost point on the perimeter of the edge. Width is the diameter of the largest circle that can be fitted into the curve of the edge (Fig. 2B). This can be done either with a digitizer or a simple engineering template. Although modified for purposes here, roundness and sharpness are measures derived from a standard agricultural engineering text (Mohsenin, 1986; but see also Lucas, 1982). Areas were taken either with a digitizer or with a polar planimeter after being drawn under a camera lucida. Analyses included bivariate plots of the logs of measurements taken to the appropriate roots and regressed against SIZE where relevant.

RESULTS

Although the canines, at first glance, appear to be simple teeth especially in comparison with postcanine teeth, microchiropteran canines are not the ellipsoidal or round cross-sectional shapes commonly seen in carnivorans (Fig. 2C; Van Valkenburgh & Ruff, 1987). These bats have a variety of acute- and obtuse-angled edges that face a variety of different directions (Fig. 1). The edges are genetically derived. They are not produced by wear from food or opposing teeth.

Because canines (and incisors for that matter) have rarely been given attention, accepted specific nomenclature for the longitudinal ridges or edges seen on bat canines does not exist. Hershkovitz (1971) gives elaborate descriptions of some of these edges but the names given depend on the serial homology of similar cusps on the molars. Palaeontologists, Butler (1978) in particular, do not agree with the terminology because serial homologies with the cusps on the molars are uncertain. Palaeontologists have also noticed these ridges or edges in mammals such as fossil cats (e.g. Beaumont, 1964) and termed them bourrelets, meaning a ridge on a stem. This is an appropriate term but one without an English equivalent.

Terminology for the edges are shown in Fig. 2A. There are two primary edges, one that runs anteriorly and one that runs posteriorly from the principal cusp (eocrista of Hershkovitz, 1971). Most bats, indeed most mammals have palates with a clear anterior-posterior axis, but because a handful of species including *Homo* have wide, parabolically-arched palates, the terms mesial (towards the midline) and distal (away from the midline) are used. Because
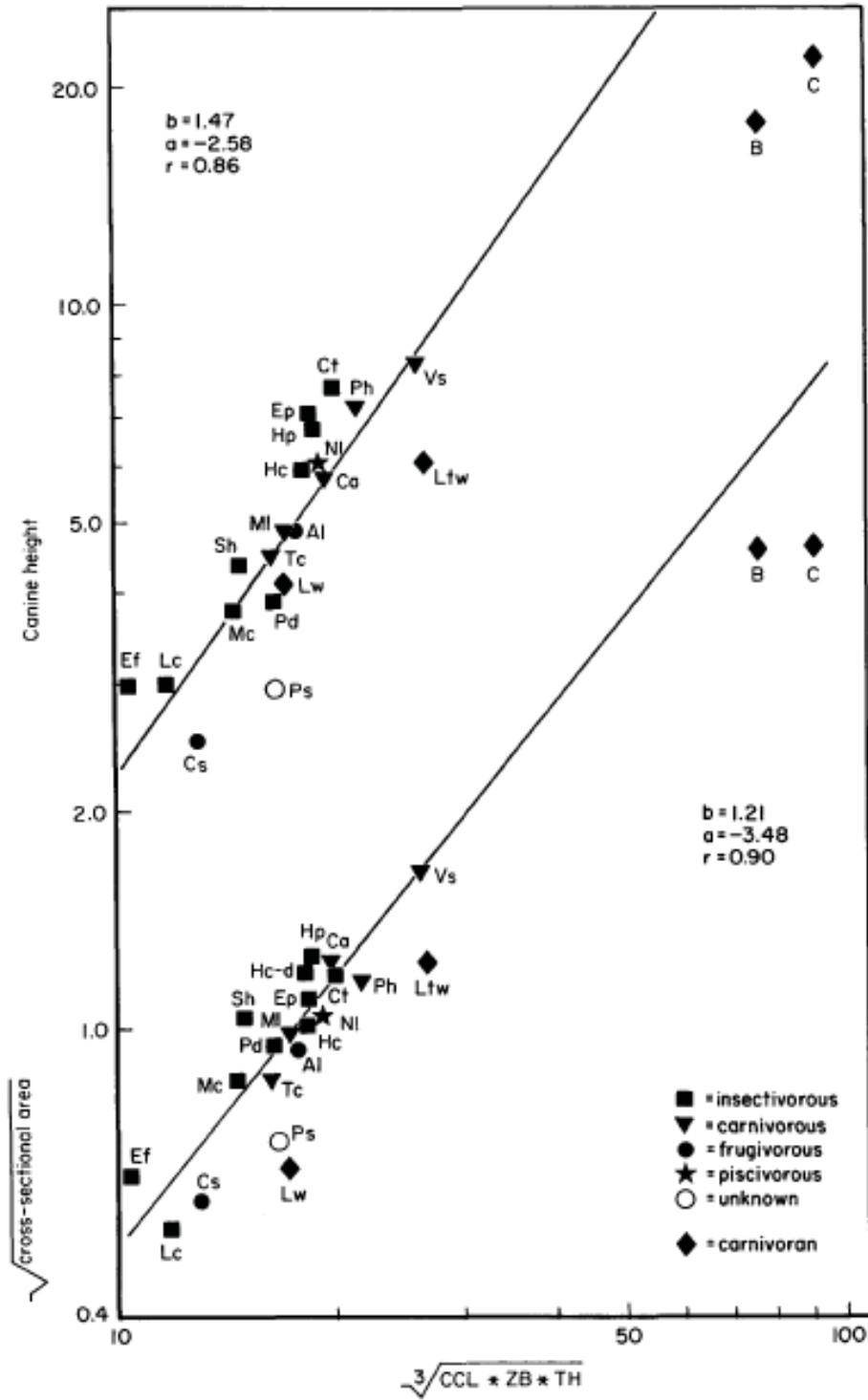
Figure 3. Two regression analyses illustrating the relationship between the thickness of the shank of the canine (square root of cross-sectional area) and the height of the canine as size increases in the bats only. The values on the abscissa are actually the components of the SIZE character (condylocanine length, zygomatic breadth and temporal height; see Materials and Methods), but linearized so as to be comparable with the values on the ordinate. Both canine measurements are positively allometric relative to size (slope, intercept and correlation are shown). Abbreviations are listed for each species in Table 1. Values for the four carnivorans have been superimposed and are not part of the regression analyses.
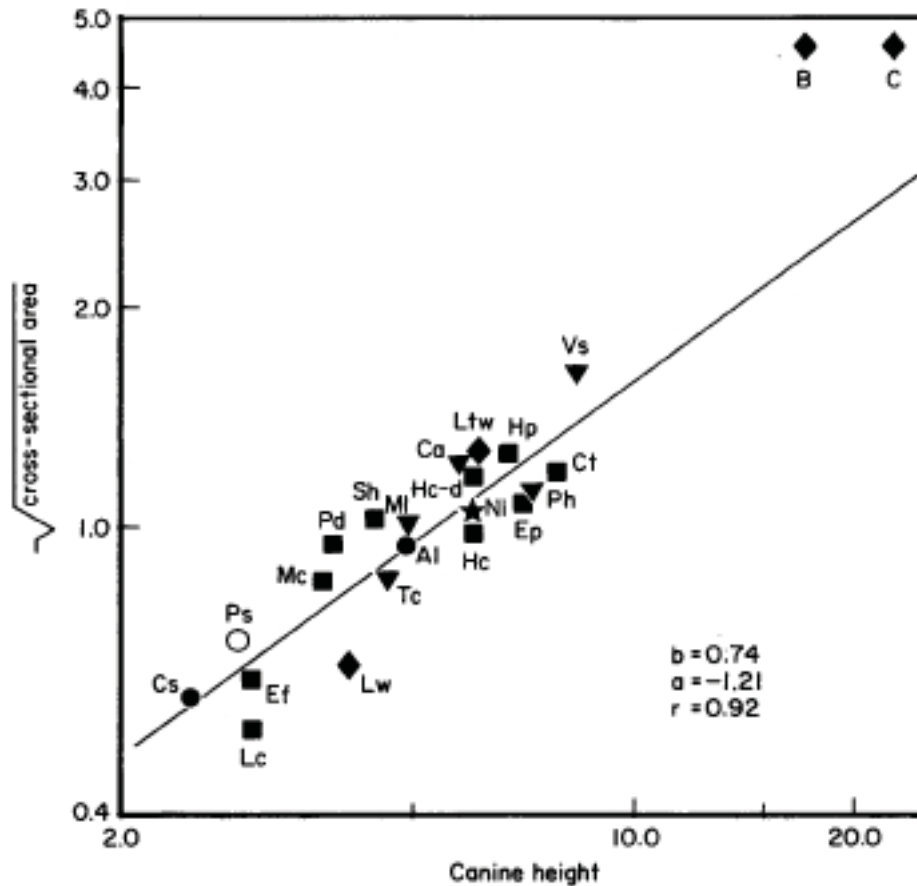
Figure 4. The thickness of a canine (square root of cross-sectional area) regressed against the height of a canine shows that height is increasing more rapidly than is thickness in bats. Larger bats generally have slender canines for their heights. This is a negative allometric relationship (slope, intercept and correlation are shown). Abbreviations are listed in Table 1, symbols are the same as in Fig. 3, and carnivorans are superimposed as in Fig. 3.

