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# Connecting morphology, function and tooth wear in microchiropterans

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A key objective in understanding the dentition of mammals is the ability to predict the function of teeth from their shape. Very few studies have used dental measurements that allow the prediction of comparative tooth effectiveness, particularly when modification in shape due to tooth wear is considered. Here, dental parameters are used in which a change in the parameter is readily interpretable in terms of change in factors such as increased force or energy required for cusps or crests to break down food. The functional parameters were measured for 3-D digital tooth reconstructions of the upper molars of the microchiropteran *Chalinolobus gouldii* at various stages of tooth wear. The changes in the majority of the parameters, such as decreased tip, edge and cusp sharpnesses, cusp occlusion relief, rake angle and fragment clearance, predict a deterioration in efficacy with increased wear. This conclusion has not been possible with alternative approaches; for instance, there was no significant change in crest length with wear, and so no change in function would be predicted from that measure. Some of the parameters did not change significantly with heavy wear, such as capture area of a crest, pointing to geometrical and design characteristics for the maintenance of shape with wear in the dilambdodont tooth form. Attrition and abrasion can be considered as wear on the relief and rake surfaces of tribosphenic-like crests, respectively. The differences in function of these two surfaces account for the differences in wear patterns. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 81–96.

ADDITIONAL KEYWORDS: confocal microscopy – dilambdodont – functional dental morphology – GIS – molar wear – morphometrics – teeth.

## INTRODUCTION

Interest in the study of functional dental morphology is long-standing (e.g. Ryder, 1878; Gregory, 1920), particularly due to the predominance of fossils that are represented only by their dentition and to the desire to interpret them in order to learn about an animal's mode of living (e.g. Fortelius, 1985; Kay, 1984; Strait, 1993b). Despite recent work demonstrating the importance of dentition to the nutritional ecology of an animal (Lanyon & Sanson, 1986; McArthur & Sanson, 1988; Pérez-Barbería & Gordon, 1998), much remains to be learned about the relationship between morphology and the action of teeth.

Teeth can be examined as tools primarily designed for the breakdown of food (Lucas, 1979; Lucas & Luke, 1984), and as with any tool, shape is a significant determinant of its mode of operation. This approach should greatly aid the interpretation of a dentition's function because an examination of tooth shape should reveal much about its manner of action. In this study, the 'function' of a tooth is directly related to the amount of force or energy required for it to fracture food. Very few studies have made use of dental measurements that can readily be interpreted in terms of effectiveness. To some extent, this is due to the difficulty of making such measurements using traditional morphometric techniques, but it is largely because a comprehensive understanding of the relationship between tooth shape and function has yet to be achieved. This study deals specifically with the function of microchiropteran molars (which can be considered dilambdodont; Freeman, 1979), but the principles are equally applicable to other tribosphenic-like teeth, e.g. of opossums, shrews, desmans, tenrecs and some primates.

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When endeavouring to assess tooth function by means of morphology, two types of dental measures can be recognized: those that primarily relate to the size of the feature being examined, and those that relate to its shape (Evans, in press). Much previous analysis has relied on size measures, e.g. comparisons of relative crest lengths (Kay, 1975; Kay, Sussman & Tattersall, 1978; Anthony & Kay, 1993; Strait, 1993b, 2001; Ungar & Kay, 1995; Dumont, Strait & Friscia, 2000); ratios of dental parts (Kay, 1975; Seligsohn, 1977) or tooth types (Freeman, 1984). For instance, studies of crest length explicitly equate the size (length) of crests with ability to divide food. It is likely that increased crest length (e.g. in folivores and insectivores compared to frugivores; Kay, 1975; Kay *et al.*, 1978; Anthony & Kay, 1993; Strait, 1993a) influences the amount of food processed. However, the effect is more complex, involving a number of trade-offs that affect the overall efficacy of food breakdown. This aspect has not been adequately addressed.

Very few investigations have tried to examine the quality of crests – the fine detail of their shape and the surrounding surfaces – and how this affects the action of teeth. When such shape characteristics have been examined, they have often related to the tooth surface as a whole (Ungar & Williamson, 2000), and any specific effect in terms of function has not been identified. Arguably, most previous measures cannot be explicitly related to dental function or are principally correlates of more informative characteristics (Evans & Sanson, 2003).

The deficit in the explanatory power of features like crest length is also apparent when trying to assess the consequences of tooth wear during an animal's lifetime. Changes in the shape of teeth will most often have an effect on their function. However, it is not usually recognized that wear does not necessarily change shape. The teeth of most herbivores, such as selenodont molars (possessed, for example, by buffalo and antelope), are essentially non-functional in their newly erupted form. A moderate degree of wear is required to transform the shape into its functional configuration (Luke & Lucas, 1983). Once this has been achieved, the tooth is constructed so that its shape, and therefore function, is static for much of its life, despite the large amount of wear that will occur (Rensberger, 1988). A point is eventually reached in such high-crowned (hypsodont) tooth forms where the tooth stops growing and the functional form rapidly degrades.

The relationship between wear and shape for tribosphenic-like teeth has generally been neglected. The implicit assumption has been that wear adversely changes their functional shape, so that the preformed occlusal morphology is fully functional and no wear is required for the tooth to operate (Luke & Lucas, 1983). However, no substantive data have been given in support of this proposition. Most studies have examined only unworn molars, in part because no reliable functional measures have been devised that allow comparison of unworn and worn teeth to test the above assumption. For instance, Ungar & Williamson (2000) suggest that crest length is unlikely to be very informative when considering change in function with wear.

Retention of good functional shape can therefore be considered a principal imperative in tooth design. The dentition can be scrutinized for design features that prevent or minimize change due to wear. Such features abound in herbivore teeth (such as the vertical enamel pillars of enamel that form the cutting edges), but have generally not been identified in tribosphenic teeth.

This study examines the upper molars of the microchiropteran *Chalinolobus gouldii* using nine functional parameters that have been developed in engineering or dental studies. These parameters can be specifically related to function; for example, a change in parameter can be used to predict an increase in force or energy for the tooth to break down food (Evans & Sanson, 2003). Several of these parameters have been recognized in the dental literature, but they have not yet been measured or placed within a comprehensive framework, and the majority have not been measured on teeth. The baseline data thereby provided for the condition of these characters in unworn teeth allow investigation of changes with increasing wear. Because the functional parameters have predictive value, relative changes in efficacy between unworn and worn molars can be measured. As change in shape most likely means a change in function, design characteristics that reduce the effect of wear on shape change, and so maintain the shape and effectiveness of the teeth, are also examined. The principles of function used here are also applicable to the lower molars; the main objective was to develop tools for the interpretation of tooth function and the influence of wear.

## Functional parameters

Arguably, the function of a tooth can be better analysed by considering the components of the tooth separately rather than attempting a measure that would purport to reveal the action of an entire tooth. Tribosphenic-like teeth can be seen as combinations of three basic tools: cusps, crests and basins. Cusps are advantageous for the penetration of food, initiating cracks in the surface, while crests play a significant role in propagating these through the material. Basins are also involved with food fracture, but their shape characteristics are more difficult to interpret and will not be considered in this work. Strictly, these components are not independent of one another (e.g. cusps often occur at the ends of crests), but it is a useful distinction to make.

The functional parameters used here are the shape characteristics that can be related to the mode of action of a tooth component. The function of the cusps and crests of microchiropteran molars are analysed with reference to the following nine criteria: tip sharpness, cusp sharpness and cusp occlusion relief for cusps; edge sharpness, rake angle, crest relief, approach angle, capture area and fragment clearance for crests. All but cusp occlusion relief are described in detail in Evans & Sanson (2003). Rake angle (the angle of the leading crest face to the line perpendicular to the direction of movement) provides an example of how these characteristics can be directly related to the force and energy required to fracture food. An increase in the rake angle (decreasing the included angle of the crest) results in less force and energy required to divide food.

