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On the cutting edge: Tooth blade sharpness in herbivorous and faunivorous mammals

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Sharp blade tips are advantageous to herbivorous and faunivorous mammals because bite forces are concentrated on the sharp blade tip and produce an initial tear in the tough foodstuff. We examine whether blade sharpness scales with body size and how tooth design and diet are related to the sharpness of the blade tip. Blade sharpness scales isometrically and the physical properties of food form a secondary influence. A high attrition/abrasion ratio is associated with sharp blades regardless of total wear rate, while high relative abrasion blunts the blades. The height of occlusal features is the main aspect of tooth design associated with sharpness.

1. Introduction

A main functional determinant of fitness is the ability of individuals to obtain energy and nutrients from their environment. The evolution of mammalian species is accordingly marked by the acquisition of behavioral, physiological, and morphological characteristics that promote feeding and digestive efficiency. Despite the extensive range of feeding specializations among mammalian species, components of the masticatory apparatus have been found to scale isometrically with body size (Fortelius 1985). Specializations in tooth shape are particularly important to the rapid breakdown and digestion of food, and not only is molar tooth shape reflective of the types of food ingested (Lucas & Luke 1984), but the linear measurements, surface areas and volumes of teeth commonly scale with isometry (Fortelius 1985, Gingerich & Smith 1985, Janis 1988). The functional units of a tooth, however, are the occluding edges or blade tips, and the extent to which the sharpness of these edges corresponds to function or conforms with the general isometric scaling of the masticatory apparatus remains unclear. Descriptions of mammalian tooth morphology have only qualitatively referred to the sharpness of the blade tip and the actual sharpness of the edges of mammalian teeth remains unknown. This study describes blade sharpness in a sample of herbivorous and faunivorous mammals and determines the extent to which sharpness scales isometrically and in accordance with other masticatory components, as well as the relationship of other factors such as crown design or diet with the sharpness of the blade tip.

1.1. What is a blade?

A blade is formed by the wear facets that mark the surfaces of cusps and lophs, and the blade tip is formed by the leading edge of the wear facets. Specifically, wear facets with leading edges that are sharp and longer than the food item to be cracked may be termed blades (Lucas & Teaford 1994). The enamel surface is worn into flat facets by contact with the opposing (occluding) tooth surface; this wear process (by tooth on tooth) is termed attrition (for a discussion and defense of this terminology, see Fortelius (1985)). Thus, each facet must have a corresponding facet on the opposing tooth, and these matching surfaces describe the occlusal relationships of the cusps. The relationship between facets and cusps is preserved even when the cusps change in relative size and position (Butler 1961). Homologous wear facets may be traced across taxa and a variety of molar morphologies and have been given numerical identities to indicate this homology (Butler 1952, 1973).

1.2. How does a blade work?

The process of food breakdown between blades, or facet surfaces, may be understood from description of tooth surfaces, the relative movement of the teeth, and the fracture behavior of food between the teeth. Blades are often described as performing a shearing action on the food stuff (Crompton & Hiiemae 1970, Kay & Hiiemae 1974), however, it is possible to be more precise in the characterization of the activity that is performed. The "shearing" that blades perform refers to the stresses upon the foodstuff. Lucas and Teaford (1994) describe two shearing modes where a notch is introduced into a hypothetical foodstuff and in which a crack will initiate and propagate in the same direction as the longest dimension of the notch. In the first shearing mode crack propagation is parallel to the loading direction and produces a cut like a hole punch, and in the second mode the crack is propagated perpendicular to the loading direction. Most bladed systems follow the latter mode and propagate cracks by point loading the blades. In contrast to loading the entire blade at once, point contacts reduce the forces associated with crack initiation. These shearing cuts can be distinguished from crack propagation that results from tensile stress. In this alternative mode of cutting, a sharp wedge induces crack propagation by forcing material apart to the right and left of the notch (Lucas & Teaford 1994).

In both shearing modes the sharpness of the blade tip is necessary to incur an initial notch in the food stuff and to promote the progress of the crack. The blade tip or leading edge of a wear facet encounters a food particle prior to the facet surface. Thus, bite forces load the blade tip before concentrating forces on the occluding facet surfaces, and the blade tip is likely to remain loaded throughout the chewing stroke. The small area of contact between a sharp blade tip and a food particle increases the intensity of the stress field in the food at the point of contact; in this way a crack is initiated in the food particle. The sharp blade tip maintains a high stress field in the foodstuff at the point of crack advancement, and thus promotes crack propagation until fracture of the food particle occurs. If the crack becomes self-propagating, the blade tip may advance through the food slightly behind the crack tip (the point of crack advancement) and reduce its wear (Lucas & Luke 1984, Lucas & Corlett 1991).

1.3. What food types are best fragmented by blades?

The elasticity and fracture toughness of a food item indicate the resistance of the material to crack propagation and ultimate fracture. Elasticity is measured by the elastic modulus: a measure of the resistance of a material to elastic deformation. Materials of low modulus are floppy and respond to stress by straining greatly. Conversely, materials of high modulus are stiff and strain only slightly in response to stress. Most solids are elastic only to very small strains and suffer breakage or non-reversible deformation at higher strains. The critical strain energy release rate, G_c, and the critical stress intensity factor, K_{Ic}, are common measures of fracture toughness. G_c refers to the energy absorbed in making a unit of area crack and K_{Ic} refers to the intensity of the stress field in a solid close to an advancing crack tip (Ashby & Jones 1980).

Blade-like dental morphologies are required to fracture dietary items of high fracture resistance. Lucas and Teaford (1994) plot values for the elastic modulus (E) versus the critical stress intensity factor (K_{Ic}) of various food items and suggest that a ratio of these values (K_{Ic}^2/E) may be used to assess fracture resistance. Dietary items of a high critical stress intensity and a low elastic modulus are pliant and tough, such as plant parenchyma, dicot leaves, rye grass, rat skin, and insect cuticle. These foods are reluctant to form cracks and a sharp blade tip is necessary to incur a notch in the food item and to promote the progress of the crack through advancement of the blade tip. Strait and Vincent (pers. comm.) find high toughness values for beetles, bovine muscle, and caterpillars. Beetles display some brittle fracture, but bovine muscle and caterpillars are too compliant for the initiated cracks to become self-propagating. The toughness values for beetles, bovine muscle, and caterpillars are comparable to those observed in eight species of leaves at different stages of maturity; most species of leaves become thicker and tougher with age (Lucas & Pereira 1990). Strait and Vincent (pers. comm.) note that bovine muscle has a toughness value that corresponds to the upper range for leaves, beetles have a mean toughness in the mid range of the leaf study, and caterpillars are close to the lowest values for young leaves.

Elastic modulus values for leaf toughness may be higher than reported in the Lucas and Pereira study, because the toughness tests measured along a 'least tough' path and avoided leaf venation. The spongy mesophyll and epidermis that form the leaf lamina provide little fracture resistance, and leaf toughness results from thick-walled veins and the surrounding bundle sheaths. The leaf venation pattern produces a direction-dependent toughness and reduces the ease of fracture. In some leaves the extension of bundle sheaths to the epithelia creates compartments between the veins. Immature leaves do not have thick-walled veins, and the thin-walled cells have a low toughness that is probably not direction-dependent; toughening of the veins may occur within a few days. The absence of thick-walled veins or bundle sheaths in some mature leaves results in leaves of a lower fracture resistance (Lucas & Pereira 1990, Lucas *et al.* 1991, Choong *et al.* 1992, Lucas & Teaford 1994).

1.4. Why is the scaling of blade sharpness important?

The scaling of blade sharpness is of special interest because the sharpness of the blade tip is functionally critical to mammals of all body size. In general the masticatory apparatus of mammals is isometric to body size, structurally as well as functionally (Fortelius 1985, 1987, 1988, Shipley *et al.* 1994), and the extent to which the scaling of blade sharpness conforms to this overall relationship affects the success with which mammals of diverse size may consume the same food. Unlike components of the masticatory apparatus, food particle size does not vary regularly with animal body size. For example, individual food items such as larvae, leaves, or seeds are always of the same size, no matter who eats them, and many foods are consumed by animals of diverse size. Because the fracture of food items may depend upon the sharpness of a blade edge, animals of diverse size are presumed to possess blade edges that are sufficiently sharp for their function and maintain a relationship with body size. Thus, this study addresses to what extent blade sharpness is size dependent and how the scaling of blade sharpness is compatible with the size-independence of the foods consumed.

