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The scaling of tooth sharpness in mammals

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The scaling of many aspects of mammalian biology remains to be thoroughly investigated. Isometric scaling of tooth sharpness over very large body size ranges appears unlikely from a theoretical viewpoint, as geometrically similar teeth will function differently in a masticatory system that scales isometrically. Taking into consideration developmental controls on tooth shape and the effects of tooth wear, tooth sharpness is predicted to be highest in small animals, with relatively lower tooth sharpness in medium and large animals. The results for small to large mammals (1–2500 kg) are reassessed to show that in this range of body size there is no isometric scaling in this body size range and that wear is probably the primary determinant of sharpness, producing sharpness that is relatively scale-independent when sufficient wear occurs. Including limited additional data on tooth sharpness for very small mammals (Microchiroptera) suggests that there may be an overall trend of isometry for functional tooth crests over the very broadest range in size (0.008–2500 kg), a hypothesis that can be tested in the future with broader taxonomic sampling.

Introduction

There has been significant interest and debate surrounding the scaling of mammalian teeth in the zoological and palaeontological literature (Pilbeam & Gould 1974, Gould 1975, Kay 1975, Fortelius 1985, Gingerich & Smith 1985, Janis 1988, Legendre & Roth 1988). In some cases, isometry of tooth size (usually molar area) with body mass has been identified, and it has been argued that isometric scaling of tooth planar area would result in isometric scaling with metabolic rate (Fortelius 1985, 1988, 1990, Lucas 2004). This would coincide with findings of isometric scaling of particular aspects of the mammalian masticatory system with body size (e.g. Fortelius 1985). However, one aspect that requires further investigation is the scaling of particular functional features of teeth with body size, and specifically how this would affect tooth function. Some work on this has been carried out for measures such as the relative development of shearing blades (e.g. Kay 1975, Strait 1993, Ungar & Kay 1995). However, it is not sufficiently known to what extent more recently discovered functional features of teeth, such as those examined in Evans (2003, 2005) and Evans and Sanson (2003, 2005a, 2006), are independent of tooth length or crown area, nor how they scale with body mass.

One important instance of the scaling of dental features is tooth sharpness, and whether isometric scaling of tooth sharpness would be expected. Three aspects of this will be considered: (1) whether geometrically similar teeth will function in the same way in a masticatory system that scales isometrically; (2) the functional consequences of different scaling regimes of sharpness; and (3) the effect of various aspects of teeth (including development and wear) on the scaling of tooth sharpness. Each of these will affect whether isometric scaling of tooth sharpness would be found in mammals. The published information on the scaling of tooth sharpness will be reviewed, and combined with newly-collected data to extend the body size range over which sharpness has been examined.

Functional scaling of tooth sharpness

In order to investigate the function of teeth in geometrically-scaled masticatory systems, we will devise two identically-shaped organisms, animal A with a body length L, and B with body length $2L$ (Table 1). The body mass of A is M_A, which is proportional to L^3; similarly, the body mass of B will be $M_B = 2^3M_A = 8M_A$. Tooth sharpness, measured as the radius of curvature at the tip or edge (tip and edge sharpnesses respectively, such that sharpness is high when radius of curvature is low) of the teeth of A will be $r_A \propto L$; for B, $r_B = 2r_A$; the volume (cusp sharpness) of the tooth will be $v_A \propto L^3$; or $v_B = 8v_A$. The maximum bite force of animals is typically proportional to the cross-sectional area of the muscle mass, and so for A will be $b_A \propto L^2$; for B, $b_B = 4b_A$.

In this example, we will assume that the application of force onto food is a major factor in tooth function. This assumption is supported by previous findings and discussions on the influence of the functional parameters on tooth function and the absolute strength of structures. Factors such as tooth sharpness will affect the minimum force required for a tooth to function, f. For instance, a blunter tooth will require greater force to penetrate or drive through food (Lucas 1979, Lucas & Luke 1984, Evans & Sanson 1998, Lucas 2004). It should be true that an animal cannot make use of a tooth that requires greater force to function than it can generate with its musculature, i.e. if $f > b$. This may be so in the literal sense (in that the animal physically cannot generate a large enough bite force) or in terms of efficiency (the animal expends substantially greater energy in processing the food than it obtains from consuming it). There will undoubtedly be some degree of plasticity in the forces that can be produced by the musculature, but there must be an upper limit to the bite force. In the present example, we will assume that, for the small animal A, the force required for the tooth to function, f_A, equals the bite force, b_A.