these latter terms can be confusing in palates with a strong anterior-posterior orientation, the terms incisor-directed edge and premolar-directed edge have been employed. However, there are other edges. A companion edge on the anterior face of the canine and lateral to the incisor-directed edge is the labial edge (quite prominent in *Phyllostomus hastatus*, Fig. 1). The fourth edge in the cross-section is the lingual. It can be seen in *Megaderma lyra* and *Noctilio leporinus*. Lastly, there is a buccal edge in *Artibeus lituratus*. Most of the buccal face of the canine is the bulge or torus of the principal cusp, which in a few is also the anterior face of the tooth.

Size of upper canine, both height and cross-sectional area, is highly correlated with body size (Fig. 3). Actual heights for the species here range from 2.0 mm to 8.5 mm. Postive allometry is occurring in both diminsions. Cross-sectional area is getting larger faster than SIZE by a factor of 1.21, and height of the canine is getting larger even faster by a factor of 1.47. However, there is a negative allometric relationship between cross-sectional area and height meaning that longer canines are relatively slender teeth ($b = 0.735$, Fig. 4).

Roundness is a ratio that gives a general idea of the edged nature of the tooth. A high ratio means that most of the tooth is part of the largest inscribed circle that can fit into the cross-section, and a low ratio means that a large proportion of area (usually indicating the presence of edges) is outside the inscribed circle. For this sample of bats *Lasiurus cinereus, Mimon co-*
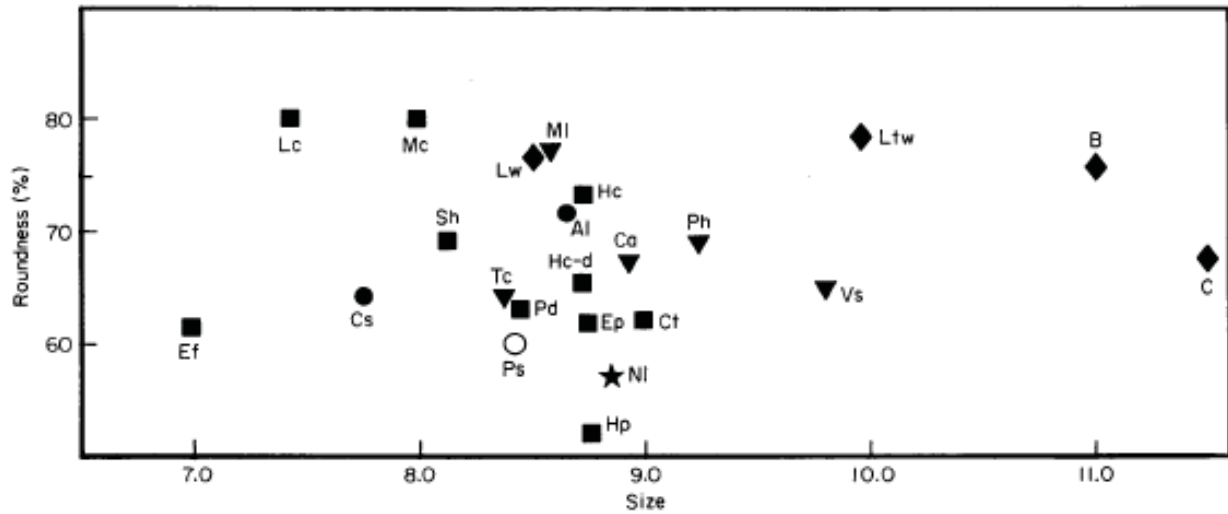
Figure 5. Roundness of a canine cross-section for each bat is plotted against SIZE. Details for the derivation of the values are in Materials and Methods, abbreviations are listed in Table 1, and symbols are the same as in Fig. 3.
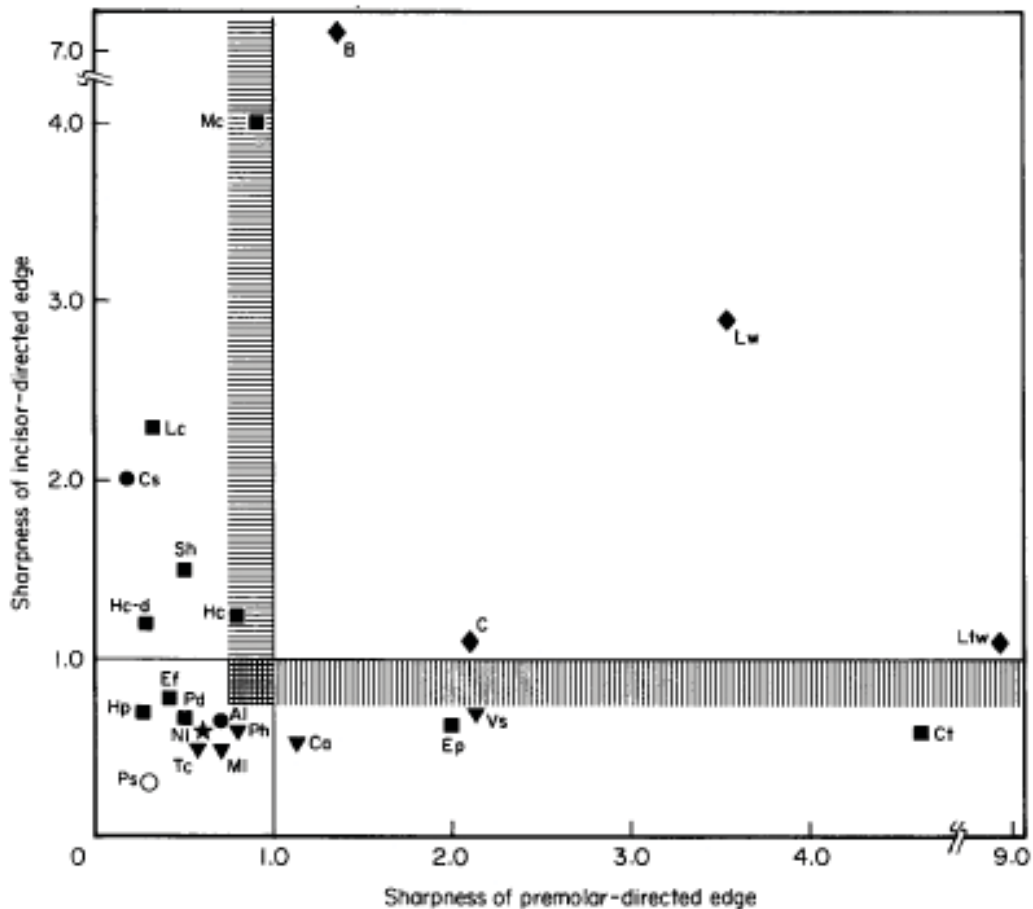