1.5. Other factors influencing sharpness

Design features of a tooth, such as the patterning of the occlusal surface, could also be associated with differences in blade tip sharpness. Consumers of tough food items differ greatly in tooth shape: for example, meat-eaters possess carnassial tooth shapes, and plant-eaters vary from selenodont forms and other lophed dental types to bilophodont shapes. Such differing crown patterns may or may not be associated with different values for blade tip sharpness. On the other hand, phylogenetically related taxa that share a crown pattern often occupy diverse ecological niches and consume different foods. Thus, there is no strict relationship between general crown type and function and whether crown type and blade sharpness are directly related is unknown.

Tooth wear and diet undoubtedly influence the countours of the blade tip to some extent. Blade

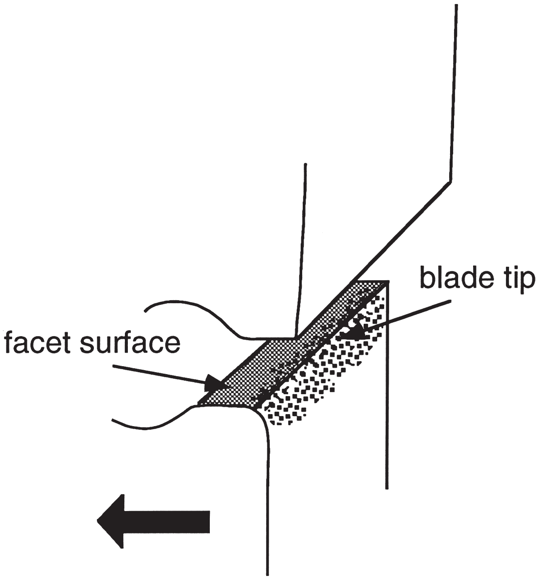

Fig. 1. A close-up of the occlusion of buccal wear facets on selenodont molars. The arrow indicates the direction of movement of the lower tooth surface relative to the upper tooth surface. The darkly shaded region indicates the presence of high attrition on the facet surface. The darkly stippled region indicates the presence of high abrasion on the buccal edge of the facet, or blade tip.

sharpness is not a preformed feature of the dentition; but must result from tooth wear during chewing. Because the blade tip forms the leading edge of a wear facet, interaction of the food stuff with the occlusal surface continuously alters the morphology of both the wear facet and the blade tip. The distinctness of the facets, including the sharpness of the edges, depends on the ratio of attrition to abrasion (Fig. 1). High bite force during the tooth-to-tooth contacts of chewing (attrition) develops the wear facets and sharpens blade tips; in contrast, food-on-tooth wear (abrasion) acts to obliterate the attrition facets and the blade tips (Rensberger 1973). The absolute amount of wear is irrelevant for sharpness; what matters is only the relative contributions of attrition and abrasion. In other words, crown height, reflecting total cumulative wear, and blade sharpness, reflecting the attrition/abrasion ratio, should be independent of each other. These wear processes are influenced by the enamel structure (Rensberger 1978, 1983, Stern *et al.* 1989, Maas 1991, 1993). Depending upon the relationship of the enamel structure to dental wear in an individual species, dental sharpness may be a reversible morphological feature; dietary changes that alter wear processes may blunt a sharp edge or sharpen a blunted edge.

The material properties of food, such as toughness and abrasiveness, control the ratio of attrition versus abrasion on the wear facet and the blade tip, and thus affect blade sharpness. Several *a priori* predictions may be made: an abrasive diet inevitably causes heavy wear on the facet surface and blade tip, and consumers of abrasive foodstuffs, such as grazers, are predicted to have blade tips that are rounded by wear and less sharp than consumers of less abrasive diets, such as meat-eaters and browsers. Meat may be considered less abrasive than plant material, and meat specialists are predicted to have sharper blade tips than herbivorous taxa. The high toughness of vertebrate tissues predicts that meat specialists will also have sharper blades than consumers of less tough prey.

2. Material and methods

Buccal facet sharpness was compared in a broad taxonomic sample of faunivorous and herbivorous mammals. The sample included species of diverse body sizes with carnassial, selenodont, and lophodont postcanine teeth. The tip of facet 1 (Butler 1952) was examined on the fourth upper premolar or carnassial of the carnivores and the first upper molar of the remaining taxa. This facet is located on the buccal edge of the tooth, on the posterior surface of the metacone. The buccal facets of the upper and lower molars that interface during the most powerful phase of the chewing cycle, known as *phase 1* (Crompton & Hiiemae 1970), are of primary importance in the mastication of “tough” foods; the high stresses necessary to fracture a tough food item are generated in this stage of the chewing cycle (Hylander *et al.* 1987).

The species examined in this study are presented in Table 1 with an indication of the dental form of the taxa, dietary category, and the approximate body size. The size classes for all species with the exception of the Carnivora are defined as follows: the mean body mass for male and female small taxa is less than 30 kg, the mean for medium taxa is greater than 30 kg and less than 150 kg, and the mean for large taxa is greater than 150 kg. Exceptions to this method of size categorization include the cervids, *Cervus elaphus* and *Rangifer tarandus*, which have a large geographic variation in body mass. Both of these species were classified as medium-sized ruminants and a mean body mass of 153 kg was used for *Cervus elaphus* (Scott 1987), and a mean body mass of 110 kg was used for *Rangifer tarandus* (Bernfield 1974). For the Carnivora, small taxa have a mean body mass that is less than 40 kg and large taxa have a body mass that is greater than 40 kg. The diet

Table 1. A list of included species and their corresponding occlussal morphologies (o.m.) and dietary habits. S = Selenodont, C = Carnassial, T = Trilophodont, B = Bilophodont, P = Plagiolophodont.

Species	O. m.	Diet	Body mass: mean male mass and species range
Order Artiodactyla			
Family **Bovidae**			
Alcelaphus buselaphus	S	Grazer: dry grass	Large: 162.5 kg; 100–225 kg
Ammotragus lervia	S	Mixed feeder	Medium: 122.5 kg; 100–145 kg male, 40–55 kg female
Antilocapra americana	S	Mixed feeder: grasses, shrubs	Medium: 53 kg; 36–70 kg
Bison bison	S	Grazer: dry grass	Large: 675 kg; 350–1 000 kg
Hippotragus niger	S	Grazer: dry grass	Large: 225 kg; 150–300 kg
Ovibos moschatus	S	Mixed feeder: grass, sedge, browse	Large: 305 kg; 200–410 kg
Sylvicapra grimmia	S	Browser: leaves, flowers, bulbs	Small: 18.5 kg; 12–25 kg
Tragelaphus scriptus	S	Mixed feeder: leaves, twigs, grass	Medium: 53.5 kg; 30–77 kg male, 24–42 kg female
Family **Cervidae**			
Alces alces	S	Browser: shrubs, trees, aquatic vegetation, bark	Large: 512.5 kg; 200–825 kg
Cervus elaphus	S	Mixed feeder: grass, forbs, woody plants, shrubs, conifers	Medium: 153 kg; 75–340 kg
Muntiacus muntjac	S	Browser: leaves, shoots, grass, fruit	Small: 21 kg; 14–28 kg
Rangifer tarandus	S	Browser: new growth, leaves, lichens, evergreen leaves, twigs	Medium: 110 kg; 60–318 kg
Family **Giraffidae**			
Giraffa camelopardalis	S	Browser: leaves	Large: 1 240 kg; 550–1 930 kg
Family **Tragulidae**			
Tragulus javanicus	S	Browser: fruits, berries	Small: 4.35 kg; 7–8 kg
Order Carnivora			
Family **Canidae**			
Canis lupus	C	Meat specialist	Large: 50 kg; 20–80 kg
Vulpes vulpes	C	Omnivore: small vertebrates, insects, fruit	Small: 8.5 kg; 3–14 kg
Family **Felidae**			
Felis sylvestris	C	Meat specialist	Small: 4.5 kg; 3–6 kg
Panthera leo	C	Meat specialist	Large: 200 kg; 150–250 kg male, 82–120 kg female
Family **Hyaenidae**			
Crocuta crocuta	C	Meat specialist	Large: 65 kg; 50–80 kg
Family **Mustelidae**			
Gulo gulo	C	Meat specialist	Small: 19.5 kg; 7–32 kg
Lutra lutra	C	Fish, crayfish, crabs	Small: 8.5 kg; 3–14 kg
Martes martes	C	Meat specialist	Small: 13 kg; 8–18 kg
Meles meles	C	Omnivore: hard and soft invertebrates, fruit, small vertebrates	Small: 13 kg; 10–16 kg
Family **Viverridae**			
Cryptoprocta ferox	C	Meat specialist	Small: 9.5 kg; 7–12 kg
Genetta tigrina	C	Small vertebrates, insects	Small: 2 kg; 1–3 kg
Order Hyracoidea			
Family **Procaviidae**			
Dendrohyrax arboreus	T	Browser: leaves, fruits, twigs and bark	Small: 2.95 kg; 1.4–4.5 kg
Procavia capensis	T	Mixed feeder: grasses, shrubs, and forbs	Small: 3.6 kg; 1.8–5.4 kg
Order Primata			
Family **Cebidae**			
Alouatta seniculus	B	Folivore	Small: 7 kg; 4–10 kg
Family **Cercopithecidae**			
Cercopithecus mitis	B	Folivore	Small: 9 kg; 6–12 kg
Colobus badius	B	Folivore	Small: 9.95 kg; 5.4–14.5 kg
Presbytis cristata	B	Folivore	Small: 6.5 kg; 5–8 kg
Order Perissodactyla			
Family **Rhinocerotidae**			
Ceratotherium simum	P	Grazer: grass	Large: 2 800 kg; 2 000–3 600 kg male, 1 400–1 700 kg female
Diceros bicornis	T	Browser: twigs, legumes	Large: 1 125 kg; 950–1 300 kg
Family **Equidae**			
Equus grevyi	P	Grazer	Large: 401 kg; 352–450 kg

