Current Trends in Dental Morphology Research

DENTAL ECOMORPHOLOGY OF EXTANT EUROPEAN CARNIVORANS

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ABSTRACT

Tooth shape was investigated in 20 species of extant European carnivorans with diverse diets. The rake angle of the upper and lower carnassial crests were measured. The rake angle is the angle of the leading surface of the crest with the direction of movement and is an indicator of the mechanical efficiency of a crest. The omnivores and meat/bone feeder were found to have very low and often negative rake angles for the carnassials. This indicates a greatly decreased effectiveness in cutting meat in these species, and may be due to conflicting constraints of needing to withstand the higher forces exerted on the teeth when consuming strong foods such as bone and vegetation. Also, rake angle was found to have no correlation with the relative length of the crest, with both the highest and lowest rake angles found in species with relatively short crests. Short crests may therefore be highly mechanically efficient, which would not have been suspected from solely measuring their length.

INTRODUCTION

The desire to understand the link between the morphology of a tooth and its function has a long history. Aristotle made broad generalisations on the shape of teeth and their basic function, describing a lion as saw-toothed and a horse tooth as broad and fit for grinding (Kay, 1975). This type of simplistic description

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seems to be very appealing and has been made many times since. However, it leaves many questions unanswered and does not attempt to quantify the function of these tooth types.

In this paper we address the relationship between carnivore tooth shape and function. Blades or crests are considered to be the most effective tooth shapes for dividing tough, ductile food such as vertebrate flesh (Lucas, 1979; Lucas and Luke, 1984), and so it is the function of crests of carnivore teeth that we will examine. Modern examinations of tooth function have associated various quantitative measures of tooth shape with the degree of 'carnivory' of the animal, i.e. the degree to which it consumes vertebrate flesh. The pioneers in this field were Crusafont-Pairó and Truyols-Santonia (1956), who devised two angular measurements of the carnassial teeth of carnivores to estimate the degree of carnivory. Van Valen (1966) also used a similar measure which he termed 'Q'. Both of these studies found a correlation between the measures and the expected degree of carnivory within groups or along lineages. Largely, these measures quantify the size of the crest, either in absolute terms or as a proportion of the length of the tooth. This is therefore similar to more recent work, which has directly measured the size and proportion of blades for individual teeth (Popowics, 2003; Van Valkenburgh, 1989).

The basic message from these studies has been that the more meat an animal eats, the longer are the crests on its carnassial teeth: hypercarnivores tend to have longer crests and smaller basins than those species that have other components to their diets, such as bone, invertebrates or plant material. Selection in hypercarnivores, therefore, appears to have been for increased crest size. It has been implied from this result that bigger is better – a longer crest improves function.

A shorter blade will decrease the amount of food cut in a single stroke, but the energy and force required to divide the food will depend on other aspects of the shape of the crest and the surrounding tooth surfaces. What is more important, then, is whether a decrease in the relative size of the crest means that the overall function of the crest has been compromised. Do teeth with a shorter blade have worse functional characteristics than those with a long blade? Are there other functions or constraints on the overall shape of short crests that reduce their functionality? For instance, eating foods that are stronger, harder or more 'intractable' (a combination of structural strength, stiffness and toughness; Evans and Sanson, 2005a) may require a strengthening of the tooth, perhaps making it more robust, that will then reduce its functionality. Do we therefore see a compromise between effective function and other factors in tooth shape?

To assess this question, we need better ways of relating the actual shape of the tooth to its function than merely the length of its crests. If we view teeth as tools for breaking down food, then this can help focus our search for the aspects of shape that most affect the tooth's function. This will also allow us to use concepts developed by engineers in the design of tools. Several measures of cusp and crest function have been developed in previous work (Evans, 2005a, 2005b; Evans and Sanson, 2003, 2005b, 2005c) that can be directly related to the force and energy for a tooth to divide food. In this study, we will examine only one, the rake angle of a crest.

The rake angle is the angle between the leading surface of a crest and a line perpendicular to the direction of tooth movement (Figure 1; Evans and Sanson, 2003). The larger this angle is, the less force will be required for a crest to divide food. This can be thought of as the 'sharpness' of a knife to some extent, where the larger this angle is, the smaller the included angle of the knife blade, and the sharper the knife appears. Two other common kitchen devices where rake angle is important are a vegetable peeler and cheese cutter. The metallic surfaces on these implements are arranged so that when the blade makes contact with the food, the rake angle is set for effective cutting. A zero degree rake angle means that the leading surface of the blade is at right angles to the direction of movement, and a negative rake angle is where the leading crest surface is ahead of the crest tip. When a blade has a negative rake angle, substantially more force will be needed to fracture food, and such a blade may even be considered 'negatively sharp', as it is contrary to what we expect from a sharp blade.