Figure 6. Sharpness ratios for the two most consistent and prominent edges among the bats, the incisor-directed edge and the premolar-directed edge. All edges less than a value of 1.0 are considered sharp, those over 1.0, blunt. Here all the bats have at least one sharp edge while the carnivorans have neither edge sharp. Nine of the 18 species of bats have both edges sharp. Details for deriving the values are in Materials and Methods, abbreviations are listed in Table 1, and symbols are as in Fig. 3.

TABLE 1. Sharpness ratios for each edge

Species	Incisor	Premolar	Labial	Lingual	Buccal
Eumops perotis (Ep)	0.64	2.03	18.89	—	—
Cheiromeles torquatus (Ct)	0.58	4.62	2.19	—	—
Scotophilus heathi (Sh)	1.50	0.53	12.31	1.71	7.00
Eptesicus fuscus (Ef)	0.78	0.42	—	0.89	1.24
Lasiurus cinereus (Lc)	2.31	0.34	—	—	4.67
Vampyrum spectrum (Vs)	0.71	2.15	4.88	—	—
Chrotopterus auritus (Ca)	0.53	1.14	5.76	—	6.07
Trachops cirrhosus (Tc)	0.58	0.51	5.20	—	—
Mimon cozumelae (Mc)	4.00	0.93	—	—	4.14
Phyllostomus hastatus (Ph)	0.62	0.79	0.45	—	6.79
Phyllostomus discolor (Pd)	0.67	0.52	1.72	—	2.81
Phylloderma stenops (Ps)	0.31	0.31	—	—	3.23
Artibeus lituratus (Al)	0.65	0.69	11.00	—	1.14
Centurio senex (Cs)	2.07	0.17	—	7.50	—
Noctilio leporinus (Nl)	0.60	0.59	—	1.54	—
Hipposideros pratti (Hp)	0.71*	0.27	2.30	—	—
Hipposideros commersoni (Hc)	1.25	0.81	7.06	—	—
H. commersoni — deep (Hc-d)	1.21	0.30	12.73	—	—
Megaderma lyra (Ml)	0.51	0.71	5.59	6.67	2.81
mean	1.08	0.94			
Bobcat (B)	7.14	1.35			
Coyote (C)	1.08*	2.09			
Long-tailed weasel (Ltw)	1.09*	8.82			
Least weasel (Lw)	2.89	3.55			

*These are asymmetrical edges and difficult to quantify because half the edge is buttressed. The ratios here represent the circle that fits inside the smallest curve of the edge, but if the circle for the buttressed side were included and averaged *H. pratti* would still be sharp at 0.9, and the coyote and long-tailed weasel would be greatly increased to 2.6 and 4.6, respectively.

zumelae, Megaderma lyra, the two mustelids and the bobcat have the roundest cross-sections (> 75%), while Hipposiderospratti and Noctilio leporinus have a lesser degree of roundness (< 60%, Fig. 5). There is no correlation between roundness and size of the bat.