Cusp occlusion relief is analogous to crest relief. In crested teeth, an opposing cusp often moves into a valley between two cusps or crests that are adjacent on the same tooth. When this occurs, friction between tooth surfaces due to food caught between the surfaces will push the teeth apart, increasing the force required. Relief behind the point at which the cusp occludes reduces friction and the tendency for occluding teeth to be separated.

When dealing with worn teeth rather than the idealised shapes of Evans & Sanson (2003, in press), the measurement of relief becomes more complicated. Relief can be considered as the area enclosed between a line running from the tip of the crest parallel to the direction of tooth movement and the relief surface (Fig. 1). The relief angle is the angle of the relief surface of the crest relative to the vector of tooth movement. An area of no relief, usually produced by wear, is often apparent immediately behind the cutting edge, and is called the wear land.

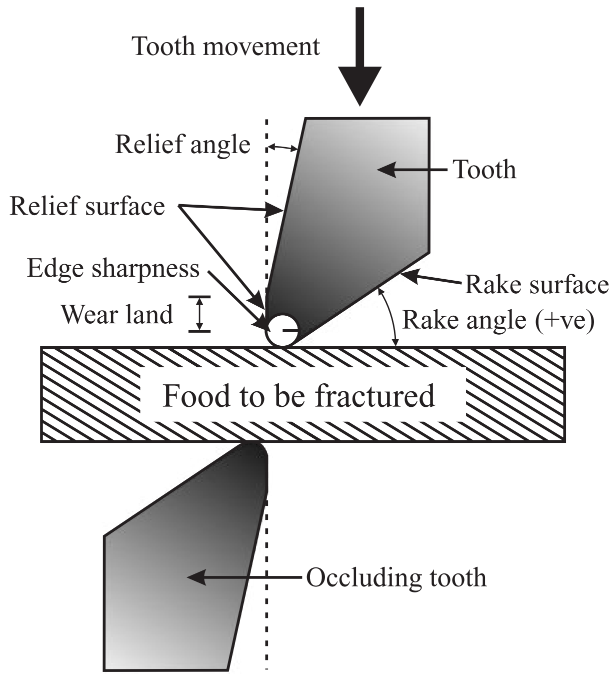


**Figure 1.** Rake angle, relief angle, wear land and edge sharpness of a crest viewed end-on. The circle radius indicating edge sharpness is enlarged for clarity, and is much smaller in actuality.

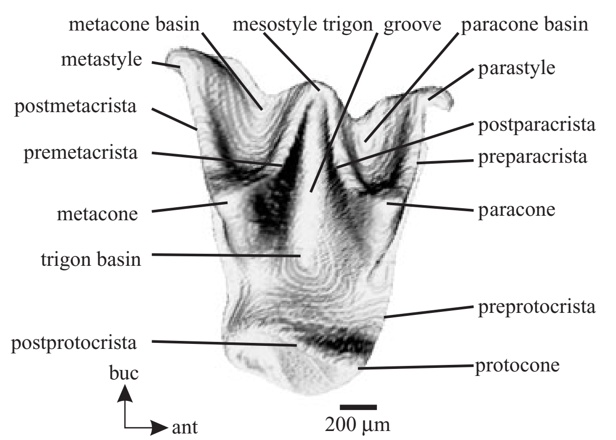


**Figure 2.** 3-D reconstruction of *Chalinolobus gouldii* upper second molar (specimen C23911), illustrating terminology. Occlusal view. *Abbreviations:* ant, anterior; buc, buccal.

## MATERIAL AND METHODS

### TOOTH WEAR

Molars of 79 specimens (Australian Museum, Sydney and Melbourne Museum, Melbourne) of the insectivorous microbat *Chalinolobus gouldii* (Vespertilionidae), were examined to survey the range and extent of molar wear. *Chalinolobus gouldii* has a body mass of *c.* 7–20 g and forearm length of 36–44 mm (Churchill, 1998). Widespread throughout Australia, it is an inhabitant of open forest, mallee, dense forest, tall shrubland and urban areas. It has been recorded feeding on a diverse range of insects, mostly beetles and moths, but also flies and orthopterans (Dixon, 1995; Churchill, 1998). Figure 2 shows the gross morphology and nomenclature used throughout the text for the upper molar. The amount and exact location of wear varies both between individuals and between teeth of the same individual; however, general trends in the wear sequence can be determined. Occasional minor

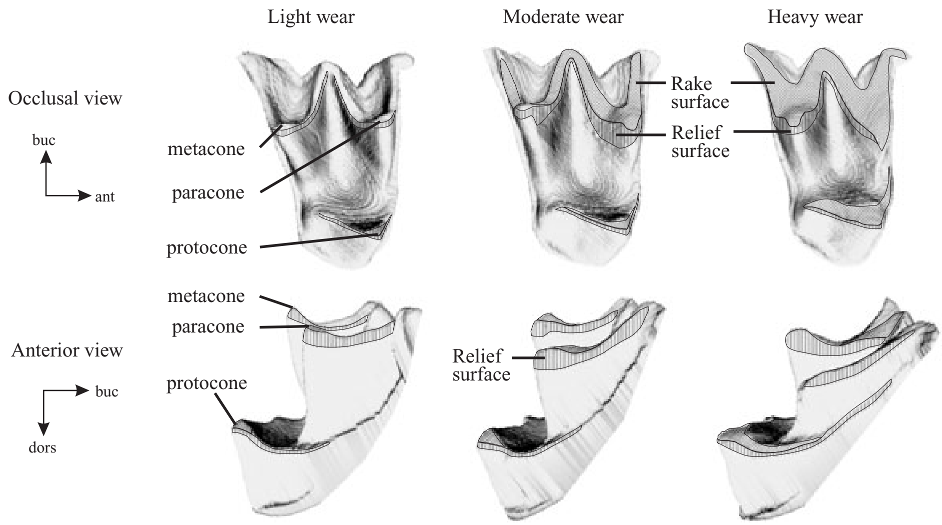


**Figure 3.** Occlusal and anterior views of the right upper second molar of *Chalinolobus gouldii*. Three wear states are shown: light (specimen C3704), moderate (C18142) and heavy wear (C3750). Wear on rake surface is shown by dotted area; wear on relief surface by vertical lines. *Abbreviations:* ant, anterior; buc, buccal; dors, dorsal.

chipping of cusps and crests can occur at any stage and in general are not considered in this discussion.

Specimens were classified visually according to a scale from 1 (no wear) to 6 (very heavily worn) for the second molars. Fraction wear states (1.25 and 1.5) were used to signify only slight changes from the unworn condition; a wear state less than 2 signifies light wear. The states are divided into light (1–1.5), moderate (2–3) and heavy (4–6) so that the gross differences and changes in shape through wear can be examined between these three states (Fig. 3). Tooth volume was tested as a quantitative measure of wear. Volume divided by length was significantly related to wear state ($P = 0.016$) although the amount of variation explained by volume was very low ($r^2 = 0.24$), so wear state appeared to be a better indicator of gross changes in morphology.

*Light wear (1–1.5)*

Light wear manifests along some of the crests as shiny attrition facets on the relief surfaces. There is little to no wear on the rake surfaces.

*Moderate wear (2–3)*

Abrasive wear on the rake surface is apparent, along with the attrition facets on relief faces. Approximately one eighth (wear state 2) to half (wear state 3) of the rake surface is exposed dentine.

*Heavy wear (4–6)*

Substantial wear has occurred, and the entire rake faces of the paracone, metacone and protoconid may be exposed dentine. The height of the paracone and metacone are substantially reduced, and at wear state 6 the tooth is essentially flat.