The principal question to be answered is: how does the scaling of sharpness affect the force required for the tooth to function? That is, how does f scale with regard to body size? For the example above, if it takes A (with a tooth of

Table 1. Two isometric animals, A and B, of length L and $2L$, respectively, and their proportions for features that relate to tooth function.

	Animal A	Animal B
Length (L)	L	$2L$
Features proportional to length, e.g. radius of curvature (r)	$r_A \propto L$	$r_B = 2r_A$
Area (a)	$a_A \propto L^2$	$a_B \propto (2L)^2 = 4L^2$
Features proportional to area, e.g. bite force (b)	$b_A \propto L^2$	$b_B = 4b_A$
Volume (V)	$V_A \propto L^3$	$V_B \propto (2L)^3 = 8L^3$
Features proportional to volume, e.g. body mass (M) and tooth volume (v)	$M_A \propto L^3$ $v_A \propto L^3$	$M_B = 8M_A$ $v_B = 8v_A$

radius of curvature r_A and volume v_A) a force of f (= b_A) to penetrate or divide food of thickness t, what force does B with radius of curvature $2r_A$ and volume $8v_A$ require to act on the same foodstuff of thickness $2t$ (also isometrically scaled; isometric scaling of food thickness is reasonable given physiological requirements of the animal and the scaling of chewing rate; Fortelius 1985)? For a tooth to maintain the equivalent function in an isometric system, the answer must be $4f$ ($b_B = 4b_A = 4f$; i.e. $f \propto L^2$), because this is the bite force generated by the larger animal. Under geometric similarity, stress between upper and lower tooth surfaces should be equivalent over all body sizes, since force is proportional to (physiological) cross-section. However, it must be determined if the force to reduce food usually does scale with L^2 for the same tooth design.

The scaling of force will depend on whether the radius of curvature of the tooth (linear) or the volume of the tooth (cubic) has the greater influence on the force required for the tooth to function. In all likelihood, both of these features will have an effect, along with other factors such as the biomechanical properties of the food (particularly structural properties; Evans & Sanson 2005b). However, the determination of the relationship between size and force will require some degree of empirical testing; it will also vary with the exact mode of function of the tooth and for different dental systems (such as protoconoid, carnassial and selenodont; the 'protoconoid-based' tooth form includes zalambdodont, dilambdodont and tribosphenic — *see* Evans 2003). In one respect, the forces that larger animals can generate with their muscles are lower than those of small animals relative to body size: for example, the force of a muscle will scale with L^2 but the mass of a limb by L^3, so at some body size an isometric animal will not be able to lift its own limbs.

In light of this, there will most probably be a discrepancy between the scaling of bite force that an animal can generate and the force required for the dentition to function (e.g. in penetrating or fracturing food). In this case, the function of the tooth will in some way be limited or constrained by the bite force that an animal can generate. Specifically, if the force required scales at a greater rate than bite force (i.e. $x > 1$ for $f \propto L^x$), at some body size the bite force will be less than the force required and so the tooth will either not function at all, or with greatly reduced efficiency.

Processes that influence tooth sharpness

We will first examine two regimes of scaling of tooth sharpness (measured as radius of curvature) and the possible functional consequences of these regimes. The forces that potentially influence scaling will then be considered, and how the relative strengths of these constraints vary with body mass.

The first situation is the isometric (or positively allometric) scaling of tooth sharpness with regard to body mass (Fig. 1a). There is likely to be a body size above which the decreased absolute tooth sharpness (higher radius of curvature) means that the force required exceeds the bite force.

Second, if sharpness is constant for all body sizes (Fig. 1b), it is likely that below a certain body mass, bite force will be insufficient for the tooth to function. At the other end of the size scale, as bite force increases and tooth sharpness remains the same, the risk of fracture of the cusp or crest will be prone to increase at some large body size.

The processes of tooth development may have an important influence on tooth sharpness. Approximately isometric scaling (the first situation considered above) might be expected from the fact that dental area and muscular cross-section have the same dimensionality, or it may be caused by developmental constraints on tooth form. This would be the case if the minimum radius of curvature that can be produced in development increases with body size. Particular properties of the developing tooth are likely to cause a change in developmental sharpness with an increase in size. The sharpness of a crest will depend on the degree of folding of the enamel epithelium, so that a more extreme folding will give higher curvature to the epithelium surface and a sharper crest or cusp. If a developing tooth is scaled up, there are likely to be three main factors that will affect surface curvature.