There can be as many as five edges on a canine (*Scotophilus heathi, Megaderma lyra,* Fig. l), but not all of these are sharp. The two sharpest edges for most bats are the posterior, premolar-directed edge and the anterior, incisor-directed edge. Several small bats have a blunt anterior edge and a sharp posterior edge, while the reverse is true for some of the large bats (Fig. 6). However, these two edges are both sharp in nine of the sampled 18 species. None of the four carnivorans have sharp edges (Figs 2C, 6, Table 1).

The labial edge on the anterior face of the canine is present in most of the species here, but it is sharp in only *Phyllostomus hastatus*. It is quite a prominent edge in *Cheiromeles torquatus* and actually forms the outer side of a deep furrow on the anterior face of the tooth. This edge is not prominent on the rounder teeth of *Eptesicus fuscus, Lasiurus cinereus* and *Mimon cozumelae* and is simply the torus, the bulge of the shank, of the principal cusp (Fig. 1, Table 1). The lingual edge is found in only a few species such as *Scotophilus heathi, Eptesicus fuscus, Centurio senex, Noctilio leporinus,* and *Megaderma lyra.* This edge is sharp only in *Eptesicus fuscus* by the criterion set above. Because of the wide palate in *Centurio* the lingual edge is in a posterior position and the primary premolar-directed edge is in a lateral,

or distal position (Fig. 1, Table 1). On the buccal side of the tooth, a fifth edge is apparent in two or three species although the torus of the principal cusp occupies this side of the canine in most of the species here. It is most prominent in *Artibeus lituratus* and *Eptesicus fuscus*, but neither is sharp (Fig. 1, Table 1).

DISCUSSION

The bite and the initiation of crack propagation

The hypothesis posed here is that the two major cutting edges on the upper canines in bats are primary tools not only for initiating food break up but for producing and directing cracks or clefts in food items in a predictable way given the configuration and positioning of the edges. Once started, cracks in the food item are directed (1) posteriorly to and expanded by the principal cusps of PM^{4}s and the cutting ectoloph of molars and (2) anteriorly to the incisors via the occluding lower canines (paths outlined in palatal view, Fig. 2A).

Bats, like most mammals, are opisthognathous, that is, the posterior (or distal) surface of the lower canine slides past the anterior surface of the upper canine when the jaw closes. The edges on the medial and lateral sides of the anterior face of the upper canine may act as guide ridges for the lower tooth. The transverse movement of the lower jaws cannot extend beyond the lateral edge, which is also where the protoconids make contact and begin to shear with the ectoloph of the upper molars. In most of the microchiropterans, particularly in the non-frugivorous cases, occlusion of upper and lower teeth has to be with 'lock and key' precision. Once occlusion has started the cusps either interdigitate because of the dilambdodont pattern of animalivores, or nest, because of the cookie-cut ter pattern of frugivores with rapid, precise registration and very little freedom of movement (Freeman, 1988). For the occluding toothrows the path initiated by the canines must be followed without deviation, or the toothrows risk deleterious malocclusion.

The lateral edge on the anterior face of the upper canine may be prominent or not, but there appears to be a zone of occlusion on the anterior face with all the species studied here. Having this zone also reinforces the idea of an autocclusal mechanism at work, but actual contact along this face between the occluding teeth is rare because there is little or no wear. The function of this edge in a species like *P. hastatus,* where the edge is sharp, may be at least twofold: first, as the lateral guide ridge for the lower canine and second, as an additional crack propagating edge. Further, and complicating any discussion of function at the anterior end of the toothrow in bats, is the fact that not all bats have a mobile mandibular symphysis. Several, particularly fruit-eating microchiropteran bats, have a fused symphysis (as do several primates including *Homo*). Fusion at the symphysis is a condition thought by many to indicate resistance to forces at the anterior end of the jaws and as an aid to transmit force from the balancing side across the symphysis to the biting side (Beecher, 1977, 1979; Hylander, 1979; Moore, 198 1). It could also mean that the frugivores are isognathous and chew bilaterally instead of chewing in the more typical anisognathous pattern (Hiiemae, 1978).

The incisor-directed edge shears past the lateral edge of the lower canine, which would extend any crack made in the prey item and direct it to the incisors. If carried to total occlusion, the cracks started by the canines would join at the incisors and a piece could be severed from
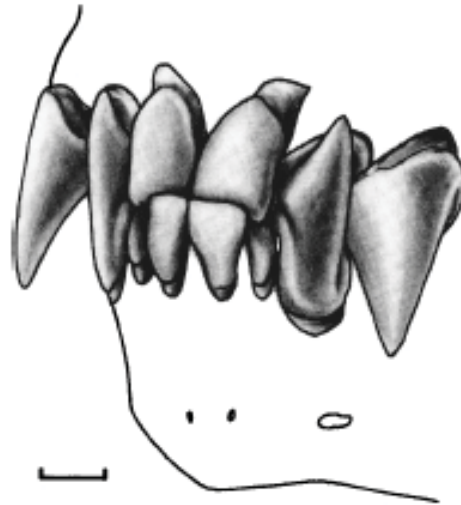
Figure 7. An illustration of the incisors and canines of ***Phyllodenna stenops,*** a bat of unknown food habits but one suspected of eating fruit (see text). This bat has an unusual overlapping, interlocking incisive occlusal mechanism. The inferior (and anterior) edges of the medial pair of upper incisors are overlapped by the superior (and posterior) edges of the medial pair of lower incisors for most of the upper pairs' breadth, but the lateral-most inferior edge of the uppers overlaps the lateral, smaller, pair of lower incisors. The entire mechanism is closely registered like puzzle pieces. Also, the lateral pair of upper incisors in this and in many species with four upper incisors are concavely sculpted to receive the tips of the lower canines as they pass by.