## FUNCTIONAL PARAMETERS

Details of the methods for generating digital models of teeth are given in Evans, Harper & Sanson (2001). Briefly, the upper molars of 20 specimens, ten with light, five with moderate, and five with heavy wear, were moulded and cast into urethane, which was then dyed with eosin, a fluorescent dye (specimen nos. C3704, C3746, C3748, C3750, C4344, C4348, C4349, C5144, C13691, C16967, C18127, C18142, C18163, C19363, C19376, C19378, C22196, C23472, C23911, C26131; Melbourne Museum).

The upper second molars were scanned with rhodamine optics using a Leica TCS confocal microscope. Scans were taken at two different resolutions: low (8 μm cubic voxel, a three-dimensional 'volume element', so that an 8 μm cubic voxel has a length of 8 μm in three orthogonal directions) using a 10× lens for entire teeth; and high (1 μm cubic voxel) using a 40× dry lens. Teeth larger than the field of view of the 10× lens (1 mm) were tiled to create a composite image of the entire object. The resulting topographical images were transformed to *x, y, z* coordinates and transferred into Surfer for Windows v. 6.04 (http://www.ssg-surfer.com), a geological mapping program. Surface data were also converted to Virtual Reality Modelling Language (VRML) files using the ElevationGrid command to generate three-dimensional reconstructions of the tooth on the computer screen.

The nine functional parameters described above were measured on confocal scans of the upper second molars. The measurement of most of these parameters was carried out in Surfer, along with a specially-written Visual Basic v. 6.0 program that interfaces with Surfer for file and data manipulations. Tooth length was measured as the three-dimensional distance from the most anterior point of the preparacrista to the most posterior point of the postmetacrista. In most instances, the functional parameters can be quantified from the confocal scans. However, for some this was not possible, so categorical differences in features were identified following observations made under a compound light microscope (45×).

The 'occlusal vector' is the vector of movement of the lower tooth relative to the upper tooth. It can be estimated as being parallel to the trigon groove, and so is the vector from a point at the buccal end of the trigon groove to a second point at the lingual end (just buccal to the trigon basin). VRML reconstructions of tooth occlusion showed that this is a good estimate of the trajectory of the lower tooth.

## Cusps

*Tip sharpness*

This was measured on high-resolution (1 μm voxel) confocal scans of the tips of cusps, ensuring no undercuts. The topographical surfaces were smoothed three times using 9 × 9 kernel with centre weighting 4 in Surfer to reduce surface noise. The curvature of the smoothed surface was calculated using the Directional Derivative : Curvature option in Surfer, which calculates the curvature of the surface in a given direction, at 10° intervals for 180°. The maximum curvature at each *x, y* point for all directions was determined. The mean curvature (in $\mu m^{-1}$) of a 20 × 20 μm area at the tip of the cusp was calculated, and the reciprocal (radius of curvature in μm) is the tip sharpness of this cusp. Tip sharpness was only measured for the metacone.

*Cusp sharpness*

This was measured on low-resolution (8 μm voxel) confocal scans of whole teeth. A plane (termed the basal plane) was fitted to three points on the tooth: the bases of the trigon, paracone and metacone basins. The position of this plane is only affected by extreme wear, as these features are usually the last to be worn. The basal plane was translated in the *z* direction so that it intersected the tip of the cusp (the highest point relative to the basal plane). The plane was translated downwards at intervals of 25 μm in the direction parallel to the normal vector of the basal plane and the volume of the cusp above the plane was calculated. Cusp sharpness measurements were taken for the volume of the cusp at 25 and 100 μm from the tip.

*Cusp occlusion relief*

A profile of the tooth along the trigon groove was obtained using Surfer. The trajectory of the cusp that occludes with the mesostyle (i.e. the hypoconid) was estimated as a line parallel to the occlusal vector starting at the mesostyle. The distance from each point of the profile from the hypoconid trajectory was measured, and the mean of these distances is the cusp occlusion relief. Cusp occlusion relief will be underestimated for some of the teeth due to minor undercutting of the surface lingual and dorsal to the mesostyle.

## Crests

*Edge sharpness*

This was measured on high-resolution (1 μm voxel) confocal scans of the postmetacrista. Processing of surface data generally follows that for calculating tip sharpness. The topographical surfaces were smoothed three times, and Curvature analysis in Surfer was used to generate a map of the maximum curvature at each point. The curvature at all positions along the crest (approximately every 1 μm) was calculated, and the edge sharpness is the reciprocal of the mean curvature of the crest. Edge sharpness was only measured for the postmetacrista.

*Crest rake*

The rake perpendicular (RKP) plane was determined, which was perpendicular to both the occlusal vector and to the length of the crest. The profile of the rake surface is the intersection between the rake surface of the crest and the RKP plane positioned at the centre of the crest. A least-squares regression line was fitted to the first 100 μm of the profile using Microsoft Excel 97; the slope of this line gives the average rake angle for the first 100 μm of the rake surface. Means and standard deviations for angles cannot be calculated in the regular manner as they are on a circular scale, and so were calculated according to Zar (1999).

*Crest relief*

Three qualitative characters relating to relief were recorded by viewing specimens under a compound microscope at 45× magnification: (1) width of wear land, (2) volume of space behind crest, and (3) relative relief angle. The wear land is the area on the relief surface closest to the cutting edge that contacts the occluding crest. This is apparent as an attrition facet. The width of the wear land was classified as: L1, absent or very small (usually apparent as a thin strip on the relief surface along the crest, approximately 50–80 μm in width); L2, moderate

(~80–150 μm); or L3, very wide (≥150 μm). Volume of space behind a crest was estimated according to the relative height of the crest above the embrasure between teeth or the trigon groove: V1, small (crest height reduced by at least 1/2 compared to unworn crest); V2, moderate (reduced by about 1/4); V3, large (full height of unworn crest). The relief angle was classified as: A1, 0° (attrition facet covering most or all of relief surface); A2, small (*c.* 1–10°); A3, large (noticeably larger than A2, ≥ 10°). A wear land that covers the entire relief surface (some crests classified as L3) and 0° relief angle (A1) can be considered equivalent, as both represent no relief behind the crest.

*Approach angle*

The profile of each crest was smoothed, using the average of four points each side of a point, and a centre weighting of four. The angle between the line connecting each pair of adjacent points and the occlusal vector was calculated using trigonometry. The mean approach angle for a crest was calculated as the mean of the absolute values for the approach angle along its length. The mean of absolute values was used, as negative and positive approach angles are functionally equivalent.

*Food capture*

For each crest, the rake surface (RKS) plane was fitted to the tip of the closest mesial cusp (paracone or metacone) and the associated stylar cusps (e.g. parastyle and mesostyle for the paracone). The profile of the crest was projected onto the RKS plane along the occlusal vector: the intersection between the plane and a line parallel to the occlusal vector passing through each point of the crest profile created a projection of the crest profile onto the plane. The area of the surface between the crest profile and the projected crest profile estimates the amount of food captured by the concavity in a crest.

*Fragment clearance*

The size and extent of flow channels for directing food off rake surfaces was qualitatively assessed by examination under a compound microscope, as it was found to be too difficult to quantitatively measure by any other means. Fragment clearance was estimated for the paracone and metacone basins. The categories of fragment clearance were: F1, poor (low crest height and absence of flow channels for directing food off the rake surface, i.e. when the rake surface is fairly flat, fragmented food would be forced against tooth surfaces rather than directed off the tooth); F2, intermediate; F3, good (tall cusps, with flow channels to direct food off the tooth surface).

### Statistical methods

Differences between the three wear states (light, moderate and heavy) for the quantitative features (tip, cusp and edge sharpnesses, rake and approach angles, and cusp occlusion relief) were tested using Kruskal–Wallis in Systat for Windows v. 10.0 (SPSS, Inc.). Qualitative features (relief wear land, volume and angle, and fragment clearance) were tested using Pearson Chi-square. Significance was determined using the exact distribution of the data using SPSS v. 10.0 (SPSS, Inc.). Significance level for all tests was $P = 0.05$.