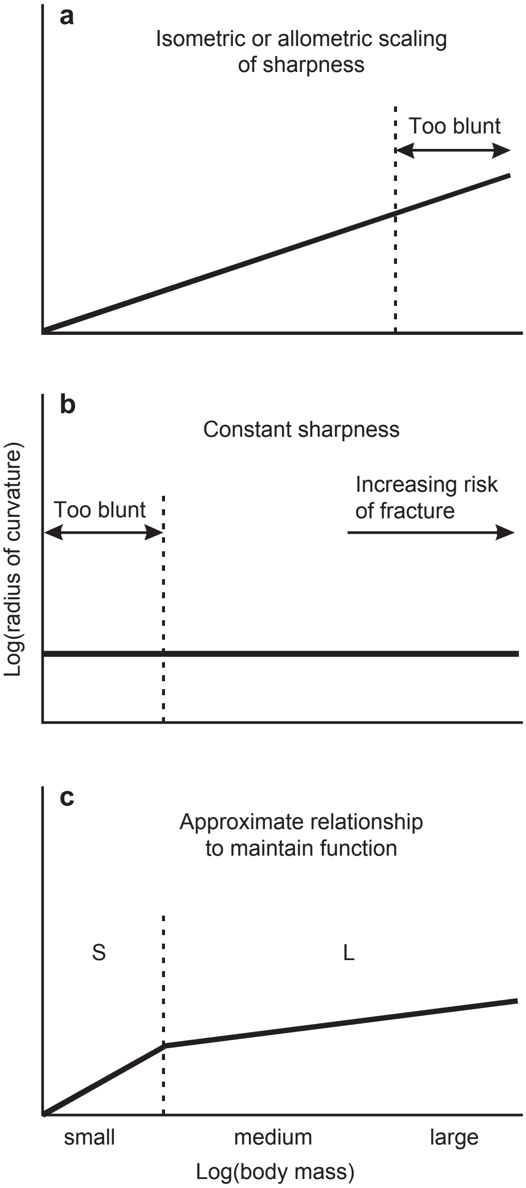

Fig. 1. Possible scaling regimes for tooth sharpness (measured as radius of curvature) *vs*. body mass. — **a**: Isometric (slope 1/3) or allometric relationship; — **b**: sharpness independent of body size (slope 0). For **a**, there is likely to be a body size above which the teeth are too blunt and require a greater bite force than can be produced, and for **b**, a body size below which the teeth are too blunt. The risk of fracture increases at large body sizes in **b**. — **c**: In order for teeth to maintain function at each body size, we may expect that tooth sharpness scales for small body size (S), and scales at a much lower rate in larger animals (L) due to the effect of wear and the risk of fracture.

First, the distance between enamel knots will be greater. This may mean that the tension forces responsible for the folding of enamel epithelium will not be as high in the larger tooth, resulting in a lower maximum curvature of the surface. Second, if enamel thickness increases with size, this may also reduce the maximum curvature possible. Either or both of these two mechanisms may result in an isometric or allometric scaling of developmental sharpness. Third, the developing tooth will be comprised of a greater number of cells, but the consequences of this on the biomechanical properties of the tissue are hard to predict. It seems unlikely that none of these possibilities would affect surface curvature and so result in scale-invariance of developmental sharpness, especially given the strong relationship between overall tooth size and body mass.

A very significant determinant of sharpness scaling is likely to be post-developmental modification of the tooth that occurs in the animal, i.e. wear. Developmental processes may indeed manufacture teeth with radii of curvature that scale isometrically, but the use of the tooth will reshape its surface. The amount and distribution of wear on a tooth will be influenced by many factors: gross tooth form, bite force, enamel thickness and microstructure, the biomechanical properties and absolute size of foods, and the relative contributions of attrition and abrasion (generally, wear on the relief and rake surfaces respectively; Evans 2005). The aspects that contribute to wear, and the degree to which they scale with body size, will be the ultimate determinants of tooth sharpness in the living and chewing animal.