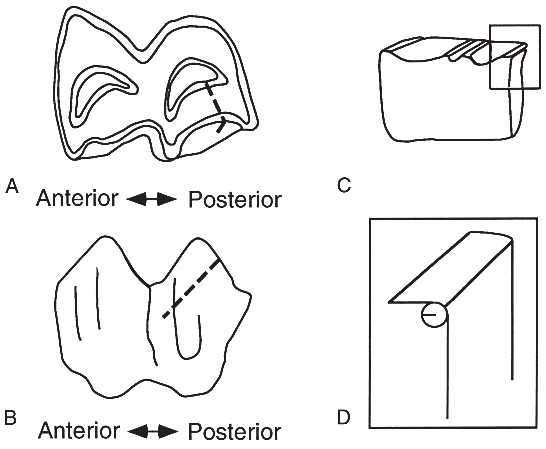

Fig. 2. Measurement of blade tip sharpness. The facet surface was cross-sectioned transversely and a circle was fit to the curve of the cross-sectioned facet tip. The radius of the circle was used as an index of blade tip sharpness. — A: Occlusal view of selenodont molar indicating the location of cross-section. — B: Buccal view of selenodont molar indicating the location of cross-section. — C: Cross-section of selenodont molar indicating the location of the blade tip. — D: Blade tip sharpness was measured as the radius of curvature of the facet edge.

and body size of each species was obtained from Nowak (1991) or Macdonald (1984). Dietary categories for the ruminants correspond with Hofmann and Stewart (1972), and indicate the amount of fibrous grass consumed versus less fibrous herbaceous material. The diet of grazing ruminants consists of at least 90% grass. Mixed feeders vary their diet seasonally and include between 10% and 90% of grass in the diet. Browsers consume at least 90% of their diet as dicotyledonous material; while most browsers feed on a mixture of leaves, shrubs, herbs and succulent items, 'succulent browsers' may take very little leaf material and concentrate mainly on fruits and buds (Hofmann & Stewart 1972, Janis & Ehrhardt 1988). The other ungulates may be assigned to the ruminant dietary categories. Of the hyraxes, *Dendrohyrax* qualifies as browser (Nowak 1991). *Procavia*, often referred to as a grazer (Walker *et al.* 1978, Janis & Ehrhardt 1988), is here considered a mixed feeder, eating 78% grasses in the wet season, but browsing extensively, 57%, in the dry season (Walker *et al.* 1978). Of the rhinos studied here, *Diceros bicornis* is a browser taking less than 5% grass even in open grasslands, while *Ceratotherium simum* is an extreme grazer (Owen-Smith 1988). Among the Carnivora, meat specialists consume a diet of more than 70% meat. In the more omnivorous taxa nonvertebrate material, such as fruit or insects, composes at least 50% of the diet (Van Valkenburgh 1989).

A sample of six specimens exhibiting a similar stage of wear was examined for each species, with the exception of *Ammotragus lervia* where only five specimens were examined. The sample described buccal tip sharpness in each species at an early wear stage. An 'early' wear stage was defined in all taxa by the presence of a well-developed buccal facet and the absence of dentine exposure at the blade tip. Although differences in wear stage exist in comparisons between taxa, the dentitions of each taxon are similarly presumed to operate with high efficiency at these early stages of wear. Specimens were also selected for the absence of enamel chipping or breakage at the blade tip. Selenodont specimens were selected with high topographical relief and unbroken ridges with the exception of the grazing taxa; high topographical relief is typically absent from the dentitions of grazers after moderate wear, and specimens that were studied had a flattened occlusal surface. Specimens of bilophodont primates with well-developed buccal facets also possessed breaching of the enamel on the lingual cusps.

Selection of unbroken facet edges may bias the results in that only the optimal tip edges are reported and compared. The percentage of damage along a facet edge may be high, particularly in grazing ruminants (Fortelius 1985); however, examination of unflawed regions of the tooth does not reflect this damage. Sharpness values therefore reflect a maximum at points along a facet edge and do not provide information on the mean sharpness of the blade as a whole. The use of maximum rather than mean sharpness was chosen because it was the easiest to define and measure.

The upper fourth premolar or first molar was molded in each specimen using Provil (Bayer Dental) or a combination of Optosil and Xantopren (Bayer Dental) mold-making materials. The molds were cast with epoxy and the buccal facet number 1 was identified on the epoxy cast. Using light microscopy the midpoint of the facet edge was identified, and perpendicular to the facet edge, a line was extended bucco-lingually at this midpoint (Fig. 2). The epoxy cast was cross-sectioned at this line using a scalpel blade and handsaw, and the cross-sectioned face was polished with fine sandpaper. The facet tip was observed at a magnification of ×30 and three tracings were obtained with a camera lucida. The cross-sectioned face was independently oriented prior to each tracing using two carpentry levels placed adjacently at 90 degrees on a metal disc. Scanned images of the traced facet tips were analyzed with the graphic software Canvas (Deneba, FL, USA). Facet tip sharpness was measured by fitting a circle to the curve of the cross-sectioned facet tip; the tracings of the facet tip were scaled to approximately the same size prior to measurement. The radius of the circle was used as an index of facet tip sharpness. The curvature of the occlusal tip of the facet surface, or blade sharpness, was measured and not the shape of the buccal crown section, or the gross curvature of the cusp or loph. The mean value of the three tracings was used for a single specimen. Anova comparisons were performed upon species means of members of different dietary, taxonomic, and size categories. Anova comparisons between species pairs were performed upon the sharpness values of individual specimens. In order to investigate the relationship of blade sharpness to body mass a regression analysis of the

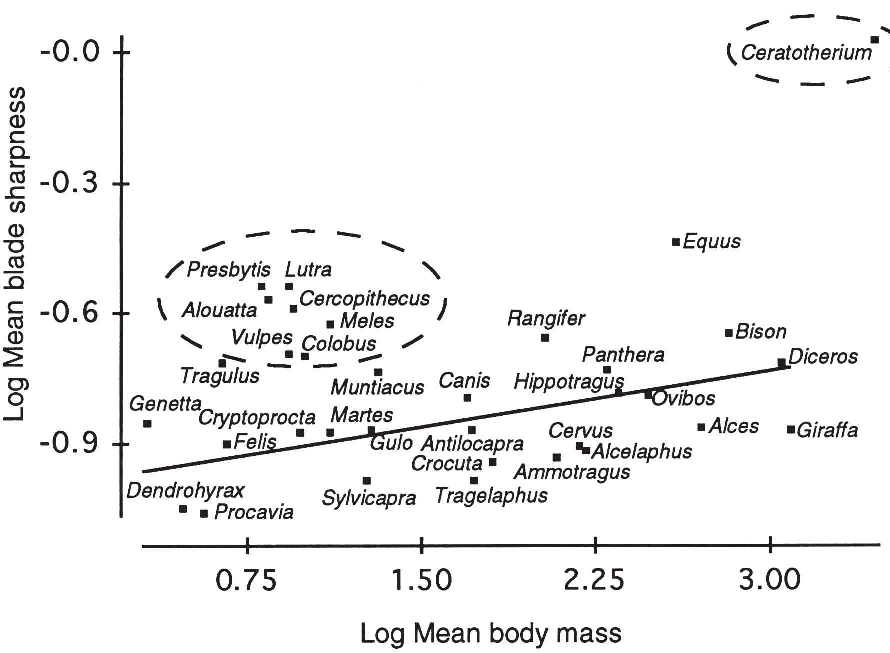

Fig. 3. Log mean blade sharpness versus log mean body mass, excluding taxa with low attrition: *Ceratotherium*, *Alouatta*, *Cercopithecus*, *Colobus*, *Lutra*, *Meles*, *Presbytis*, and *Vulpes*, ($y = 0.075x - 0.967$, $r^2 = 0.206$).