Principal components analysis (PCA) was carried out using Systat. Volume ($mm^3$) and area ($mm^2$) measures were reduced to linear measures by cube root and square root transformation, respectively, and all quantitative values logged. Analyses were undertaken for functional parameters relating to the following five groups of variables:

1. Entire data set, including tooth length, which was included in all analyses.
2. Paracone and related crests: tip and cusp sharpness of paracone; cusp occlusion relief of mesostyle; rake and approach angles, relief and capture area of pre- and postparacristae; fragment clearance of paracone basin.
3. Metacone and related crests: as for paracone except for variables relating to metacone and pre- and postmetacristae.
4. Interloph crests: parameters relating to postmetacrista and preparacrista.
5. Intraloph crests: parameters relating to premetacrista and postparacrista, and cusp occlusion relief of the mesostyle.

Relief angle was omitted from the PCAs where there was no variation in relief angle over wear. Non-metric multidimensional scaling (NMDS) was carried out using Primer 4.0 (Plymouth Marine Laboratory) on the same five groups as the PCA. Pairwise difference between the wear groups was tested using analysis of similarity (ANOSIM) and the influence of each factor on the dissimilarity between groups using similarity percentages (SIMPER). A significance level of 3% was used for the SIMPER analyses.

## RESULTS

### Functional parameters

*Cusps*

*Tip sharpness:* lightly worn cusp tips had significantly higher sharpness than worn specimens, indicated by the smaller radius of curvature of the cusp (25.6 ± 2.6 μm vs. 50.3 ± 8.0 μm; mean ± SE; Table 1).

**Table 1.** Functional parameters relating to cusps (mean ± SE) for paracone and metacone for three wear states in *Chalinolobus gouldii*. $N = 10$ for light, $N = 5$ for moderate and heavy. *Abbreviations:* me, metacone; pa, paracone. $^*P < 0.05$; NS, not significant

| | Cusp | Wear: Light | Moderate | Heavy | $P$ | |
|---|---|---|---|---|---|---|
| Tip sharpness (µm) | me | 25.6 ± 2.6 | 47.5 ± 10.6 | 50.3 ± 8.0 | 0.009 | * |
| Cusp sharpness to 25 µm ($10^3$ µm$^3$) | pa | 57.9 ± 6.0 | 62.6 ± 17.2 | 85.7 ± 4.4 | 0.056 | NS |
| | me | 54.8 ± 10.3 | 72.8 ± 15.0 | 94.3 ± 22.7 | 0.353 | NS |
| Cusp sharpness to 100 µm ($10^3$ µm$^3$) | pa | 1127.9 ± 82.7 | 1464.7 ± 288.9 | 1895.6 ± 132.8 | 0.018 | * |
| | me | 1084.6 ± 118.0 | 1626.0 ± 73.0 | 1670.6 ± 280.7 | 0.034 | * |

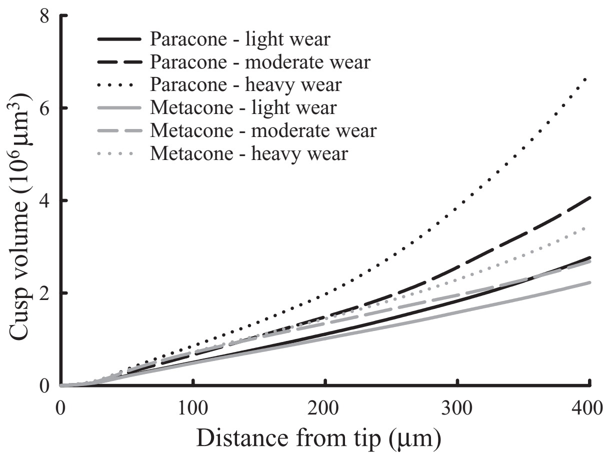


**Figure 4.** Mean cusp sharpness for the first 400 µm from the tip of the paracone and metacone of upper molars for three wear states in *Chalinolobus gouldii*.

*Cusp sharpness:* This is approximately equal for the paracone and metacone of unworn teeth; on average it is slightly higher for the metacone (i.e. smaller volume; Table 1; Fig. 4). In general, the cusp sharpness of the main upper cusps decreases as the teeth wear (particularly for sharpness to 100 µm), so that cusp volume for a given distance from the tip increases. This is more apparent for the paracone, where cusp sharpness decreases more substantially than for the metacone. However, there is variation in this general pattern. The majority of unworn cusps have high cusp sharpness. Most moderately worn cusps have only slightly lower cusp sharpness, but in a few individuals the cusps with moderate wear have even lower cusp sharpness than some highly worn cusps.

*Cusp occlusion relief:* the relief behind the mesostyle for three wear states, represented by the space between the surface of the trigon groove and the path of the hypoconid, is shown in Figure 5. Cusp occlusion relief is very high at low wear (average distance between trigon groove and path of hypoconid is 129.71 ± 11.45 µm) and decreases significantly with increasing wear (33.20 ± 5.96 µm; $P = 0.001$; Table 2). At high wear, the mesostyle is worn away, leaving essentially no relief. In some specimens, wear at the lingual end of the trigon groove and in the trigon basin shows that the hypoconid contacts the upper tooth surface, signifying the lack of relief.

Cusp occlusion relief is also apparent at the points where the protoconid and the protocone occlude (the parastyle on the upper molar and the entocristid/postmetacristid junction on the lower molar, respectively), but was not quantified in this study.

*Crests*

*Edge sharpness:* the results for edge sharpness measurements are shown in Table 3. Edge sharpness of the postmetacrista in the unworn state is 14.4 ± 2.1 µm. After large amounts of wear, this increases significantly to 24.4 ± 3.0 µm.

*Crest rake:* several of the unworn crests have a small amount of negative rake for 10–50 µm from the crest edge. When the rake angle for the first 100 µm is calculated, all unworn ectoloph crests have a positive angle (Table 3). After a small amount of wear, any small amount of negative rake originally present is removed. At higher wear states, the rake angle of all crests is highly negative and significantly different from the unworn state (all $P < 0.01$; Table 3). The most anterior crest (preparacrista) has the highest positive angle when unworn (31.81 ± 2.89°), and the smallest negative angle when worn (–29.76 ± 8.75°) compared to the other three crests. However, all of them have approximately the same change in angle between unworn and highly worn (~60°).

*Crest relief:* the crests of lightly worn molars have a small ridge on the relief surface along the crest edge. Attrition occurs first on this ridge, creating the facet that is seen on lightly worn teeth. This attrition facet,