The ratio of attrition to abrasion will be a significant factor in tooth sharpness (Popowics & Fortelius 1997). Attrition is tooth–tooth contact of relief surfaces, and will tend to sharpen an edge through the removal of dental material from the relief surface (Fig. 2). Wear on the rake surface by food (abrasion) will more likely blunt the edge. Foods that require large bite force (i.e. high structural strength) are likely to result in high degrees of attrition; low attrition will probably result where only a small bite force is needed. Abrasive diets will cause greater amounts of abrasion, rounding the crest edge. Many other factors will affect the degree to

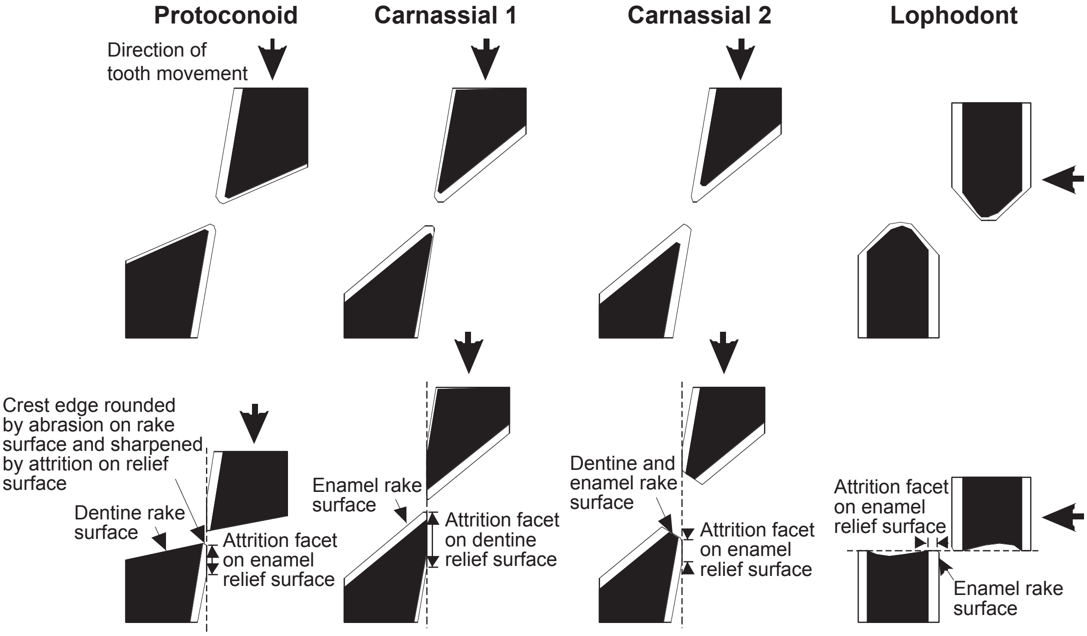

Fig. 2. Wear and enamel distribution in protoconoid, carnassial and lophodont forms. After wear, the protoconoid crest typically has an attrition facet on the relief surface that is enamel, and the rake surface is dentine. Two general types of the carnassial form occur among mammals and are distinguished by the following characteristics shown here: in carnassial 1, the cutting edge is formed by the rake enamel following wear, and so the relief surface of the crest is mostly dentine and the rake surface is enamel; in carnassial 2, the relief enamel forms the cutting edge, and so the relief surface is enamel and the rake surface is both dentine and enamel. Carnassial 1 is typical of felids and hyaenids, and carnassial 2 of canids and mustelids. The arrangement of enamel is very different in lophodont forms, which display horizontal movement. Direction of tooth movement shown by large arrow.

which each of these types of wear occur, including the precision of occlusion, the crown shape, the biomechanical properties of the foods (*see* fig. 12 in Popowics & Fortelius 1997) and the bite force. To a large extent these factors will be closely related to the diet, and so it might be expected that dietary type would affect sharpness to a greater extent than body size, at least among animals in a limited size range.

If the factors that dictate the amount of wear on teeth are largely independent of the size of the tooth, then you may expect there to be no scaling of tooth sharpness in worn teeth. For example, if the amount of attrition and abrasion were the primary dictates of sharpness, it would seem that the maximum sharpness that can be produced through wear is likely to be relatively scale-independent. Also, there is likely to be an approximate scale-independence of the effects of the biomechanical properties of foods on the wear process that may be another cause of scale-independence of sharpness. Scale-invariant factors such as cell size, exogenous grit particle size, enamel prisms and thickness of decussation zones may also contribute to a lack of sharpness scaling following wear.

Wear is more likely to even out sharpness in small and large animals: wear in small animals is more likely to blunt a tooth (given the decrease in edge sharpness with moderate to high wear in *Chalinolobus gouldii*; Evans 2005) as compared with that in a large animal (where the worn enamel edge is likely to be substantially sharper than the rounded unworn state of herbivores; *see* Fig. 2).