log-transformed mean blade sharpness for each species versus the log-transformed mean body mass for the males of each species was performed. Mean blade sharpness for each species was also multiplied by a tooth area measure (tooth length × width) in order to produce an approximation of planar area. The log-transformed planar area was also regressed against the log-transformed body mass values.

Measurement error was assessed by obtaining six sharpness measures from a single individual of *Cervus elaphus* and by calculating the standard deviation of these independent measures. Anova comparison of blade sharpness between 6 individuals of *Rangifer tarandus* with extremely low molar relief and 6 individuals with high molar relief determined the extent to which molar height due to tooth wear contributed to differences in blade sharpness.

3. Results

Differences in blade sharpness observed among species were not a result of measurement error or the degree of molar height due to wear. Six measures of an individual specimen of *Cervus elaphus* had a standard deviation of 0.019 around a mean blade sharpness of 0.097. Anova comparison of 2 samples of reindeer, *Rangifer tarandus*, containing 6 specimens each with high and low molar relief did not indicate a significant difference in blade sharpness between molars of different heights; ($F = 0.838$, $P = 0.381$).

The regression analysis of log-transformed mean blade sharpness versus log-transformed mean body mass was significant only for those taxa that shape their blade tips through high attrition. The rhinoceros, *Ceratotherium simum*, was excluded from the analysis because of its high body mass and the high abrasion on its dental surfaces. The primates, *Alouatta seniculus*, *Cercopithecus mitis*, *Colobus badius*, and *Presbytis cristata*, and the carnivores, *Lutra lutra*, *Meles meles*, and *Vulpes vulpes*, consume less tough foods than the remaining herbivorous and carnivorous taxa, and thus high attrition does not shape their blade tips. The exclusion of these taxa from the regression analysis resulted in a significant relationship between log mean body mass and log mean blade sharpness ($F = 6.24$, $P = 0.025$; Fig. 3). The regression of log-transformed planar area versus log-transformed body mass was also significant and indicated isometric scaling (F-ratio: 112, P: 0.001, slope = 0.679, $S.E. = \pm 0.064$).

In contrast, blade sharpness was not observed to differ according to body size in a sample of Carnivora that specialize on meat or in a sample of selenodont artiodactyls that included browsers, mixed feeders and grazers. Members of the Carnivora of small and large size did not have significant differences in blade sharpness ($F = 1.467$,

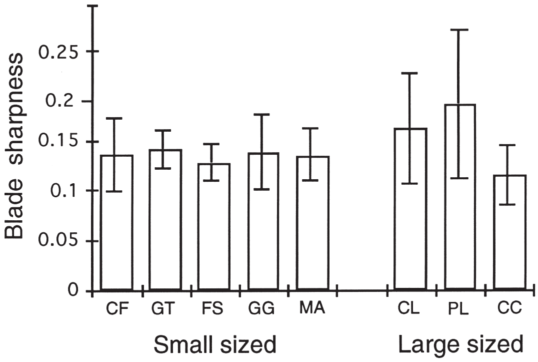

Fig. 4. Blade sharpness in carnivores of small and large body size that specialize on meat. No significant difference in blade sharpness exists between carnivores of small and large body size. Standard deviations for mean blade sharpness are indicated by the error bars. Abbreviations for taxa are as follows: *Cryptoprocta ferox*, CF; *Genetta tigrina*, GT; *Felis sylvestris*, FS; *Gulo gulo*, GG; *Martes martes*, MA; *Canis lupus*, CL; *Panthera leo*, PL, and *Crocuta crocuta*, CC.

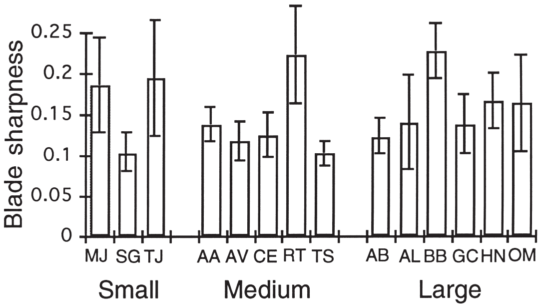

Fig. 5. Blade sharpness in artiodactyls of different body sizes. No significant difference in blade sharpness exists between size categories. Standard deviations for mean blade sharpness are indicated by the error bars. Abbreviations are as follows: *Muntiacus muntjac*, MJ; *Sylvicapra grimmia*, SG; *Tragulus javanicus*, TJ; *Antilocapra americana*, AA; *Ammotragus lervia*, AV; *Cervus elaphus*, CE; *Rangifer tarandus*, RT; *Tragelaphus scriptus*, TS; *Alcelaphus buselaphus*, AB; *Alces alces*, AL; *Bison bison*, BB; *Giraffa camelopardalis*, GC; *Hippotragus niger*, HN; *Ovibos moschatus*, OM.

$P = 0.271$; Fig. 4). The artiodactyls of small, medium, and large size also did not differ in blade sharpness ($F = 0.306$, $P = 0.742$; Fig. 5). Table 2 lists the results of these anovas in addition to the results of the subsequent between-group comparisons.

Dietary differences were not associated uniformly with differences in blade sharpness. For a sample of Carnivora of small size, consumers of meat, a tough, soft foodstuff, had sharper facet edges than consumers of non-vertebrate material, a weak, abrasive foodstuff ($F = 32.857$, $P = 0.0012$; Fig. 6). Differences in blade sharpness among artiodactyls of different dietary categories were not significant ($F = 1.441$, $P = 0.278$; Fig. 7); browsing and mixed-feeding artiodactyls did not have sharper facet edges than grazers that consume a higher amount of abrasive material. Furthermore, the grazing perissodactyl, *Equus grevyi* (Grevy's zebra), with a mean sharpness index of 0.186 ± 0.025 did not differ significantly in blade

Table 2. Anova results from comparisons of blade sharpness between groups. A significant difference between groups is denoted by an asterisk (*).

Groups compared	*F*-ratio	*P*-value	*d.f.*
Small vs. large carnivores	1.467	0.271	(1, 6)
Small, medium, large artiodactyls	0.306	0.742	(2, 11)
Meat specialists vs. nonvertebrate-eating carnivores	32.857	0.0012*	(1, 6)
Browsing, mixed-feeding, grazing artiodactyls	1.441	0.278	(2, 11)
Equus grevyi vs. grazing artiodactyls	0.063	0.825	(1, 2)
Meat-specializing carnivores vs. artiodactyls	0.418	0.525	(1, 20)
Browsing hyrax vs. mixed-feeding hyrax	0.023	0.882	(1, 10)
Browsing hyrax vs. browsing rhinoceros	9.548	0.011*	(1, 10)
Meat-specializing carnivores vs. hyraxes	10.666	0.011*	(1, 8)
Browsing vs. grazing rhinoceros	32.065	0.0002*	(1,10)
Browing rhinoceros vs. browsing artiodactyls	0.442	0.535	(1,5)
Grazing rhinoceros vs. grazing artiodactyls	217.370	0.0046*	(1, 2)
Browsing artiodactyls vs. folivorous primates	11.821	0.009*	(1, 8)
Hyraxes vs. folivorous primates	32.212	0.005*	(1, 4)
Meat-specializing carnivores vs. folivorous primates	43.375	0.0001*	(1, 10)