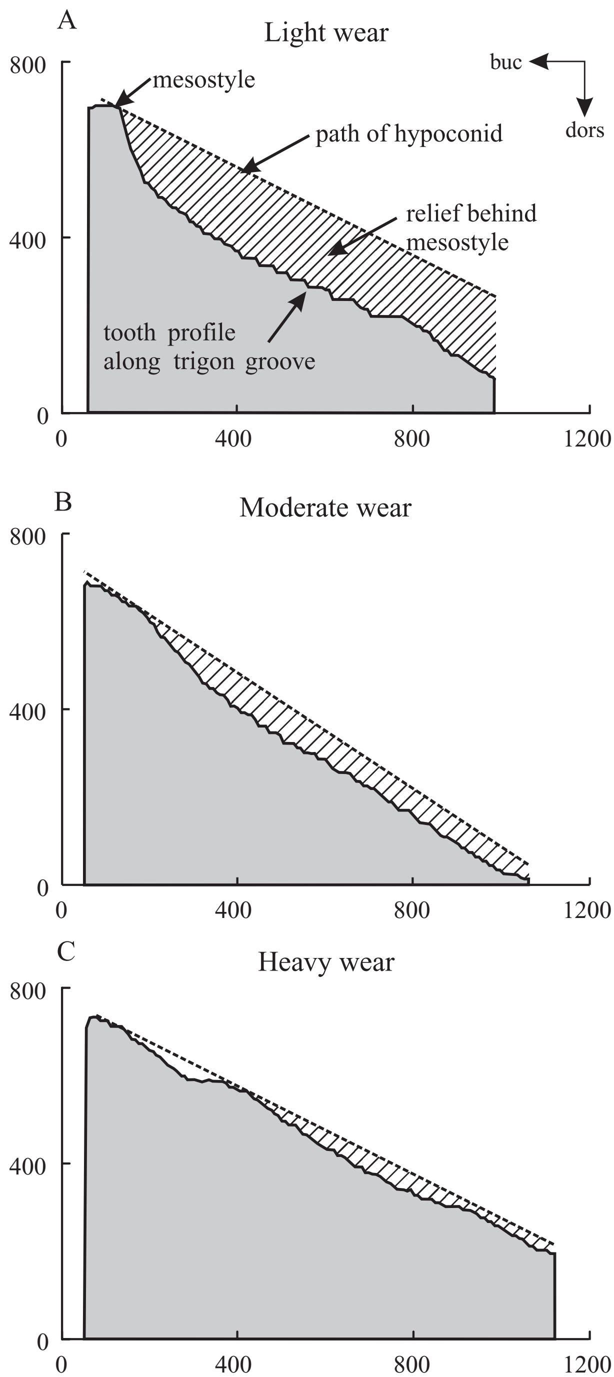


**Figure 5.** Changes in cusp occlusion relief behind the mesostyle for three wear states in *Chalinolobus gouldii*. Grey area is profile of tooth surface along trigon groove; dashed line signifies path of occluding hypoconid (occlusal vector); hatching signifies relief behind mesostyle. A, light; B, moderate; and C, heavy wear. Axes measurements in µm.

or wear land, is approximately the same width for the length of the crest, and its presence maintains the relief behind it. The crests are also relatively high above the associated valleys, giving a large volume behind them.

As wear progresses, the raised ridge is removed and the attrition facet extends down the relief surface. In general, the wear land increases in width with wear, which was significant for three of the four crests (Table 3). The relief angle does not greatly increase with higher abrasion wear as the relief surface is fairly flat (see below). As the crest becomes worn and the distance between it and the adjacent valley decreases, the volume of space into which food can flow decreases. On the relief surface of some crests is a small, shallow concavity (such as behind the postprotocrista) that would also contribute to relief of the crest, particularly at later wear stages. The overall effect of these parameters is that some relief is maintained but it is reduced compared to the unworn teeth.

*Approach angle:* the approach angle for ectoloph crests of unworn or lightly worn teeth is approximately equal, being between 36 and 43° (Table 3). This angle generally increased with tooth wear. The change is highly significant for those crests that occlude with the crests of the protoconid (i.e. preparacrista and postmetacrista; $P = 0.001$), and also significant for the postparacrista ($P = 0.014$; Table 3).

*Food capture:* in unworn teeth, capture area is largest in the crests posterior to a cusp (postmetacrista and postparacrista; Table 3). There is significant change in the capture area from unworn to worn crests only in the postparacrista ($P = 0.011$; $P > 0.05$ for all other crests).

*Fragment clearance:* in unworn teeth, the ectoloph crests are substantially higher than the adjacent paracone and metacone basins, and the rake surface is directed down into the basins, guiding divided food off the buccal edge of the tooth. Divided food that is on the buccal side of the ectoloph crests would flow off the rake surfaces across the basins. The height of the paracone and metacone basins remains essentially constant but the depth of these flow structures is reduced with greater wear. In heavily worn specimens, the rake surface may be lower than the basin and so the fragments must be forced against the slope to be pushed off the rake surface and out towards the buccal side of the teeth. This has the effect of reducing the capacity to gather and direct food off the rake surface. Table 2 summarizes the quantitative differences in clearance with wear. The reduction in fragment clearance occurs more quickly in the paracone than the metacone.

**Table 2.** Cusp occlusion relief (mean ± SE) and fragment clearance (median, minimum and maximum in parentheses) for paracone and metacone basins and trigon groove for three wear states in *Chalinolobus gouldii*. $N = 10$ for light, $N = 5$ for moderate and heavy. *Abbreviations:* meso, mesostyle; para, paracone basin; meta, metacone basin. ***$P \leq 0.001$.

| | | Wear | | | | |
|---|---|---|---|---|---|---|
| | Feature | Light | Moderate | Heavy | $P$ | |
| Cusp occlusion relief (μm) | meso | 129.71 ± 11.45 | 59.05 ± 13.59 | 33.20 ± 5.96 | 0.001 | *** |
| Fragment clearance (qual) | para | 3 (3, 3) | 2 (2, 3) | 1 (1, 1) | <0.001 | *** |
| | meta | 3 (3, 3) | 3 (2, 3) | 2 (1, 2) | 0.001 | *** |

**Table 3.** Functional parameters relating to upper molar ectoloph crests (mean ± SE, or median (minimum, maximum) for qualitative data) for three wear states in *Chalinolobus gouldii*. $N = 10$ for light, $N = 5$ for both moderate and heavy. *Crest:* prpac, preparacrista; popac, postparacrista; prmec, premetacrista; pomec, postmetacrista. *Wear land:* 1, small; 2, moderate; 3, large. *Volume of space behind crest:* 1, small; 2, moderate; 3, large. *Relief angle:* 1, zero; 2, small; 3, large. *$P < 0.05$; **$P < 0.01$; ***$P \leq 0.001$; NS, not significant

| | | Wear | | | | |
|---|---|---|---|---|---|---|
| | Crest | Light | Moderate | Heavy | $P$ | |
| Edge sharpness (μm) | pomec | 14.4 ± 2.1 | 19.7 ± 3.3 | 24.4 ± 3.0 | 0.016 | * |
| Rake angle (°) | prpac | 31.81 ± 2.89 | –16.45 ± 5.03 | –29.76 ± 8.75 | 0.001 | *** |
| | popac | 20.95 ± 4.79 | –35.52 ± 2.87 | –41.95 ± 6.53 | 0.001 | *** |
| | prmec | 18.95 ± 3.05 | –11.76 ± 10.78 | –37.73 ± 8.18 | 0.005 | ** |
| | pomec | 14.61 ± 5.35 | 5.06 ± 13.06 | –40.78 ± 5.95 | 0.009 | ** |
| Relief – wear land (qual) | prpac | 1 (1, 2) | 2 (2, 3) | 1 (1, 2) | 0.001 | *** |
| | popac | 1 (1, 1) | 2 (1, 3) | 2 (1, 2) | 0.086 | NS |
| | prmec | 1 (1, 2) | 1 (1, 3) | 2 (1, 3) | <0.001 | *** |
| | pomec | 1 (1, 1) | 2 (1, 2) | 2 (1, 3) | 0.017 | * |
| Relief – volume behind crest (qual) | prpac | 3 (3, 3) | 3 (2, 3) | 2 (1, 2) | 0.001 | *** |
| | popac | 3 (3, 3) | 3 (1, 3) | 1 (1, 2) | 0.008 | *** |
| | prmec | 3 (3, 3) | 3 (2, 3) | 2 (1, 3) | 0.004 | *** |
| | pomec | 3 (3, 3) | 3 (2, 3) | 2 (1, 2) | <0.001 | *** |
| Relief – angle (qual) | prpac | 2 (2, 2) | 2 (2, 2) | 2 (2, 3) | 1.000 | NS |
| | popac | 2 (2, 2) | 2 (2, 2) | 2 (2, 2) | 1.000 | NS |
| | prmec | 2 (2, 2) | 2 (2, 2) | 2 (2, 2) | 1.000 | NS |
| | pomec | 2 (2, 2) | 2 (2, 2) | 2 (2, 2) | 0.499 | NS |
| Approach angle (°) | prpac | 38.56 ± 1.13 | 46.17 ± 1.28 | 56.42 ± 1.76 | 0.001 | *** |
| | popac | 42.76 ± 1.10 | 40.49 ± 4.29 | 49.36 ± 1.27 | 0.014 | * |
| | prmec | 36.12 ± 1.19 | 40.40 ± 4.52 | 39.04 ± 3.36 | 0.822 | NS |
| | pomec | 37.78 ± 0.76 | 40.35 ± 0.98 | 50.02 ± 1.51 | 0.001 | *** |
| Capture area ($10^3$ μm$^2$) | prpac | 26.87 ± 1.94 | 26.72 ± 5.18 | 18.34 ± 2.43 | 0.084 | NS |
| | popac | 67.37 ± 5.03 | 73.11 ± 8.85 | 31.65 ± 4.60 | 0.011 | * |
| | prmec | 47.90 ± 2.94 | 39.71 ± 3.70 | 33.77 ± 7.57 | 0.153 | NS |
| | pomec | 63.47 ± 3.07 | 64.13 ± 6.92 | 78.88 ± 13.45 | 0.597 | NS |