A significant interaction between development and wear will be the thickness of the enamel exposed after wear. The edge sharpness and function of a blade will be affected by the thickness of the enamel. For a cross-section through the enamel (Fig. 3a), the edge has a maximum bluntness when it is rounded at the top to a semi-

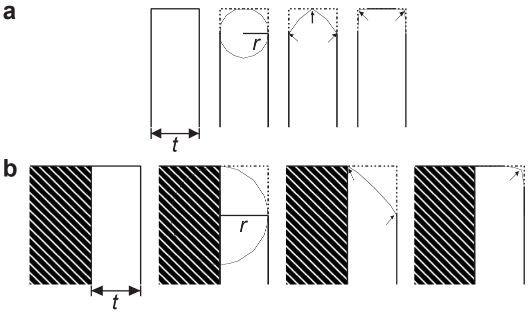

Fig. 3. The relationship between enamel thickness and sharpness. The figure shows cross-sections through the enamel of a tooth. — **a**: The bluntest that enamel of thickness *t* can be is where the top is rounded to a semi-circle of radius $r = t/2$. Any other rounding regime will create an area of higher curvature and therefore higher sharpness, indicated by small arrows on the two examples on the right. — **b**: Where the enamel is supported on one side by dentine (shaded area), the bluntest that the edge can be is a radius of curvature of $r = t$. Maximum bluntness will then scale with enamel thickness, so that a thinner edge is likely to be sharper than a thick edge.

circle with radius $t/2$, where t is the thickness of the enamel edge. Any other rounding will have a higher curvature (i.e., lower radius of curvature) at some point (shown by arrows in Fig. 3a), and so be a sharper edge. If the enamel edge is supported on one side by dentine (Fig. 3b), then the maximum bluntness will be t.

The scaling of enamel thickness with body size is therefore liable to affect the scaling of edge sharpness. Maximum bluntness will scale with enamel thickness, so that a thinner edge is likely to be sharper than a thick edge. If the sharpness of an edge were directly related to the thickness of the enamel, then any scaling of enamel thickness with body size (e.g. isometric or allometric) would be reflected in the scaling of sharpness. This effect may only be relevant over very large body size ranges, due to any variance in enamel thickness and wear regime at the same size.

The one main factor that may cause allometric scaling of tooth wear with size is bite force. Larger animals generate higher bite forces on (approximately) equivalent dental materials, which is likely to increase the wear rate and may change the proportion of attrition:abrasion, leading to a roughening of the attritial face. This cannot be the case for dental area as a whole, but may be important for occlusion of individual dental features such as cusps and crests. However, the extent to which this is the case is unknown.

Even though high attrition is likely to sharpen a tooth to some extent, there may be a maximum sharpness that can be produced through this method. Tooth-on-tooth wear will remove enamel from the relief surface, such that the resulting cutting edge may be fragmented and chipped, perhaps only at the microscopic scale, rather than sharp and precisely angled. Such an effect may be exacerbated by large bite force, resulting in a rougher or more rounded edge.

Given these possible scaling regimes and caveats, we can try to integrate them and speculate on how their relative influence will differ with body size. We will presume that the teeth of an animal will be as sharp as possible, accounting for the increased risk of fracture at high sharpness and bite force. If there is a minimum radius of curvature that can be produced in small animals, which cannot be significantly increased by wear, then the sharpness of the teeth of small animals is dictated by overall tooth shape and is the product of development (perhaps followed by minimal wear, which may slightly increase sharpness compared to the unworn state). Tooth sharpness would decrease (increase in radius of curvature) with increasing body size in small animals (Fig. 1c). At intermediate body sizes, the sharpness that can be produced by wear is probably greater than that formed in development, increasing sharpness relative to the unworn state. The sculpting of the edge by wear will produce tooth sharpness that is more scale-independent. This also ameliorates the effect of teeth being too blunt at large body sizes. However, the additional constraint of risk of tooth fracture in larger animals will prevent tooth sharpness from being too high (Fig. 1c).

From this, we expect that maintaining high tooth sharpness is more important in small animals than large ones. Tooth sharpness may then be relatively constant in large animals. This gives larger animals relatively sharper teeth than small animals. It is not known which of developmental or wear processes could produce the sharper crest.