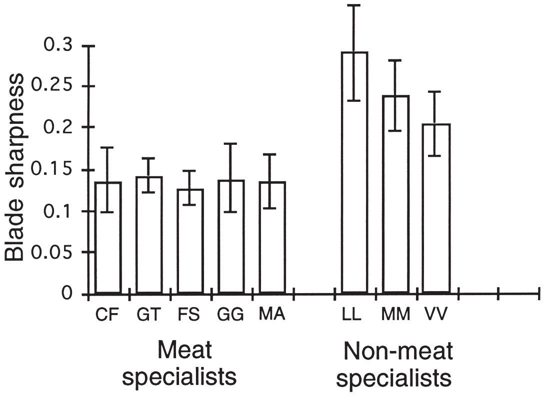

Fig. 6. Blade sharpness in a sample of carnivores of small body size. Carnivores specializing on meat have significantly sharper carnassial blades than non-meat specialists ($F = 1.467$, $P = 0.271$). Standard deviations for mean blade sharpness are indicated by the error bars. Abbreviations for taxa are as follows: *Cryptoprocta ferox*, CF; *Genetta tigrina*, GT; *Felis sylvestris*, FS; *Gulo gulo*, GG; *Martes martes*, MA; *Lutra lutra*, LL; *Meles meles*, MM; and *Vulpes vulpes*, VV.

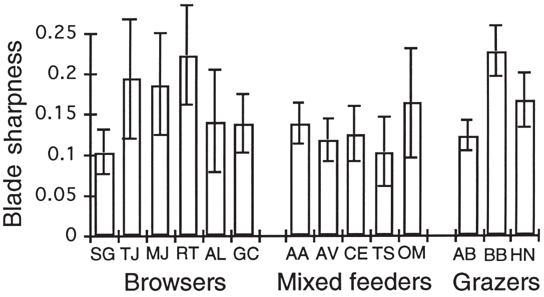

Fig. 7. Blade sharpness in browsing, mixed feeding, and grazing artiodactyls. No significant difference in blade sharpness exists between dietary groups. Standard deviations for mean blade sharpness are indicated by the error bars. Abbreviations are as follows: *Sylvicapra grimmia*, SG; *Tragulus javanicus*, TJ; *Muntiacus muntjac*, MJ; *Rangifer tarandus*, RT; *Alces alces*, AL; *Giraffa camelopardalis*, GC; *Antilocapra americana*, AA; *Ammotragus lervia*, AV; *Cervus elaphus*, CE; *Tragelaphus scriptus*, TS; *Ovibos moschatus*, OM; *Alcelaphus buselaphus*, AB; *Bison bison*, BB; *Hippotragus niger*, HN.

sharpness from the artiodactyl grazers ($F = 0.063$, $P = 0.825$). Comparison of Carnivora that specialize upon meat with the artiodactyls indicated that significant differences in sharpness do not exist ($F = 0.418$, $P = 0.525$).

Blade sharpness in the browsing hyrax, *Dendrohyrax arboreus*, did not differ significantly from blade sharpness in the mixed-feeding species, *Procavia capensis* ($F = 0.023$, $P = 0.882$). Furthermore, neither hyrax differed in sharpness from the artiodactyls ($F = 4.54$, $P = 0.051$). The blade sharpness of the browsing hyrax, *Dendrohyrax*, differed significantly from the sharpness of the browsing rhinoceros, *Diceros*, ($F = 9.548$, $P = 0.011$), and the hyrax had sharper blade tips. The hyraxes also have sharper blade tips than the carnivoran meat specialists ($F = 10.666$, $P = 0.011$).

The browsing rhinoceros, *Diceros bicornis*, had a mean sharpness index of 0.194 ± 0.082, and had sharper blades than the grazing rhinoceros, *Ceratotherium simum,* with a mean sharpness index of 0.186 ± 0.025, ($F = 32.065$, $P = 0.0002$). Comparison of *Diceros* with browsing artiodactyls did not show significant differences in sharpness ($F = 0.442$, $P = 0.535$); however, comparison of *Ceratotherium* with grazing artiodactyls indicated the blunter edges of the teeth of the grazing rhinoceros ($F = 217.37$, $P = 0.0046$).

The folivorous primates were found to have buccal facet edges of lower sharpness. A sample of browsing artiodactyls have significantly sharper blades than the folivorous primates ($F = 11.821$, $P = 0.009$; Fig. 8), as do the hyraxes ($F = 32.212$, $P = 0.005$; Fig. 9). The carnivorans that specialize on meat also have sharper blades than the folivorous primates (F-ratio = 43.375, $P = 0.0001$).

4. Discussion

4.1. Primary and secondary influences upon blade tip sharpness

The observed isometric scaling of blade tip sharpness corresponds with the isometric scaling of other components of the masticatory system, and suggests that body size may be the primary determinant of blade tip sharpness. Thus, not only do the dimensions, surface area, and volume of a tooth scale with isometry but the tooth's first point of contact with food, the blade tip, also has a one to one relationship with body size. Isometric scaling between blade tip sharpness and body mass is likely to be apparent, however, only across a broad size range. For example, no size effect was observed between small and large-sized meat-eat-

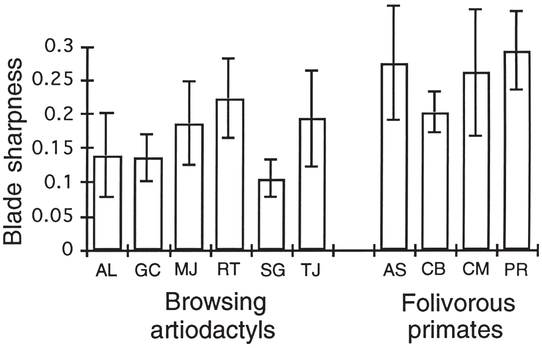

Fig. 8. Blade sharpness in browsing artiodactyls and folivorous primates. Browsing artiodactyls have significantly sharper buccal facet edges than do folivorous primates ($F = 11.82$, $P = 0.009$). Standard deviations for mean blade sharpness are indicated by the error bars. Abbreviations are as follows: *Alces alces*, AL; *Giraffa camelopardalis*, GC; *Muntiacus muntjac*, MJ; *Rangifer tarandus*, RT; *Sylvicapra grimmia*, SG; *Tragulus javanicus*, TJ; *Alouatta seniculus*, AS; *Colobus badius*, CB; *Cercopithecus mitis*, CM; *Presbytis cristata*, PR.

ers; only *Panthera* is large enough (approximately 200 kg) to show a blunter blade tip. This factor is likely to account for the absence of an isometric scaling coefficient in the regression analysis of blade tip sharpness against body mass; isometry was observed, however, in the regression of planar area against body mass.

Because diet controls the attrition to abrasion ratio on the facet surface and blade tip, diet is likely to be a secondary but more proximate influence upon the sharpness of the blade edge. Dietary components that generate greater attrition or abrasion or vice versa will have the effect of obliterating a blade tip sharpness that correlates strongly with size. For example, species with high attrition and low abrasion have sharpened the blade tip beyond the original size-correlated value, such as is the case among selenodont artiodactyls. The consumption of tough vegetation results in a generally high rate of attrition and sharp blade tips among selenodont artiodactyls of nearly all sizes, and thus confounds a size effect. Alternatively, species with high abrasion and low attrition have blunted the sharper blade tips that would correlate with body mass, such as is the case for the small-sized *Muntiacus* and *Tragulus*. The diets of these species may not be sufficiently tough to mask abrasion, and a low level of attrition and an accumulation of abrasion characterizes the dentitions.

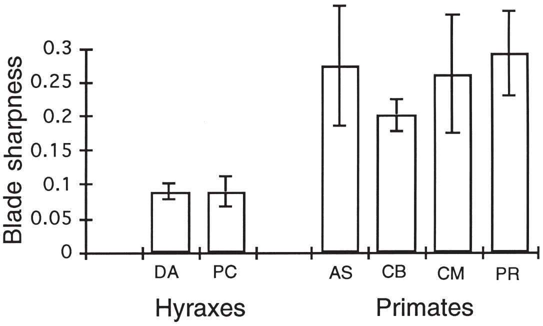

Fig. 9. Blade sharpness in hyraxes and primates. Hyraxes have significantly sharper buccal facet edges than primates ($F = 32.21$, $P = 0.005$). Standard deviations for mean blade sharpness are indicated by the error bars. Abbreviations are as follows: *Dendrohyrax arboreus*, DA; *Procavia capensis*, PC; *Alouatta seniculus*, AS; *Colobus badius*, CB; *Cercopithecus mitis*, CM; *Presbytis cristata*, PR.