the main body of the prey. Mechanisms like these would be particularly useful in species that clip off inedible parts of their prey before eating them. Upper and lower incisors fit together in a variety of unique ways, the most unusual appearing in Phylloderma stenops. The incisors here fit like interlocking, slightly overlapping, puzzle pieces and surely perform some precise nipping function (Fig. 7). In addition to fused mandibulae, Phylloderma has short canines, closely adjacent teeth, a raised buccal stylar shelf that joins with the sharp edges of the premolars to create a sharp perimeter, and widened trigonal basins on the upper molars. These are characteristics supporting frugivory (Freeman, 1988), which would make Phylloderma the only frugivorous phyllostomine. In species where there are four upper incisors, the lateral pair are often sculpted by wear to accommodate the tips of the lower canines as they pass by. In several, the lateral edge of the medial pair of incisors shears past the medial edge of the lower canines. Upper incisors do not always meet lower incisors, and in Centurio and Artibeus there is a conspicuous gap between upper and lower incisors when the jaws are closed (Freeman, 1988).

The premolar-directed cutting edge or crest is usually posterior on the tooth (lateral or distal in Centurio). Once the initial puncture is made in a prey item, this edge initiates the crack or cleft made in the food and, with the help of the tall apices of the fourth premolars, extends the crack right to the ectoloph of the molariform row. One or both lower premolars shears with the long cutting edge of the premolar-directed edge, and the lingual face of **C'** is often scalloped to accommodate one or both of these premolariform teeth. The premolar-directed edge forms an interloph with the anterior crest or precrista of the adjacent upper premolar to receive the protoconid of PM,. Not all lower premolars occlude snugly inside the upper canines or with the oc-

cluding upper premolars, but where there is contact there is often wear. In *Vampyrum* there is an additional lower premolar, two of the three lower premolars are low crowned, and none of the lower premolars contact the upper teeth. On the other hand in *Centurio* sharp, antero-posteriorly compressed canines along with similarly shaped premolars and the raised and sharpened buccal stylar shelf of the molars form an outer sharpened perimeter around a wide, parabolically-shaped dental arcade much like a cookie cutter. This sharpened edge around the perimeter of the palate is thought to function as a sharp, serrated knife as it cuts through the moderately tough skin of a soft fruit without squeezing out the soft interior (Freeman, 1988). The lower postcanine toothrow nests inside the perimeter of the upper toothrow, and the lower canines fit like puzzle pieces beside the upper canines (medially and only slightly anteriorly).

Some peculiarities of the premolar-directed crest must be mentioned. *Artibeus lituratus* has a trenchant crest, meaning that instead of one edge running from tip to posterior cingulum there are two with a small trench nestled in between. Interestingly, the buccal cusps on PM^4s and upper molars of this species and many other fruit-eating bats are also trenchant. Having a trenchant crest creates two problems: first, the lingual-most edge of the pair is measured in this analysis as the posterior crest and is sharp (Table 1); and second, the buccal edge of the pair, which is not quite as sharp, is not similar to any other edge on the buccal side of the canine of other bats. The trenchant nature of the tooth leaves a very sharp edge with which to shear with the opposing tooth, and, because these trenchant crests appear on canines, premolars and molars of several frugivorous species, it is logical to conclude that they may be particularly advantageous for cutting through skins of fruits. Crests in older bats can become trenchant with wear with a thin valley of dentine exposed between the two sides of enamel resulting in sharp enamel edges, but the ones mentioned here, frugivorous or otherwise, are not a result of wear.

In several species there is a secondary cusp on the premolar-directed crest. *Megaderma lyra* bears a second, smaller cusp, which neatly occludes with PM_3 and PM_4. The lower third premolar occludes with the crest from the tip to the secondary cusp, and PM_4, occludes with the crest running from the secondary cusp to the cingulum and ending at the anterior crest or precrista of PM^4. This interloph arrangement that functions to receive the lower protoconid is a characteristic functional unit that regularly occurs along the ectoloph of the molars (Freeman, 1984). Whereas the secondary cusp in *Megaderma* is located near the base of the canine, the secondary cusp in confamilial, *Cardioderma* and not included in this sample, is a prominent blade that occupies over 50% of the length of the shaft.

Another species, *Hipposideros commersoni,* has a secondary cusp on the premolar-directed edge. The edge from tip to small cusp is slightly trenchant but not beyond. Two cross-sections were taken of this species-the standard one ventral to the cusp and a second one, dorsal to the cusp. The deeper cut (dorsal) shows how elongated the posterior edge of the upper canine becomes after the level of the secondary cusp. While both are sharp the deeper one is one of the sharpest in the study (Table 1). Again, occlusion with the lower premolars is fairly intricate as in *Megaderma.* Although *H. pratti* does not have a secondary cusp it does have an unusually robust canine with a long premolar-directed edge that gives the cross-section a dagger-like, bladed appearance (Fig. 1). However, only the tip and *c.* one-third of the height shears with PM_3. The fourth lower premolar does not appear to shear with the blade-like edge

and the tip simply nestles into a cingular depression at its base. The anterior face dorsal to the cross-section of *H. pratti* is flattened to accommodate occlusion with C^1 for about one-half of the latter's height. This flattened surface is well anterior to the gingival margin because of the procumbency and broadness of the tooth. *Hipposideros commersoni* is a sit and wait predator that specializes on large beetles that walk by its low perch (Vaughan, 1977). Both hipposiderids have features typical of bats that consume large, hard prey i tems (Freeman, 1984).