It is not expected that the full predictions of the above discussion will be borne out, but it should set the stage for the types of patterns and

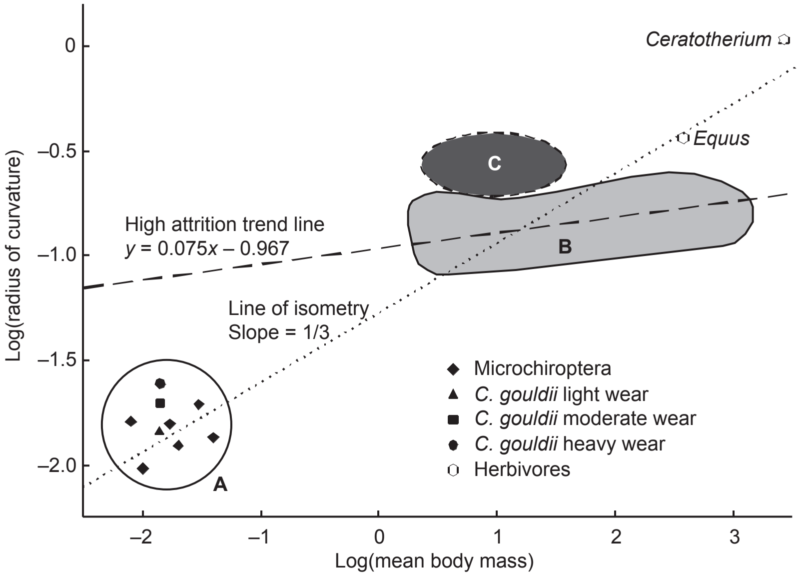

Fig. 4. Edge sharpnesses of a wide range of body masses and dietary types. A, small insectivorous microchiropterans; B, high attrition medium to large body masses; C, low attrition medium body masses. High attrition trend line for data in B and *Equus*; line of isometry of slope 1/3 shown passing through the middle of microchiropterans. A, data from Evans (2005) and Evans and Sanson (2005a) for microchiroptera, including *Chalinolobus gouldii*; B, C and herbivores, data from Popowics and Fortelius (1997).

data that are required to fully dissect the final influences on the scaling of tooth sharpness.

Empirical data on tooth sharpness

The only substantial measurement of tooth crest sharpness has been carried out by Popowics and Fortelius (1997). They argued for an isometric scaling of wear-derived tooth sharpness with body size among mammals. The minimum radius of curvature of transverse cross-sections through tooth crests of a wide range of faunivorous and herbivorous mammals was measured; when regressed against body mass, no significant relationship was found. If animals with 'low attrition' were excluded (mostly animals of small body mass with blunter teeth, including *Vulpes*, *Lutra*, *Alouatta* and *Colobus*, and the large *Ceratotherium*), then there was a marginally significant relationship using Model I regression with a slope of 0.075. Popowics and Fortelius (1997) also plotted body mass *vs*. radius of curvature multiplied by tooth area (length × width), which gave an exponent of 0.679 ± 0.064 S.E. However, it was actually intended to regress an estimate of 'blade area' (radius × tooth length), for which the expected slope for isometric scaling would be 0.667 (an area to a volume). From the similarity between this empirical and the expected slopes, it was erroneously concluded that there was an isometric relationship between body size and blade sharpness, and that body size was the main determinant of blade sharpness. It is likely, however, that the result of a 0.679 slope reflects the scaling of tooth area alone, with radius of curvature being nearly constant with respect to body mass in this data set. These data have now been reanalysed using a Model II regression, which accounts for error in both X and Y variables. The slope of the major axis was 0.053, with 95% confidence limits of –0.002 to 0.108. The slope within the high-attrition sample is therefore not significantly different from zero, showing size-invariance of sharpness for this sample.

For the range of body masses investigated by Popowics and Fortelius (1997), it appears that wear regime is more important than body size in determining tooth sharpness, as the regression of tooth sharpness and body size 'was significant only for those taxa that shape their blades through high attrition' (Popowics & Fortelius 1997: p. 79). This is also indicated by the lack of significant differences in comparisons of blade sharpness, such as between small, medium and large artiodactyls. The sharpest teeth were found in the smallest animals, and the bluntest in the largest, but small animals that eat 'less tough foods' have the bluntest teeth apart from the large *Equus* and *Ceratotherium* (Fig. 4).