4.2. The importance of crown design

Sharpness does not appear to depend directly on occlusal patterning, however the height of the occlusal features may strongly influence the sharpness of the blade tip. Because diet shapes the blade tips of species of all crown types, sharp blade tips were observed among each of the different crown types studied (selenodont, lophodont, carnassial) and different sharpness values were also found in morphologically homogenous groups. Crown types with sharp blade tips have morphological features, such as high cusps or lophs, which interface with an occluding surface at high bite force, but the details of the dental design vary and there is a strong phylogenetic component. Although the occlusal pattern does not appear to affect sharpness, the high height of occlusal features may be necessary to accommodate the high attrition that shapes sharp blade tips.

4.2.1. Brachydont crown designs

Low crown height accounts for the bluntness of the cutting edges of primate teeth relative to taxa with a high-crowned, secondary (wear-maintained) occlusal morphology. Primates select a diet of low toughness and have a preformed occlusal morphology, meaning that the crown is fully functional upon eruption and therefore necessarily low in height. Sharp blade tips can only be maintained under relatively high attrition, which in turn is incompatible with maintenance of a preformed occlusal shape. Crown height thus emerges as a fundamental variable controlling blade sharpness, for the simple reason that only attrition will maintain sharpness, and low-crowned teeth can only afford relatively limited attrition.

Leaf-eating primates select plant material of a low toughness that does not require sharp blade tips or extreme bite force to be fractured. Relative to ungulates, primates are limited to either non-abrasive foods that can be processed with low occlusal stress, or to energy-rich foods which need to be eaten only in small quantities. The ability to feed manually may allow primates to be more selective in their diet relative to other herbivores. Young leaves are of a lower toughness than mature plant material (Lucas & Pereira 1990, Lucas & Teaford 1994), as well as easier to digest and higher in protein (Struhsaker 1975, Marsh 1981). Colobus monkeys have been found to prefer young leaves to mature ones (Marsh 1981), and new leaves and leaf buds were a large portion of the diet of *Presbytis cristata* (Bernstein 1968) and of *Alouatta seniculus* (Gaulin & Gaulin 1982).

Carnivore carnassials are also essentially preformed, but their design may accommodate considerable wear. Carnassial blades are sharp in meat-eating forms and blunter in those that consume non-vertebrate material, reflecting the toughness of vertebrate tissue as a food and the high attrition that goes with chewing tough foods (Fig. 10). Vertebrate tissues require the application of high force to fracture and the resulting high attrition of the carnassial facet maintains a sharp facet edge. The non-meat specialists consume less tough food stuffs that may fracture with lower applied force, and the facets of their low crowned carnassials undergo less attrition than those of meat specialists. For example, the otter, *Lutra*, consumes fish (Nowak 1991), and this muscle tissue is likely to be less tough than the tissues of tetrapods. Likewise, the badger, *Meles*, consumes a high proportion of earthworms which are weak and fragile (Kruuk 1989, Strait & Vincent, pers. comm.). The sharp carnassials of meat-eaters are quite high, and meat-eaters may have increased carnassial crown height just as eaters of tough plant parts have increased molar postcanine tooth height more generally. Undoubtedly, the size of the particle to be chewed influences blade depth and thus crown height, but the simple association among carnassial teeth of sharp blades with high crowns must be recognized as significant. In fact, we suggest that a high level of attrition is the main reason for the evolution of high-crowned carnassials among carnivores.

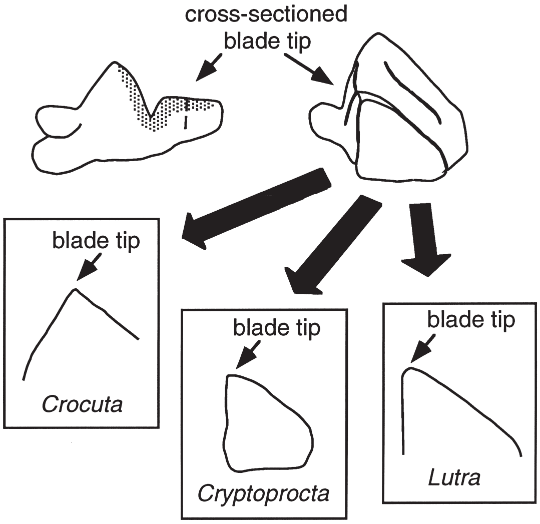

Fig. 10. Cross-sections of the metastylar blade on the upper carnassial. High attrition of the carnassial facet results in a sharp blade tip among meat specialists, such as *Crocuta* and *Cryptoprocta*. Relatively lower attrition and higher abrasion in non-meat specialists, such as *Lutra*, results in less sharp blade tips.

4.2.2. Selenodont crown designs

The functional surfaces of ruminant teeth are entirely shaped by wear and both high crowned and low crowned teeth may maintain sharp blade tips through the re-sharpening effect of attrition. The high tooth volume found in ruminants relative to primates accommodates these extensive wear processes and may be the key to maintaining sharp blade tips during the consumption of various plant materials. Blade sharpness was similar between meat-specializing carnivores and ruminants because both vertebrate and plant food stuffs require the application of high force to fracture, and high attrition characterizes the carnassial facets of meat specialists and the facets of the selenodont ruminants. The absolute wear rate is higher in the den-

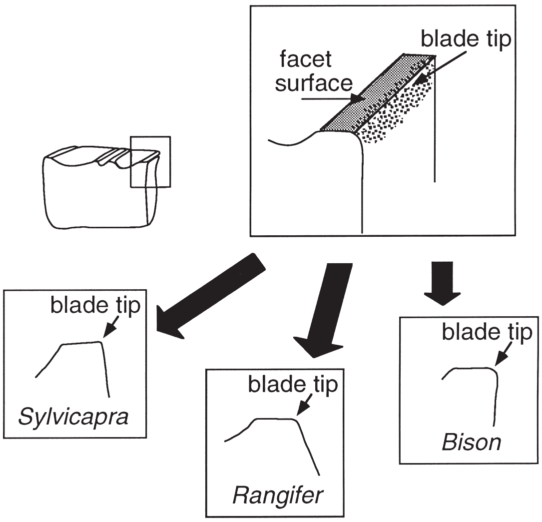

Fig. 11. Buccal facet tip sharpness on the upper first molar of selenodont artiodactyls. The darkly shaded region indicates the location of high attrition on the facet surface. The darkly stippled region indicates the location of high abrasion on the blade tip. Browsing artiodactyls with high attrition and low abrasion, such as *Sylvicapra*, maintain sharp blade tips. Browsing and mixed feeding artiodactyls with low attrition and high abrasion, such as *Rangifer*, have less sharp blade tips. Grazing artiodactyls with high abrasion and high attrition, such as *Bison*, have less sharp blade tips.

tition of an herbivore than of a carnivore, however, because of the greater amount of food processed. Furthermore, attrition rates on ruminant teeth are higher than those on primate teeth. Many browsing ruminants will choose the youngest plant parts available, but they are likely to ingest a wide variety of plants of varying toughness. It is difficult for ruminants to be as selective in feeding as primates, because ruminants select plants with the incisors and tongue instead of the hands. Because ruminants ingest a greater volume of food per day they cannot afford to be as choosy as primates over plant food texture. Thus, even browsing ruminants are likely to have high attrition on their dental surfaces, and the level of attrition will increase with the toughness of the plant parts consumed.

Blade tip sharpness did not differ between dietary categories of selenodont artiodactyls possibly because within each dietary category attrition is at least high enough to match abrasion. Differences in the absolute amount of wear (abrasive and attritial) between dietary categories, however, results in differences in the rate of crown reduction, and the crown will wear down faster in grazers than in mixed-feeders and browsers (Solounias *et al.* 1994). Most browsing ruminants have low wear rates (Solounias *et al.* 1994). They consume forbs and leaves of different maturity, as well as bark, twigs, and fruit, which all vary in degree of toughness. Even the less tough plant parts, however, are still likely to be tougher than the nonvertebrate material consumed by some carnivores (fish, soft invertebrates), and will have a sharpening effect upon the blade tip by increasing attrition. In this way, differences in blade sharpness that were observed among carnivores of different diets were not observed among ruminants of different diets because most plant parts consumed are tough enough to generate sufficient attrition to hide the effect of abrasion.