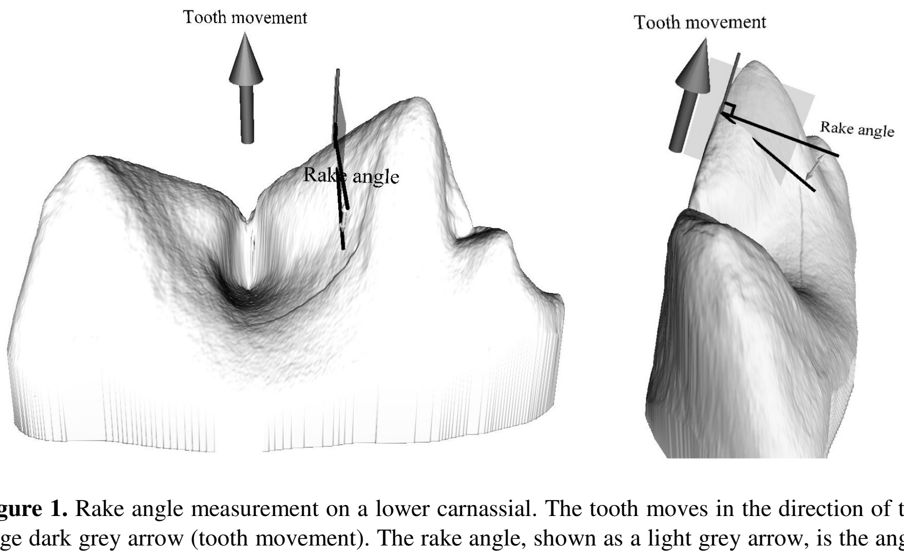

Figure 1. Rake angle measurement on a lower carnassial. The tooth moves in the direction of the large dark grey arrow (tooth movement). The rake angle, shown as a light grey arrow, is the angle between the leading surface of a crest and a line perpendicular to the direction of tooth movement

Scraping butter off the surface of a block with a knife uses a negative rake angle – only a small amount of material is removed because of the ineffective use of the input force for dividing food.

This study examined crest function in carnivorans by looking at the rake angle of the carnassial blade of 20 species of extant European carnivorans. This will test whether those animals that have a higher proportion of meat in their diet have more effective crests, as measured by the rake angle. Also, we will be able to see whether species with a relatively short crest are able to maintain a high rake angle. The results presented here are only the preliminary results for this study.

METHODS

The carnassial teeth, upper P4 and lower M1, of 20 species of extant European carnivorans (Table 1) were scanned using a Nextec Hawk 3D laser scanner. This digitises the x,y,z coordinates of single points using a range-finding laser at 30 µm intervals across the surface. Only teeth with very light wear and in good condition (no major chips or cracks) were used, and each species is represented by one specimen. The tooth surface was reconstructed from the point cloud data using Surfer for Windows version 8, a geographic information systems (GIS) package. To estimate the occlusal vector (the direction of tooth movement), a plane was fitted to the attrition facet of the main crest. The occlusal vector was then the vector that lay within this plane and was perpendicular to a line connecting the tips of the cusps at the end of the crest. This may not perfectly represent the true occlusal vector during occlusion, but appears to be a reasonable estimate and is straightforward to calculate.

Table 1. Dietary grouping of the 20 species used in this study, based on Nowak (1999).

Dietary group	Species
Meat	*Canis lupus, Felis silvestris, Genetta genetta, Lynx lynx, Mustela eversmannii, Mustela nivalis, Vormela peregusna*
Meat/Bone	*Gulo gulo*
Meat/Nonvertebrate	*Alopex lagopus, Canis aureus, Martes foina, Martes martes, Mustela erminea, Mustela lutreola, Mustela putorius, Vulpes vulpes*
Nonvertebrate/Meat	*Herpestes ichneumon*
Fish/Meat	*Lutra lutra*
Omnivore	*Meles meles, Ursus arctos*

The rake perpendicular (RKP) plane is a plane parallel to the occlusal vector and perpendicular to the long axis of the crest. The profile of the rake surface is the intersection between the rake surface and the RKP plane. Two such profiles were found by positioning the RKP plane half-way between the anterior end of the crest and the carnassial notch, and half-way between the posterior end of the crest and the carnassial notch. If no carnassial notch was present (e.g. in the upper carnassial of most mustelids), then the lowest point of the crest was taken as the position of the notch. A least-squares regression line was fitted to the profile for a distance along the profile of 0.2 times the length of the tooth.

Tooth length was measured as the three-dimensional distance from the most anterior point to the most posterior point of the tooth. Crest length is the length of the crest when projected onto a plane perpendicular to the occlusal vector (Evans and Sanson, 2003). This represents the length of the cut made by the crest as it divides food.

The diets of the 20 species were categorised using dietary information in Novak (1999) as feeding on meat (predominantly meat in diet), meat/bone (including significant amounts of large bone), meat/nonvertebrate (mostly meat but significant amounts of nonvertebrate food), nonvertebrate/meat (more nonvertebrate food than meat), fish/meat (mostly fish) or omnivore (consuming many different food types as well as meat, such as nuts, berries, fruits and vegetation). Table 1 shows the classifications used here.