### PCA AND NMDS

There is a fairly high degree of separation among wear states along Factor 1 of the PCA plot using the entire data set (Fig. 6A). Many of the functional parameters were very highly correlated with Factor 1. Parameters with absolute correlations between 0.94 and 0.80 were as follows: fragment clearance; approach angle for preparacrista and postmetacrista; relief volume; rake angle; paracone volume to 100 μm; capture area for postparacrista; and cusp occlusion relief. Tooth length had a correlation of 0.172 with Factor 1. Factor 2 was not highly correlated with any of the variables, with the third highest correlation being with tooth length (0.608). The plots using subsets of the data displayed similar patterns.

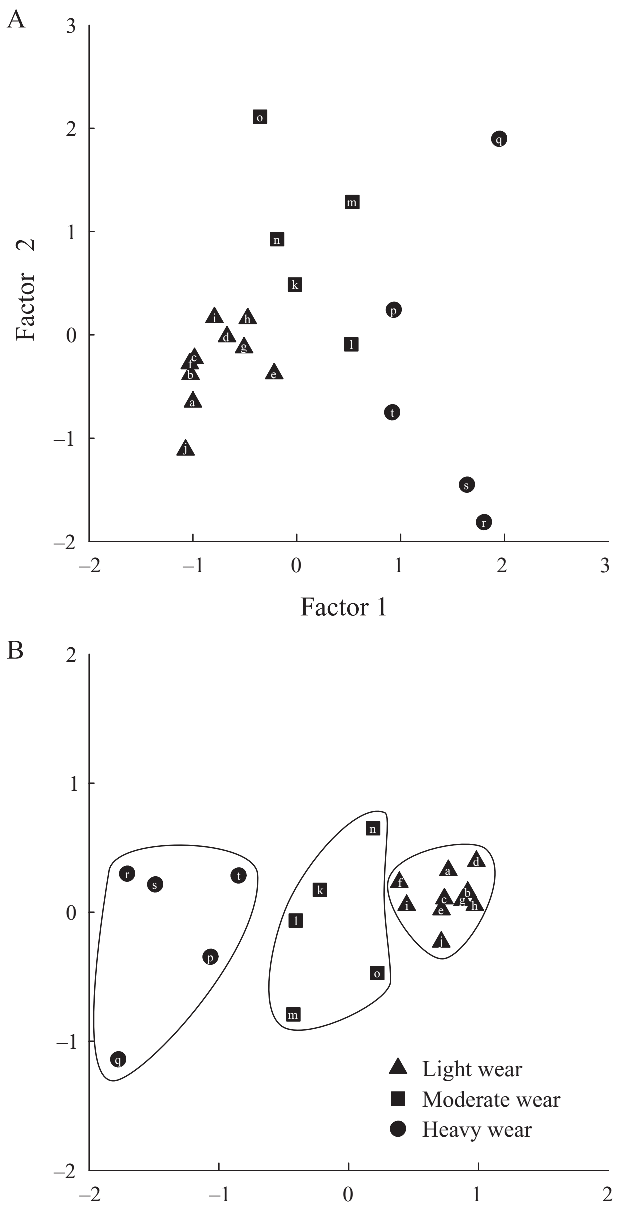


**Figure 6.** A, PCA (Factor 1 vs. Factor 2) and B, 2-D NMDS plots for all functional parameters for three wear states in 20 individuals of *Chalinolobus gouldii*. Letters indicate individual specimens: a–j, light wear; k–o, moderate; p–t, heavy.

NMDS plots showed a clustering of individuals with similar wear states (light, moderate and heavy), which was very tight for the ten lightly worn specimens in most plots (Fig. 6B). The moderate wear group was always found between the light and heavy wear groups. Stress for all 2-D plots was < 0.10, and plots for subsets of the data were similar. ANOSIM for all variables found a significant difference between light-moderate, light-heavy and moderate-heavy (significance level < 0.01%, < 0.01% and 0.08%, respectively). SIMPER analyses found that cusp occlusion relief contributed most to the differences between groups (average 10.61% for the three between-group comparisons), followed by rake angles of postparacrista (6.97%), postmetacrista (6.42%), premetacrista (6.30%) and preparacrista (6.24%), tip sharpness (5.70%), capture of postparacrista (4.69%) and edge sharpness (4.31%).

## DISCUSSION

### Functional parameters

The nine functional parameters of crests and cusps measured in this study have a predictable influence on the function of teeth. As a result, the changes in tooth shape that result from wear can be assessed, most often directly in terms of force or energy required for a component to function. Changes that occurred following heavy wear that would lead to an increase in the force and/or energy required are as follows: larger radius of curvature for cusp tips and crest edges (tip and edge sharpnesses); larger volume of a cusp for a given distance from the tip (cusp sharpness); diminished relief behind cusp occlusion points (cusp occlusion relief); decreased rake angle (from positive to negative); increased wear land behind three crests; decreased volume behind crests; and decreased flow of material off rake surfaces (fragment clearance). The effect is perhaps largest for rake angle, which changed by approximately 60° in all of the crests examined. A significant difference in the forces required to fracture plant material occurs between blades with rake angles of 0° and 30° (N. Aranwela, pers. comm.) Individuals of the same wear state clustered in the NMDS plots (Fig. 6B), and significant differences between lightly, moderately and heavily worn molars were found in the ANOSIM analysis.

In contrast to this, a decrease in the force for the teeth to operate would result from the larger approach angle of three of the four crests due to increased mechanical advantage of the crests. There was no significant change in wear land for postparacrista, relief angle for all crests and approach angle for premetacrista. Change in capture area is not as straightforward to interpret: the removal of the entire area of capture would mean less food trapped and divided by crests, but a large increase in area would require greater forces and not necessarily improve overall effectiveness. There was no significant change in capture area for three of four crests.

Overall, it would be expected that the function of these teeth would deteriorate significantly with wear, requiring more force and energy to process food. There are two independent lines of evidence that support the prediction that increased force and energy will be required. Insectivorous shrews increase the efficiency of the jaw mechanics with age, increasing the available bite force (Carraway *et al*., 1996; Verts, Carraway & Benedict, 1999). It was only presumed in these studies that worn teeth were less effective at dividing food. Wear scratches on the enamel relief surface of crests appear to be deeper or wider at higher wear states of *C. gouldii* (my unpubl. data). Deeper or wider scratches may require the application of greater bite force (Teaford, 1988; Ungar & Spencer, 1999; although see Maas, 1994 for an alternative view), supporting the proposal that this is necessary for worn teeth. Other possible explanations for deeper scratches include a change in enamel structure that makes it easier to scratch at greater depths into the tooth or further down the relief surface (e.g. different hardness or structure at various enamel depths; Ferreira *et al*., 1985; Maas, 1993).