For grazers and mixed-feeders, as the extent of attrition increases with the consumption of tough grass, so does the extent of abrasion. The proximity of grasses to the earth means that grass is often coated with minerogeneous grit and is more abrasive than plant parts that are growing further from the earth's surface, such as leaves. The contact of hard mineral particles with the facet surface causes high abrasive wear and rounds the blade tip. The high rate of attrition on the facet surface which corresponds to the high toughness of the plants consumed appears, however, to be sufficient to re-sharpen a blade tip blunted by abrasive wear.

Most browsing ruminants that consume less tough plant parts do not consume highly abrasive foods, therefore the blade tip is not abraded to the extent that it is in mixed feeders and grazers. If abrasive foods are consumed, the lesser rate of attrition can permit the accumulation of abrasion on the blade tip in these forms. The high blade sharpness of some browsers, such as *Alces*, *Giraffa*, and *Sylvicapra* suggest that the facets are formed and maintained through relatively high attrition (Fig. 11). In other selenodont browsers, especially ones with a tendency towards frugivory, such as *Muntiacus* and *Tragulus*, the rate of attrition on the facet surface is insufficient to re-sharpen the facet tip. An absence of re-sharpening has also been observed in herbivorous rodents that consumed less tough foods (Rensberger 1978). The dental surfaces of hypsodont forms (consumers of tough foods) with high attrition rates were not associated with abrasive microwear; however, the dental surfaces of brachydont forms (consumers of less tough foods) with low attrition rates exhibited high detrital abrasion. Mixed-feeding ruminants vary their diets seasonally between browse and grasses and variation in the sharpness of blade tips of mixed-feeders can be attributed to seasonal variation in the attrition/abrasion ratio (as observed by Solounias & Moelleken 1992).

A factor which might exaggerate the apparent lack of differences between browsers and grazers is that the sharpness measurements ignored the irregular wear ("damage") on enamel edges, commonly seen in grazers. The measurement itself is, of course, true, but mean sharpness along the edge is overestimated in the forms with more damage, i.e., the grazers. The significance of this factor is difficult to assess, since no attempt was made to overcome the formidable difficulties involved in measuring mean sharpness.

4.2.3. Other crown designs

The plagiolophodont postcanine teeth of hypsodont horses, although derived from a lophodont ancestry, are morphologically and functionally similar to the selenodont molars of ruminants (Fortelius 1985), and a similar blade sharpness fits this pattern. All living horses are grazers of relatively uniform size and *Equus grevyi* was selected for comparison with grazing ruminants. This grazing zebra has a blade sharpness similar to that of the ruminants.

The small and lophodont hyraxes had the sharpest cutting edges encountered in this study, with no apparent difference in sharpness between the browser, *Dendrohyrax arboreus*, and the seasonal mixed feeder, *Procavia capensis*. A similar abrasion/attrition ratio can be plausibly postulated for these forms with high abrasion and attrition in the mixed feeder relative to the browser. The molars of the mixed-feeding species are characterized by higher buccal edges in order to accommodate the increased wear. The significantly higher blade sharpness of hyraxes in comparison to ruminants is a strong indication of the effect of body size on blade sharpness.

The lophodont browsing rhinoceros, *Diceros bicornis*, was found to have a molar blade sharpness comparable to that of ruminants and the zebra. In relation to size, these were the sharpest teeth found in the study, and the browsing rhino concentrates very large bite forces on a small blade tip area. The grazing rhinoceros, *Ceratotherium simum*, has very blunt blade tips and abrasion must be high. It is unclear why attrition is low in this grazer and not in others. The molar edges of *C. simum* are rounded by abrasion and true wear facets are absent. It might be illuminating to compare the shape and size of grass particles from this species with those from grazers with attrition-dominated occlusal surfaces. It may well be that the mode of comminution is different.

4.3. Functional morphology of blade tip sharpness

The ability of mammals of different body sizes to break down the same foods may be in part a result of the relationship between blade sharpness and body mass. Masticatory features such as tooth size and bite force are roughly isometric with body size, and the sharpness of the blade is also likely to scale isometrically. The matched isometric scaling of blade sharpness and muscular bite force with body size would mean that an increase in absolute force of the bite would be associated with a commensurate increase in the bluntness of the blade. The facet surface bears the majority of occlusal force during the tooth-to-tooth contacts of chewing; however, the blade tip is likely to be loaded against food prior to the tooth-to-tooth contacts. The absolutely lesser bite forces present in small-sized taxa would be concentrated on an absolutely sharper blade tip and the absolutely greater bite forces produced by large-sized taxa would be distributed over an absolutely blunter blade tip. In this way small-sized taxa, such as hyraxes, and large-sized taxa, such as rhinoceroses, are able to produce nearly equivalent stress fields in a foodstuff and can fracture the same foods. Blunt edges in small species would not concentrate the small bite force sufficiently, while the strong bite of a large species would fracture a very sharp blade tip.

Only certain combinations of mechanical and dietary food properties may be compatible with

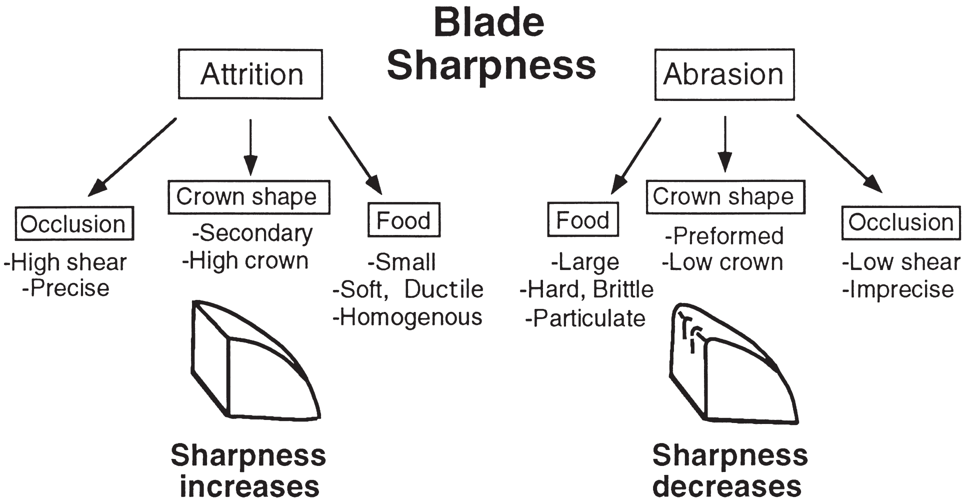

Fig. 12. A summary of secondary influences upon blade tip sharpness.

long-term maintenance of sharp blades. As noted above, folivorous primates are confined to the consumption of less tough plant parts in order to limit attritial wear of the low crowned occlusal surface. The blade tips are not sharp and abrasive wear would be particularly detrimental to the blade tips without the sharpening effect of high attrition. Therefore, to maintain a degree of sharpness on the blade tip and to preserve the ability for tearing young leaf material, folivorous primates must avoid not only tough plant materials, but also less tough foods that are abrasive, such as immature grass shoots. In order to form a sharp blade tip meat-specializing carnivores must also restrict their diet and consume only tough vertebrate tissues. The ingestion of less tough food or brittle food items reduces the extent of attrition on the blade through diminished bite force, and less sharp blade tips result. Blunting of the blade tip reduces the efficiency of fracture of tough vertebrate materials because bite forces are dispersed over a broader occlusal area. Therefore, supplementing a diet of meat with insects, fruits, or worms will result in a less sharp blade tip and reduced efficiency in fracturing vertebrate tissues. Specializing upon meat ensures the maintenance of a sharp blade tip through high attrition.

Such “eco-functional” channeling is not essential for the presence of sharp blade tips in ruminants because of the generally high toughness of plant materials. Browsing ruminants may consume a wide variety of plant materials and still maintain sharp blade tips, because even plant parts of lower toughness (with the exception of immature leaves) are sufficiently tough to be associated with high attrition. The consumption of more abrasive foods is generally accompanied by an increase in toughness of the plant tissue and consequently higher attrition on the facet surface. The dietary flexibility of ruminants is important because of the low nutrient quality of plant material and the necessity for large mammals to consume a large volume of plant food. Although dietary restrictions are not necessary to ensure blade sharpness, abrasive or tough foods will cause higher crown wear, and ruminants with lower crowned teeth may adhere to a less tough and less abrasive diet in order to preserve crown height.