A secondary, additional cusp on the upper canine, would enhance the shearing mechanism of the upper and lower teeth by functioning as an additional serration and by increasing the bladed condition of the tooth. Perhaps an analogous and definitely experimental situation occurs in the 'evolution' of simple man-made spears where lappets were added to the base of the blade to stop the spear penetrating too far. These lappets were found to inflict additional wounds and later were developed into substantial blades of their own (feather-staves of Dean, 1915).

Explanation of shape diversity

Three different phenomena could be affecting the shapes of cross-sections in bat teeth. First, similarity in canine shape might be a function of phylogenetic distance. Second, bats of similar size may have similarly shaped canines for allometric reasons and face relatively similar problems with stresses and strains or have similar constraints due to development. Finally, bats might share similar shapes of teeth when they have dietary similarity because natural selection has produced convergent shapes that function similarly. If the latter were true then similarity in form could indicate similar diets for distantly related bats. Unfortunately, allometric changes in shape and shape change caused by natural selection may be difficult to separate.

Closely related taxa may have similarly shaped teeth based on recency of common ancestry independent of functional similarity. Sample sizes here are not large enough to support or refute that notion, but it is true that the vespertilionids have similar shapes (Fig. 1) as do many of the species of phyllostomids. However, closely related phyllostomids, *Mimon* and *Phyllostomus*, have different canine shapes and potentially different diets (Honeycutt & Sarich, 1987a; Gardner, 1977). Canines of the smaller *Mimon*, possibly a more insectivorous species, look more like the wedge-shaped canines found in vespertilionids. *Centurio* and *Artibeus* are both stenodermine phyllostomids but are from different tribes (Owen, 1987) and have different canine shapes. *Artibeus lituratus* is a large, robust bat that eats a variety of fruits of different sizes, other flower parts and insects, whereas *Centurio* is probably an obligate frugivore and eats ripe fruit (Gardner, 1977; Freeman, 1988). *Centurio* is one of the smallest bats in the study and has an elongate, bladed premolar-directed edge (Table 1).

Does a change in size significantly change the shape of the canine? A size series involving three closely related monotypic phyllostomids are *Trachops*, *Chrotopterus* and *Vampyrum* (Fig. 1). All three have the same basic triangular shape, but the edges of the largest, *Vampyrum*, are not as acute as the other two and the edges of the smallest, *Trachops*, are the sharpest (Fig. 1, Table 1). The same can be said for the closely related *Phyllostomus hastatus, P.*

discolor and *Phylloderma stenops* (Honeycutt & Sarich, 1987b), where the smallest has the sharpest edges. Sharp edges in smaller bats to blunter edges in larger bats is not a surprising allometric change, and, indeed, there is a significant correlation between sharpness of the premolar-directed edge (dimensionless ratio) and SIZE. Although the largest bat here, *Vampyrum*, does have stouter canines relative to its height, the allometric relationship for these bats as a whole indicates that the demands for height are increasing faster than the demands for strength (as indicated by the square root of the cross-sectional area, Fig. 4). This negative relationship of height to width (Fig. 4) is counter to McMahon's (1973) evidence that height increases as the 2/3 power of diameter, that is that tall trees or long bones are not isometric enlargements of small trees and small bones but are stouter and therefore of necessity, stronger. Here big bats have relatively slender canines, a phenomenon which may be due to the teeth not being weight-bearing structures as are femora or tree trunks but also because they are tools that penetrate prey. The heights of the canines are also positively related to the size of the skull (SIZE, Fig. 3). Why does this positive allometry occur? Do larger bats have longer teeth because they take larger prey that may be covered by proportionally thicker layers of protection? Or perhaps they are long, because there is little or no hard, brittle material within to break them. Bones of prey of the carnivorous bats, namely small birds and mammals, are fragile compared to wildebeest long bones, and prey of hyaenas. Indeed, the obligate carnivore here, *Vampyrum*, does have slightly stouter canines, but at the same time its cross-sectional shape is much like that of *Eumops perotis,* a large insectivore known to eat large insects (Vehrencamp, Stiles & Bradbury, 1977; Ross, 1967). Emerson & Radinsky (1980) found the same relationship of length (anterior-posterior) to height in 11 modern didelphid species that they measured, that is, height increased more rapidly than length relative to a size measurement. Confounding the issue, however, is that the largest microchiropterans have higher basal metabolic rates (McNab, 1983) and have abandoned insectivory for the majority of their diet; thus determining whether changes in shape are because of size increase or because of a change in diet may be difficult.

Several papers have been written on the importance of canines in primates (Every, 1965, 1970; Lucas, 1981; Maier, 1984). The Every studies explore the use of canines as weapons and the self-sharpening phenomenon that occurs (see also Osborn & Lumsden, 1978). In studies that might be relevant to the procuring and crack propagation role, Maier (1984) believes that the size of the anterior teeth in primates increases with increased frugivory and that "small insectivorous forms do not even need very prominent canines." This may be true in some terrestrial insectivores but flying insect eaters have prominent canines and flying fruit eaters have smaller canines (Freeman, 1979, 198 1 a, 1984, 1988).

Lucas (1979) suggests that the shapes and configurations of mammalian teeth are largely an evolutionary response to the types and textures of food eaten. From his research with primates Maier (1984) states "that anterior teeth are more directly correlated with the gross structure of food and they may more directly reflect ecological adaptations of a species." For a bat canines are certainly on the 'front line' of the action and may be the most readily changed for dietary requirements. Processing of foods by bats begins with the penetration of the tip of the canine into the food item. In general the sharper the tip of a bat's canine tooth, the smaller the force required for penetration (Freeman, in preparation). Once the tip is in the item, cracks or

clefts in the food would proceed based on the shape of the shank of the tooth, and how the topography of the tooth directs these cracks anteriorly toward the incisors and posteriorly toward the postcanine teeth. Food processing or break up is caused by crack propagation and the propagation of cracks in brittle materials is most effective if initiated at the beginning of a sharp crack. An example is the crack formed by the sharpened edge of a blade. In soft, non-brittle, materials the apex of the initial cleft is soon blunted or rounded off and more stress must be applied to make the crack propagate (Wainwright *et al.*, 1976; Lucas, 1979). This is why the blade must remain in the material to divide it, because the crack will not progress beyond the blade.