There are some important implications of decreased tooth efficacy with wear. Greater energy and possibly time (in number of chews) must be expended in processing food, leaving less time and energy for other important processes, including food searching and gathering, and social interactions (Lanyon & Sanson, 1986; McArthur & Sanson, 1988; Logan & Sanson, 2002). Carraway *et al*. (1996) concluded that older animals must switch to a diet of softer food. Their search for such a dietary shift assumes that the worn teeth have retained the ability to divide 'soft' food; however, worn teeth may be equally ineffective in dividing 'soft' and 'hard' foods. An increase in efficiency of jaw mechanics would then be more important, as was found to occur in shrews (Verts *et al*., 1999).

The majority of the parameters used in this study have been at least alluded to in the functional dental literature. Lucas (1982) clearly explained the significance of tip sharpness to cusp function and measured it on human cusps by fitting conic sections to cusp profiles. It has since been measured in bat canines (Freeman & Weins, 1997) and lemur molars (Yamashita, 1998). Both tip sharpness and cusp sharpness were shown to be significantly related to the force and energy for a cusp to operate (Evans & Sanson, 1998). Rake and relief are common terms in the literature of engineering tool design. They have previously been briefly outlined or described by some authors (e.g. Osborn & Lumsden, 1978), but apparently no attempt has been made to measure these parameters. The concept of approach angle has been discussed previously in terms of mechanical advantage (Abler, 1992; Evans & Sanson, 1998) and its functional significance demonstrated for model teeth (Worley & Sanson, 2000), but the term was not used (and has been indirectly referred to elsewhere in the form of 'point cutting'). The importance of capture in bladed systems has been recognized for a long time (e.g. Van Valen, 1969; Freeman, 1979; Abler, 1992) but attempts have rarely been made to quantify it in the various tooth forms in which it occurs. Popowics & Fortelius (1997) measured edge sharpness of crest profiles from a variety of mammals by fitting a circle to the curved part of the profile (see Evans, 2003 for further discussion). Fragment clearance has been included previously in analyses of tooth function (Seligsohn, 1977; Sanson, 1980; Frazzetta, 1988). No reference to relief behind points of cusp occlusion has been found in the dental literature, but this can be considered merely a specific instance of relief.

Crompton, Wood & Stern (1994: 330) were under the impression that the angle between the 'vertical shearing surfaces and horizontal occlusal surfaces' (the relief and rake surfaces, respectively) of a crest is almost always a right angle. In fact, more efficient cutting will be achieved if this angle is minimized, which will increase the rake angle. They also concluded that cutting efficiency would be decreased if the cutting edges are rounded, due to the lack of the right angle between the rake and relief surfaces. It is true that the efficiency of the crest will be decreased, but it would be more accurate to say that this is because such rounding will decrease edge sharpness (increase the radius of curvature of the crest edge) and create negative rake on the crest, which will tend to force crests apart when food is between them.

## Crest size

Crest size or length has been used as an indicator of crest function in previous studies, and it is therefore useful to compare any change in length due to wear with alterations in the functional parameters discussed above. In general, three-dimensional length of crests has been used as a surrogate for function. In this study it was not found to significantly change with heavy wear (sum of 3-D lengths of all ectoloph crests: light wear $3080.3 \pm 88.0$ µm; moderate $3141.7 \pm 136.6$ µm; heavy $3136.2 \pm 109.3$ µm; Kruskal–Wallis test statistic = 0.509; $P = 0.775$).

The length of a cut made by a crest is another good representation of its size, i.e. the two-dimensional length of the crest when projected onto a plane perpendicular to the occlusal vector (Evans & Sanson, 2003). A shorter two-dimensional length indicates that the effective size of the crest has decreased, as it will now divide less food with one stroke. Two-dimensional crest length did on average decrease by about 10% (light $2335.4 \pm 81.7$ µm; moderate $2346.2 \pm 89.4$ µm; heavy $2039.9 \pm 123.4$ µm) but this was not significant (Kruskal–Wallis = 4.669; $P = 0.097$). Results were very similar if crest length was standardized according to tooth length.

Therefore, a comparison of function based solely on crest length would detect no change in shape or function with the extreme alteration in molar shape with wear that occurs in *C. gouldii*. This substantial change is displayed very clearly, though, by the decrease in effectiveness in the majority of the tooth components according to the nine functional parameters.

### SHAPE AND FUNCTION MAINTENANCE DURING WEAR

Despite the noticeable change in tooth shape that occurs with wear, several of the features retain good functional aspects even after heavy wear, or even verge upon improvement. The design means that the teeth will retain many aspects of effective shape longer than may be expected.

#### *Food capture*

A concave crest is able to maintain its shape to some degree merely through use. If the entire cavity is filled with food, all of which has been broken down, then the middle of a concave crest will divide more material than the ends, and may be under greater pressure (or certainly under pressure for a longer time) from the food. Wear on the rake surface of a crest by food abrasion is at least partly determined by the amount of material it divides and by the pressure exerted on the surface, so greater wear will occur in the middle compared to the ends. The thickness of enamel along the length of a crest will influence how it wears. Thinner enamel on the middle of crests compared to the ends will cause the middle to wear more rapidly compared to the ends. Enamel thickness along a crest does not appear to have been quantified before, but in the specimens of *C. gouldii* examined it appears thicker towards the cusp ends of the crests (the lingual end of ectoloph crests; also found in several other microchiropteran species, e.g. *Hipposideros diadema*, and appears to be the case from micro-CT scans of *Eptesicus* sp. molars; pers. observ.). The greater amount of dentine that must be worn at the buccal end of the crests would have the same effect as the thicker enamel on the other end, reducing the rate at which the height of the crest is decreased. Both of these parameters will preserve or possibly even increase the concavity of the crest, as was found in the worn crests of *C. gouldii*.

#### *Cusp sharpness*

Wear in the centre of the crests on two-crested cusps (such as the paracone and metacone) also maintains higher cusp sharpness to some extent. Thicker enamel on the rounded, lingual faces of the cusps will mean their height is maintained, and greater wear on the rake surface of the adjoining crests will maintain high cusp sharpness. To a limited extent, this occurs on the upper molars, where in some instances a highly worn cusp has higher cusp sharpness than moderately worn ones.