This suggests that the amount of attrition is the primary determinant of tooth sharpness in these animals. For animals with high attrition, this generates a very slight increase in radius of curvature with body size (*b* = 0.053), but at a significantly lower rate of increase than that predicted by isometry (*b* = 0.333). This indicates that the sharpness produced by wear is relatively size-independent. However, it is not known to what extent increased bite force in large animals contributes to the slight decrease in tooth sharpness with size, which may cause greater rounding of the attrition surface, or increased risk of fracture (which to some extent can be considered part of the same process). It was hypothesised that increased risk of tooth fracture may cause a decrease in the tooth sharpness at larger body sizes. Sharper edges would then be more likely to be removed, resulting in a decrease in sharpness.

The influences that were considered by Popowics and Fortelius (1997) to be 'secondary', including amounts of attrition and abrasion, are more likely to be primary determinants of sharpness for animals of the size range examined (2–2500 kg). Wear modifies or obliterates to a large extent any effect that body size *per se* has on tooth sharpness. The absolute amount of wear is therefore not 'irrelevant' to sharpness, as was suspected by Popowics and Fortelius (1997: p. 76) — a critical amount of wear would be necessary to generate sufficient attrition to sharpen crests, as shown by the blunt teeth of animals eating weak foods which only require lower bite forces (referred to as the 'mabra group', or minute abraded brachydonts, by Fortelius & Solounias 2000).

We can use the data on edge sharpness from Evans (2005) and Evans and Sanson (2005a) to further investigate this relationship. Within these microchiropterans, there is not a very good relationship between body size and sharpness (Fig. 4). This does not appear to be due to the differences in diet, and to some extent may be attributable to the relatively high variability of edge sharpness within species (particularly *Rhinolophus blasii*).

If these data are added to the dataset of Popowics and Fortelius (1997), the relationship between sharpness and body size can be examined at a broader scale, as the body size of the microchiropterans used here is substantially smaller than the smallest included in the previous study (0.008–0.040 kg *vs*. 2–2500 kg). Edge sharpness of these species is significantly higher (i.e. radius of curvature is lower) than that of the larger species (Fig. 4). This supports several of the points raised earlier: that constant sharpness for all animals is unlikely, as high tooth sharpness is probably more important for function in smaller animals. The higher sharpness in small animals is more likely to be due to a scaling of the maximum tooth sharpness that can be produced through developmental processes compared to increased tooth sharpness from wear, as it is significantly reduced with wear (Evans 2005), but also to the scaling of enamel thickness.

However, for the entire dataset there is an approximation to isometry, as a line with a slope of 1/3 passes through *Equus*, *Ceratotherium*, and groups A and B (Fig. 4). This would not be expected from the above discussion. However, the expected pattern of a slower increase in radius of curvature at larger sizes (Fig. 1c) is still apparent.

Discussion

The occlusal morphologies of mammalian teeth have been categorised as primary (the tooth shape is functional upon eruption) and secondary (significant wear is required for the shape to be functional, and the functional form is substantially different from the unworn state; Fortelius 1985). This distinction is apparent in the degree of difference between the unworn and worn states of the forms shown in Fig. 2. The protoconoid and carnassial forms can be considered primary, and herbivore lophodont forms are secondary. However, substantial wear does occur in these primary forms, and the resulting morphology differs to some extent from the unworn state (Fig. 2). These worn forms can be considered as primary-derived occlusal morphologies, and have their own distinctive patterns (such as the position of enamel on the rake or relief surfaces). For instance, the main occluding cutting edge of the carnassial 1 form (e.g. felids and hyaenids) is comprised of the rake surface enamel, in contrast to the carnassial 2 form (e.g. canids and mustelids), where the relief enamel surface fills that role. The enamel surfaces of these two forms would be expected to show differences in their enamel prism microstructure and orientation that reflect the divergence in function of the enamel surfaces, with the rake enamel and relief enamel carrying out the majority of the cutting function in carnassial forms 1 and 2 respectively.