Descriptions of canine function in the literature lead one to believe that different canine shapes allow contrasting methods of penetration (Osborn & Lumsden, 1978; Lucas, 1979, 1982; Luke & Lucas, 1983). Mechanically the triangular or sharpened ellipsoid (blade-like) shapes are better at dividing soft materials than a round shape because there is an increase of surface energy at the edges (Wainwright *et al.*, 1976: 41, 154). This is the reason why surgical needles, which are triangular in cross-section, rather than round needles are used for stitching flesh. These needles actually cut through the skin. Canines with edges should generate a swift, slicing penetration while conical canines generate a strong, crushing penetration. Canines with edges on them should have better speed while conical canines should have greater strength. It would be especially advantageous for small flying mammals that eat tough or soft foods, like insects or skin-covered vertebrates or fruits, to have edged teeth—triangular or polygonal or ellipsoidal—not round teeth.

That conical canines have greater strength has been demonstrated by Van Valkenburgh & Ruff (1987). For a terrestrial predator such as a hyaena that picks up much of its food by group kills or by the more leisurely scavenging method, speed would be less critical. Further, hyaenas cannot afford to have canines that are long and bladed because they eat bones from large prey. Even the short conical canines and premolars that they do have show the highest incidence of breakage among families of large carnivorans (0.35, 0.40; Van Valkenburgh, 1988a).

Van Valkenburgh & Ruff (1987) suggest that the rounder canines of cats are stronger along the antero-posterior axis and are resistant to breakage. This is important because cats have particularly deep bites that may encounter bone. Hyaenas, too, have rounder canines and these blunt, round teeth definitely encounter and actually break bones. Dogs, on the other hand, have canines that are more compressed medio-laterally (more elliptical) and make quick, shallow bites that are less likely to encounter bone. The extremely compressed canines of sabretooth cats are strongly suspected of being good for cutting soft parts without bone or thick skin, and because the moment arm of resistance is short, the bite itself was probably as great or greater than that of extant felids (Emerson & Radinsky, 1980; Van Valkenburgh & Ruff, 1987). Beyond this latter study, which is a careful interpretation of canine characteristics in the light of beam theory, little has been written on the effect of shape of canine teeth on penetration. There is some evidence that felids, unlike microchiropterans, have stouter canines relative to their heights (Emerson & Radinsky 1980, Appendix 11). Van Valkenburgh (1988a) also states that "compared with those in other carnivores, the premolar and canine teeth of hyenas are relatively large in cross- sectional area and presumably stronger for their body

weight." There were no directly comparable figures from Van Valkenburgh & Ruff (1987) or Van Valkenburgh (1988b) to support the idea that extant terrestrial carnivores have shorter, stouter canines—and ones without edges—compared with flying predators that have long, slender and edged canines. The four carnivorans in this study exhibit stouter canines with increasing height, a positive allometric relationship, but the sample size is small and represents two different carnivoran families (Fig. 4).

CONCLUSION

There appear to be three basic shapes for the upper canine in microchiropteran bats: those with sharp incisor-directed edges, those with sharp premolar-directed edges, and those with both edges sharp. No bats in this study have blunt anterior and posterior edges as do the carnivorans represented here. The incisor-directed edge would initiate cracks in prey and direct them to the incisors while the premolar-directed edge would direct cracks to the ectoloph of the postcanine teeth.

Canines in bats are slender and long for their size, even for carnivorous species, a phenomenon which may be related to the lack of hard, brittle, potentially tooth-breaking substances in their prey. Whether bats are capturing insects on the wing, gaffing fish or insects from the water's surface, or transporting a heavy item and eating it in a roost may make a difference to canine shape. Van Valkenburg & Ruff (1987) suggest that eating behaviour affects the shape difference seen in carnivorans. The flying predator has edged canines that would penetrate prey with a swift, slicing puncture while the terrestrial predators today have round or oval canines that would penetrate prey with great strength.

Finally, although canine teeth appear to be simple they are the first teeth in the toothrow to be dealing with prey items and to initiate a rather complex sequence of food break up. Compared with other mammals the triangular-shaped or edged canine seen in microchiropteran bats could have significant functional advantages because food is being gathered with little aid from the forelimbs. Understanding how the edges of these less complex unicuspid teeth may propagate cracks could lead to a greater understanding of not only how cracks are extended by the lower occluding teeth, but also how the more complex, multicuspid postcanine teeth break up foods.

ACKNOWLEDGEMENTS

REFERENCES

BEAUMONT, G. DE, 1964. Remarques sur la classification des Felidae. *Eclogae geologicae Helvetiae, 57:* 837–845.

BEECHER, R. M., 1977. Function and fusion at the mandibular symphysis. *American Journal of Physical Anthropology, 47:* 325–335.

BEECHER, R. M., 1979. Functional significance of the mandibular symphysis. *Journal of Morphology, 159:* 1 17–1 30.

BOHLIN, B., 1940. Food habit of the machaerodonts, with special regard to *Smilodon. Bulletin Geologiska Institut Universitet Upsala, 28:* 156–174.

BUTLER, P. M., 1978. Molar cusp nomenclature and homology. In P. M. Butler & K. A. Joysey (Eds), *Development, Function and Euolution of Teeth:* 439–453. London: Academic Press.

DEAN, B., 1915. Evolution of arms and armor. *American Museum Journal, 1915:* 357–362.

EMERSON, S. B. & RADINSKY, L., 1980. Functional analysis of sabertooth cranial morphology. *Paleobiology, 6:* 295–312.

EVERY, R. G., 1965. The teeth as weapons, their influence on behaviour. *Lancet, 1*: 685–688.

EVERY, R. G., 1970. Sharpness of teeth in man and other primates. *Postilla, 143:* 1–30.

FREEMAN, P. W., 1979. Specialized insectivory: Beetle-eating and moth-eating molossid bats. *Journal of Mammalogy, 60:* 467–479.

FREEMAN, P. W., 1981a. Correspondence of food habits and morphology in insectivorous bats. *Journal of Mammology, 62:* 166–173.