#### *Relief*

The incidence and ratio of wear on the rake and relief surfaces will influence the amount of relief of a crest,

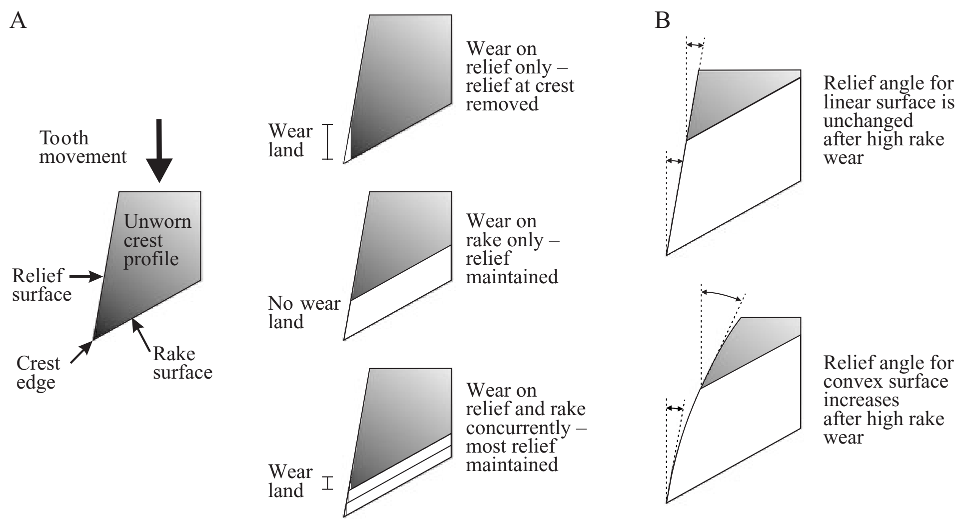


**Figure 7.** A, the effect on the relief behind a crest of relative wear on the rake and relief surfaces. If wear only occurs on the latter, then relief behind the crest is removed (as represented by a large wear land). If wear only occurs on the former, relief is maintained. For the more realistic situation where wear occurs on both surfaces concurrently, substantial relief (indicated by small wear land) is maintained. B, relief angle is maintained after wear on rake surface for a linear relief surface, but increases if relief surface is convexly curved. Tooth profile is represented by shaded areas; unshaded areas represent tooth removed by wear.

particularly the size of the wear land (Fig. 7A). Wear on only the relief surface would cause the majority of the relief to be removed, increasing the wear land. If the rake surface were also worn, then no wear land would be produced, and relief would be preserved. If sufficient wear occurs on both the rake and the relief surfaces, then relief will be maintained. *Chalinolobus gouldii* molars have a high degree of wear on the rake surface relative to wear on the relief surface, reducing the wear land on the relief surface and maintaining relief.

From this, it appears that some abrasive wear is beneficial in maintaining the relief of the tooth. There is substantially more wear on the rake than relief surface. This may be due to a greater force being applied to the former, or that the applied force is perpendicular to it compared to almost parallel to the relief surface. The component of the force directed into the tooth is therefore smaller on the relief surface, resulting in the removal of less dental material. The relative enamel thicknesses (thin on the rake surface and thick on the relief) would also contribute, so that enamel on the rake surface is rapidly removed, particularly for areas close to the crests. Once the enamel is breached, the differential hardness of dentine and enamel, along with the microstructure arrangement of enamel prisms (where they are perpendicular to the force on the relief surface and so resist wear to a greater extent; Stern, Crompton & Skobe, 1989) would also play a part.

A non-zero relief angle can be maintained during wear when the relief surface is straight, and will even increase given a convex curvature of the relief surface (Fig. 7B). Relief surfaces, particularly those on the lingual side of upper molar cusps, are either straight or slightly concave, so that relief is maintained as tooth wear progresses.

### *Edge sharpness*

The edge sharpness of crests was found to significantly decrease with wear. The substantial change in other parameters of crest shape (such as rake angle) may have been expected to produce a major change in edge sharpness, but the small increase in radius of curvature (from 14 to 24 μm) suggests that there are characteristics preventing this. These are likely to include enamel microstructure. An enamel edge will wear more slowly than the surrounding dentine, resulting in a ridge of enamel higher than the dentine (Rensberger, 1973). This will produce a sharper cutting edge compared to a crest of dentine only. Enamel prisms in the relief surface of crests are arranged parallel to the rake surface, so that when prisms are removed by wear, a sharp edge is retained (as has been found in the opossum; Stern *et al*., 1989).

All of these features point to controlled wear in tribosphenic-like molars. Wear cannot be avoided, but teeth can be shaped to influence which regions of the tooth wear more than others. Proportions of cusps and crests, and distribution and structure of enamel, can encourage wear in particular areas during use, allowing effective function to be maintained.

## Functional relationships of attrition and abrasion of crests

Two types of wear surfaces result from tooth wear (Every & Kühne, 1971; Kay & Hiiemae, 1974; Osborn & Lumsden, 1978): *abrasion* surfaces, which are relatively rough and rounded with non-parallel scratches; and *attrition* surfaces, which are essentially planar, with a polished appearance and largely parallel scratches. Abrasion is thought to be the result of tooth–food contact, and attrition chiefly due to tooth–tooth contact, with scratches caused by hard particles between the tooth surfaces (Teaford & Walker, 1983a, b).

When these two types of wear are related to the dental surfaces on which they occur, we find that there is a constant relationship between the function of a crest surface and the type of wear that occurs on it (Figs 3, 7). When two crests occlude, no tooth–tooth contact occurs on the rake surface of the ectoloph crests: all wear must be due to tooth–food contact, producing a rough ‘abrasion’ wear surface. Conversely, where relief surfaces contact those of opposing crests, wear due to tooth–tooth contact occurs and the result is planar ‘attrition’ wear surfaces. It may be that a small amount of dental material is removed from the relief surface through abrasion. However, due to the very clear attrition facet just behind the crest edge, and the observation that there is very little evidence of wear (either by tooth–food or tooth–tooth contact) on the relief surface beyond the attrition facet, we can conclude that abrasion wear on the relief surface is probably inconsequential to any change in tooth shape with wear.

The disparity in the form of wear is due to the differences in function of the surfaces on which they occur. Therefore, the action of a surface can be determined by the type of wear found on it. Attrition can only occur on the relief surface of a crest. One without attrition wear and with an abrasion wear surface will almost certainly be a rake surface. This has been implicit in previous reconstructions of tooth occlusion (e.g. Butler, 1952; Mills, 1966, 1967; Crompton & Hiiemae, 1970; Crompton, 1971; Greaves, 1973), but the specific correlation with the functional rake and relief surfaces has apparently not been made.

The situation is slightly different in herbivorous forms, such as selenodont artiodactyls. These differ from the tribosphenic type considered here in that the relief surface is composed of both enamel (at the crest edge) and dentine (further away from the crest edge; Evans, 2003). The dentine basin behind the enamel attrition facet will only be worn by abrasion of food, as tooth–tooth contact is not possible due to the shape of the crests. However, any attrition wear will only occur on a relief surface, thus allowing it to be identified as such. In addition, the relief surface of one crest is often contiguous with the rake surface of the adjacent one, although there will still be no attrition wear on the latter, which is usually the lateral surface of an enamel crest, either on the side of the tooth or next to a dentine basin. The identification of relief surfaces according to this definition will be more difficult in some herbivorous teeth where the attrition facets may be removed by large amounts of abrasion (Popowics & Fortelius, 1997).

## CONCLUSIONS

Previous measures designed to assess the functional effectiveness of teeth (such as those based on crest length) do not consider differences in tooth action due to tooth shape, and are not particularly informative when comparing worn teeth. Other more recently developed methods also lack the ability to explain the action and efficacy of individual cusps and crests. The powerful functional measures elaborated and measured in this study allow the determination of changes in efficacy with the change in shape resulting from wear in tribosphenic-like teeth.

Following substantial wear, many of the functional parameters were significantly altered, indicating a decrease in the efficacy of the tooth in breaking down food. These features include tip, edge and cusp sharpnesses, cusp occlusion relief, rake angle, fragment clearance and some measures of crest relief. Only approach angle improved for some crests.

Wear is a constraint on shape that may not be inherent in the operation of unworn teeth, and should be considered when examining their function. Therefore, we can presume that it must have been a highly influential selective force in shaping teeth. Although not as adapted as other tooth forms (e.g. selenodont molars) to cope with high wear and maintain function, there are significant features of the teeth that mean that some valuable features are retained with wear. Shape may be maintained through geometrical relations of wear or through specific morphological adaptations; for example, capture area did not change with wear for most crests. For many tooth forms, the function of a dental surface can be determined by the type of wear found on it. Attrition can only occur on the relief surface of a crest, and a surface with only abrasion wear is most likely to be a rake surface.

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