All of the taxa examined in Popowics and Fortelius (1997) have primary-derived (carnassial) or secondary occlusal morphologies. This differs from the microchiropteran species, which were in a very light state of wear and so have a primary occlusal morphology (other than the *Chalinolobus gouldii* specimens that were moderately to heavily worn and can be considered primary-derived). Therefore, the primary tooth shape, which is the result of developmental processes, has a greater influence on the sharpness of the microchiropteran form than on the larger carnivores and herbivores. The tooth form of large animals with primary occlusal morphologies (e.g. bears, humans, pigs) is basically rounded cusps and usually lacking in crests (either primary or secondary crests), and the importance of crest sharpness is lower. Therefore, we would expect that the erupted tooth form (resulting from development) has a greater influence in the microchiropterans as compared with that in herbivores, and so any patterns that are apparent in the erupted occlusal morphology (such as allometric scaling of sharpness for unworn cusps) will have a greater influence. This would be expressed as a scaling in sharpness in these forms but not in the secondary crest edges. Despite the very wide range of occlusal morphologies and dietary types examined in this enlarged sample, all have the fundamental similarity of the presence of a leading edge on the blade that concentrates forces on food, assisting fracture. It is the curvature of this leading edge that has been measured for all species.

A substantial limitation on interpretation of the enlarged dataset, however, is the strong phylogenetic signal that is likely to be present. The group of bats added here, representing animals of very small body size, may arguably be seen as a single data point as they all are part of a single monophyletic group distinct from the other groups studied. However, we do not attempt to test the apparent isometric relationship in the current paper, in part because of the limitations of the data available. Moreover, given the diversity of factors that can contribute to sharpness, we consider strict isometry across the full range of mammals to be unlikely.

These patterns must, however, be re-examined when sharpness data for small mammals with secondary occlusal morphologies such as rodents become available. If wear were a scale-independent process, then we may expect rodent sharpness to lie along the 'High attrition' trend line in Fig. 4. However, there would very likely be strong selection pressure for sharp crest edges in these small mammals, and factors such as specialised enamel microstructure (Rensberger 1978, von Koenigswald 1980), thin enamel ridges and lower bite force (reducing the risk of fracture) may allow a decrease in the radius of curvature in comparison to the larger animals. We suggest that sampling sharpness in rodents and other small mammals in the future may help to resolve the paradox that different scaling patterns emerge at different ranges in body size.

The extent to which major differences in the methodologies of the current work and Popowics and Fortelius (1997) affect the results (such as an approximation to isometry) is not known. Pilot studies showed that the measured radius of curvature was highly correlated with the resolution at which the surface was digitised (A. R. Evans unpubl. data). This would be expected for a surface that has a fractal nature to some extent. Cusp tips and crest edges were digitised at the highest resolution achievable for the confocal microscope with a dry lens (1 μm for ×40) and then smoothed by a fixed amount to obtain a digitised surface that should represent the contours of the surface at a very fine level but still removing extremely high sharpness values due to the small amount of noise present. It is very likely that radius of curvature values obtained through this method would be smaller than those of sectioned profiles for the same specimen. The smallest radius of curvature quantified for the microchiropterans was 4.7 μm, which is probably well below that obtainable from profiles viewed at ×30 magnification. The calculation of surface curvature from splines fit to the three-dimensional surface, which is the method used by the Surfer software, is more objective than fitting by eye. If Popowics and Fortelius' (1997) method tended to underestimate the sharpness as compared with the new values included here, the approximation of isometry would be removed and the levelling out of sharpness at high body mass would be more apparent.

In conclusion, the data on edge sharpness compiled here largely support the predictions made above: that at small body sizes (< 1 kg) sharpness will be more closely correlated with body size as developmental processes, such as enamel thickness, may have a greater influence on the final tooth sharpness and there is a lesser risk of tooth fracture. For larger animals (1–2500 kg), the degree of attrition appears to be the main factor in determining sharpness: for animals of high attrition, tooth sharpness is close to constant, and when there is lower attrition, tooth sharpness is lower for the same body size. Wear is therefore the dominant determinant of sharpness within size classes. The putative overall isometric scaling between large and small animals may be related to the scaling of enamel thickness, or the influence of increased bite force.

However, the current level of taxonomic sampling, which is strong from bats, carnivores, and ungulates, is not yet sufficient to allow generalizations to all mammals. In addition, significantly more information is needed for these topics: unworn tooth sharpness and the scaling of the maximum sharpness produced by development; the maximum sharpness that can be produced by attrition; the effects of body size (bite force) on attritial sharpness; the effects of the biomechanical properties of diet on wear; scaling patterns within dietary types; the influence of thickness and microstructure of enamel on sharpness and how this varies with diet; and data on small mammals with secondary occlusal morphology. It must be certain that, whatever constraints each body size and dietary type faces, there will be strong selection for a tooth shape that wears in such a way as to maintain function, and there may be very many ways of achieving this.

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