FREEMAN, P. W., 1981b. A multivariate study of the family Molossidae (Mammalia, Chiroptera); Morphology, ecology, evolution. *Fieldiana, Zoology, 7:* 1–173.

FREEMAN, P. W., 1984. Functional cranial analysis of large animalivorous bats (Microchiroptera). *Biological Journal of the Linnean Society, 21:* 387–408.

FREEMAN, P. W., 1988. Frugivorous and animalivorous bats (Microchiroptera): dental and cranial adaptations. *Biological Journal of the Linnean Society, 33:* 249–272.

GARDNER, A. L., 1977. Feeding habits. In R. J. Baker, J. K. Jones, Jr. & D. C. Carter (Eds), Biology of bats of the New World family Phyllostomatidae. Part II. *Special Publications, The Museum, Texas Tech University, 13:* 293–350.

HEPBURN, H. R. & JOFFE, I., 1976. On the material properties of insect exo-skeletons. In H. R. Hepburn (Ed.), *The Insect Integument:* 207–235. Amsterdam: Elsevier.

HERSHKOVITZ, P., 1971. Basic crown patterns and cusp homologies of mammalian teeth. In A. A. Dahlberg (Ed.), *Dental Morphology and Evolution:* 95–150. Chicago: University of Chicago Press.

HIIEMAE, K. M., 1978. Mammalian mastication: a review of the activity of the jaw muscles and the movements they produce during chewing. In P. M. Butler & K. A. Joysey (Eds), *Development, Function and Evolution of Teeth:* 359–398. London: Academic Press.

HONEYCUTT, R. L. & SARICH, V. M., 1987a. Albumin evolution and subfamilial relationships among New World leaf-nosed bats (family Phyllostomidae). *Journal of Mammalogy, 68:* 508–517.

HONEYCUTT, R. L. & SARICH, V. M., 1987b. Monophyly and molecular evolution within three phyllostomid bat genera. *Journal of Mammalogy, 68:* 518–525.

HYLANDER, W. L., 1979. Mandibular function in *Galago crassicaudatus* and *Macaca fasicularis*: An in vivo approach to stress analysis of the mandible. *Journal of Morphology, 159:* 253–296.

KURTEN, B., 1952. The Chinese Hipparion fauna. *Commentationes Biologicae Societas Scientiarum Fennica,* 13: 1–82.

LUCAS, P. W., 1979. The dental-dietary adaptations of mammals. *Neues Jahrbuch Geologie und Palaontologie Monatshefte, 8:* 486–512.

LUCAS, P. W., 1981. An analysis of canine size and jaw shape in some Old and New World non-human primates. *Journal of Zoology, London, 195:* 437–448.

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

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

LUKE, D. A. & LUCAS, P. W., 1983. The significance of cusps. *Journal of Oral Rehabilitation, 10:* 197–206.

MAIER, W., 1984. Tooth morphology and dietary specialization. In D. J. Chivers, B. A. Wood & A. Bilsborough (Eds), *Food Acquisition and Processing in Primates:* 303–330. New York: Plenum Press.

McMAHON, T., 1973. Size and shape in biology. *Science, 179:* 1210–1204.

McNAB, B. K., 1983. Energetics, body size, and the limits to endothermy. *Journal of Zoology, London, 199:* 1–29.

MELLETT, J. S., 1985. Autocclusal mechanisms in the carnivore dentition. *Australian Mammalogy, 8:* 233–238.

MOHSENIN, N. N., 1977. Characterization and failure in solid foods with particular reference to fruits and vegetables. *Journal of Texture Studies, 8:* 169–193.

MOHSENIN, N. N., 1986. *Physical Properties of Plant and Animal Materials.* 2nd Edition. New York: Gordon & Breach Science Publishers.

MOORE, W. J., 1981. *The Mammalian Skull.* Cambridge: Cambridge University Press.

OSBORN, J. W. & LUMSDEN, A. G. S., 1978. An alternative to "thegosis" and a re-examination of the ways in which mammalian molars work. *Neues Jahrbuch Geologie und Palaontologie Abhandlungen, 156:* 371–392.

OWEN, R. D., 1987. Phylogenetic analyses of the bat subfamily Stenoderminae (Mammalia: Chiroptera). *Special Publications, The Museum, Texas Tech University, 26:* 1–65.

PORTER, F. L., 1978. Roosting patterns and social behavior in captive *Carollia perspicillata. Journal of Mammalogy, 59:* 627–630.

ROSS, A., 1967. Ecological aspects of the food habits of insectivorous bats. *Proceedings of the Western Foundation of Vertebrate Zoology, 1:* 205–264.

VAN VALEN, L., 1979. The evolution of bats. *Evolutionary Theory, 4:* 103–121.

VAN VALKENBURGH, B., 1988a. Incidence of tooth breakage among large predatory mammals. *American Naturalist, 131:* 291–302.

VAN VALKENBURGH, B., 1988b. Carnivore dental adaptations and diet: a study in trophic diversity within guilds. In J. L. Gittleman (Ed.), *Carnivore Behavior, Ecology and Evolution.* Ithaca: Cornell University Press.

VAN VALKENBURGH, B. & RUFF, C. B., 1987. Canine tooth strength and killing behavior in large carnivores. *Journal of Zoology, London, 212:* 379–397.

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

VEHRENCAMP, S. L., STILES, F. G. & BRADBURY, J. W., 1977. Observation on the foraging behavior and avian prey of the neotropical carnivorous bat, *Vampyrum spectrum. Journal of Mammalogy, 58:* 469–478.

VINCENT, J. F. V., 1980. Insect cuticle: a paradigm for natural composites. In J. F. V. Vincent & J. D. Currey (Eds), The mechanical properties of biological materials. *34th Symposium of the Society of Experimental Biology:* 183–210. Cambridge: Cambridge University Press.

VINCENT, J. F. V., 1982. *Structural Biomaterials.* New York: John Wiley &Sons.

WAINWRIGHT, S. A., BIGGS, W. D., CURREY, J. D. & GOSLINE, J. M., 1976. *Mechanical Design in Organisms.* Princeton: Princeton University Press.