5. Conclusions

Blade tip sharpness is likely to be determined primarily by an isometric relationship with body size, however, the combined effects of diet and crown design may further influence the sharpness of the blade tip. Blade sharpness is size dependent as are other components of the masticatory apparatus, and prior to tooth wear sharpness is likely to scale isometrically across a broad size range. The physical properties of food are proposed to be a secondary influence on sharpness because they determine the nature of the wear on the blade tip during a lifetime of chewing. Very tough food items, such as vertebrate tissues, mature plant parts, and grasses require high bite forces and produce attrition on the wear facets (Fig. 12). This high rate of attrition will re-sharpen blade tips that have been blunted by abrasives, such as the silica associated with grasses. Blades are blunted either when abrasion is very high, as in extreme grazers, or when attrition is very low due to the softness of the food eaten. The correlation between blade sharpness and high crowned teeth or high crowned morphological features on teeth suggests that the extensive attritial wear that maintains sharp blade tips rapidly wears the tooth crown. Specific occlusal patterns are not, however, generally predictive of blade sharpness.

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References

Ashby, M. F. & Jones, D. R. H. 1980: Engineering materials 1: An introduction to their properties and applications. — Pergamon Press, Oxford.

Banfield, A. W. F. 1974: The mammals of Canada. — University of Toronto Press, Toronto.

Bernstein, I. S. 1968: The lutong of Kuala Selangor. — Behav. 32: 1–16.

Butler, P. M. 1952: The milk-molars of Perissodactyla, with remarks on molar occlusion. — Proc. Zool. Soc. Lond. 121: 777–817.

Butler, P. M. 1961: Relationships between upper and lower molar patterns. — Int. colloq. on evolution of lower and non-specialized mammals. Kon. V1., Acad. Wet. Lett. Sch. Kunst, Belgie. Brussels 1: 117–126.

Butler, P. M. 1973: Molar wear facets of early Tertiary North American primates. — Symp. 4th Int. Cong. Primat. 3: 1–27.

Choong, M. F., Lucas, P. W., Ong, J. S. Y., Pereira, B., Tan, H. T. W. & Turner, M. 1992: Leaf fracture toughness and sclerophylly: their correlations and ecological implications. — New Phytol. 121: 597–610.

Crompton, A. W. & Hiiemae, K. 1970: Molar occlusion and mandibular movements during occlusion in the American opossum, Didelphis marsupialis L. — Zool. J. Lin. Soc. 49: 21–47.

Fortelius, M. 1985: Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. — Acta Zool. Fennica 180: 1–76.

Fortelius, M. 1987: A note on the scaling of dental wear. — Evol. Theory 8: 73–75.

Fortelius, M. 1988: Isometric scaling of mammalian cheek teeth is also true metabolic scaling. — In: Russell, D. E., Santoro, J.-P. & Sigogneau-Russell, D. (eds.), Proceedings of the VIIth International Symposium on Dental Morphology, Paris 1986. Memoires du Museum national d'Histoire naturelle, Paris, Serie C, 53: 459–462.

Gaulin, S. J. C. & Gaulin, C. K. 1982: Behavioral ecology of Alouatta seniculus in Andean cloud forest. — Int. J. Primat. 3: 1–32.

Hofmann, R. R. & Stewart, D. R. M. 1972: Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. — Mammalia 36: 226–240.

Hylander, W. L., Johnson, K. R. & Crompton, A. W. 1987: Loading patterns and jaw movements during mastication in Macaca fascicularis: a bone-strain, electromyographic, and cineradiographic analysis. — Am. J. Phys. Anthr. 72: 287–314.

Janis, C. & Ehrhardt, D. 1988: Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. — Zool. J. Linn. Soc. 92: 267–284.

Kay, R. F. & Hiiemae, K. M. 1974: Jaw movement and tooth use in recent and fossil primates. — Am. J. Phys. Anthrop. 40: 227–256.

Kruuk, H. 1989: The social badger, ecology and behavior of a group-living carnivore (Meles meles). — Oxford University Press, Oxford.

Lucas, P. W. & Corlett, R. T. 1991: Quantitative aspects of the relationship between dentitions and diets. — In: Vincent, J. F. V. & Lillford, P. J. (eds.), Feeding and the texture of food: 93–121. Cambridge University Press, Cambridge.

Lucas, P. W. & Luke, D. A. 1984: Chewing it over: basic principles of food breakdown. — In: Chivers, D. J., Wood, B. A. & Bilsborough, A. (eds.), Food acquisition and processing in primates: 283–301. Plenum Press, New York.

Lucas, P. W. & Pereira, B. 1990: Estimation of the fracture toughness of leaves. Funct. Ecol. 4: 819–822.

Lucas, P. W. & Teaford, M. 1994: Functional morphology of colobine teeth. — In: Davies, A. G. & Oates, J. F.

(eds.), Colobine monkeys: their ecology, behavior and evolution: 173–203. Cambridge University Press, Cambridge.

Lucas, P. W., Choong, M. F., Tan, H. T., Turner, I. M. & Berrick, A. J. 1991: The fracture toughness of the leaf of the dicotyledon Calophyllum inophyllum L. (Guttiferae). — Phil. Trans. R. Soc. Lond. B. 334: 95–106.

Maas, M. C. 1991: Enamel structure and microwear: An experimental study of the response of enamel to shearing force. — Am. J. Phys. Anthrop. 85: 31–49.

Maas, M. C. 1993: Enamel microstructure and molar wear in the greater galago, Otolemur crassicaudatus (Mammalia, Primates). — Am. J. Phys. Anthrop. 92: 217–233.

Macdonald, D. 1984: The encyclopedia of mammals. — Facts on file, New York.

Marsh, C. W. 1981: Diet choice among red colobus (Colobus badius rufomitratus) on the Tana River, Kenya. — Folia Primatol. 35: 147–178.

Nowak, R. M. 1991: Walker's mammals of the world. — The Johns Hopkins University Press, Baltimore. 5th ed.

Owen-Smith, N. 1988: Megaherbivores. — Cambridge University Press, Cambridge.

Rensberger, J. M. 1973: An occlusion model for mastication and dental wear in herbivorous mammals. — J. Paleont. 47: 515–528.

Rensberger, J. M. 1978: Scanning electron microscopy of wear and occlusal events in some small herbivores. — In: Butler, P. M. & Joysey, K. A. (eds.), Development, function, and evolution of teeth: 415–438. Academic Press, London.

Rensberger, J. M. 1983: Effects of enamel structure on wear. — Am. J. Phys. Anthrop. 60: 343–344.

Scott, K. M. 1987: Allometry and habitat related proportions in the post-cranial skeleton of the Cervidae. — In: Wemmer, C. (ed.), Biology and management of the Cervidae: 65–80. Smithsonian Institution Press, Washington, D. C..

Shipley, L. A., Gross, J. E., Spalinger, D. E., Thompson Hobbs, N. & Wunder, B. A. 1994: The scaling of intake rates in mammalian herbivores. — Am. Nat. 143: 1055–1082.

Solounias, N. & Moelleken, S. M. C. 1992: Tooth microwear analysis of Eotragus sansaniensis (Mammalia: Ruminantia), one of the oldest known bovids. — J. Vert. Paleont. 12: 113–21.

Solounias, N., Fortelius, M. & Freeman, P. 1994: Molar wear rates in ruminants: a new approach. — Ann. Zool. Fennici 31: 219–227.

Stern, D., Crompton, A. W. & Skobe, Z. 1989: Enamel ultrastructure and masticatory function in molars of the American Opossum, Didelphis virginiana. — Zool. J. Linn. Soc. 95: 311–334.

Struhsaker, T. T. 1975: The red colobus monkey. — Chicago University Press, Chicago.

Teaford, M. F. & Glander, K. E. 1991: Dental microwear in live, wild trapped Alouatta palliata from Costa Rica. — Am. J. Phys. Anthrop. 85: 313–319.

Van Valkenburgh, B. 1989: Carnivore dental adaptations and diet, a study of trophic diversity within guilds. — In: Gittleman, J. L. (ed.), Carnivore behavior, ecology and evolution: 410–436. Cornell University Press.

Walker, A., Hoeck, H. N. & Perez, L. 1978: Microwear of mammalian teeth as an indicator of diet. — Science 201: 908–910.