RESULTS

Rake angle is plotted against tooth length in Figure 2 for the upper and lower carnassials. *Ursus arctos* is the only species to have negative rake angles for both the upper and lower crests. *Gulo gulo* and *Meles meles* have negative rake angles for the upper crest and lower crest respectively. Despite being positive, the lower crest rake angle of *G. gulo* is more than 10º below all of the species other than the two that are negative. These three species are either omnivores or meat/bone feeders. For the upper crest, the remaining species range between 3.4º for *Mustela putorius* and 28.1° for *Canis aureus*; for the lower, they cluster more tightly between 19.5° for *Felis silvestris* and 36.8° for *Vulpes vulpes*. In both crests, there does not appear to be any grouping of the species according to diet other than the omnivores and meat/bone feeder. There is no significant correlation between tooth size and rake angle for all of the species ($R^2 < 0.1$, $p > 0.25$ for both upper and lower). The group of meat/bone feeders and omnivores, representing a hard or imtractable-feeding group, were significantly different from the remaining species (Mann-Whitney U test statistic = 0.000, $p = 0.002$ for both upper and lower).

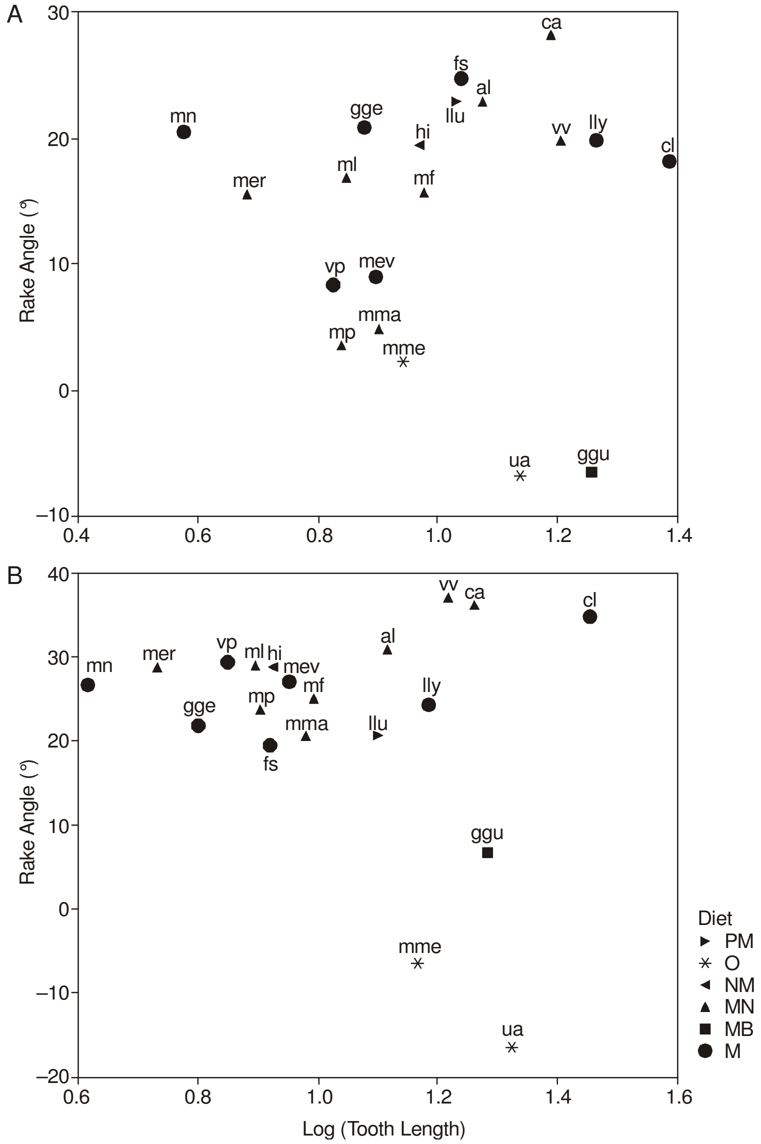

Figure 2. Tooth length versus rake angle for 20 carnivoran species for the upper (A) and lower (B) carnassials. Omnivores and the meat/bone feeder have lower rake angles than the other feeding groups. Abbreviations: al – *Alopex lagopus*; ca – *Canis aureus*; cl – *Canis lupus*; fs – *Felis silvestris*; gge – *Genetta genetta*; ggu – *Gulo gulo*; hi – *Herpestes ichneumon*; llu – *Lutra lutra*; lly – *Lynx lynx*; mer – *Mustela erminea*; mev – *Mustela eversmannii*; mf – *Martes foina*; ml – *Mustela lutreola*; mma – *Martes martes*; mme – *Meles meles*; mn – *Mustela nivalis*; mp – *Mustela putorius*; ua – *Ursus arctos*; vp – *Vormela peregusna*; vv – *Vulpes vulpes*; M – meat; MB – meat/bone; MN – meat/nonvertebrate; NM – nonvertebrate/meat; O – omnivore; PM – fish/meat

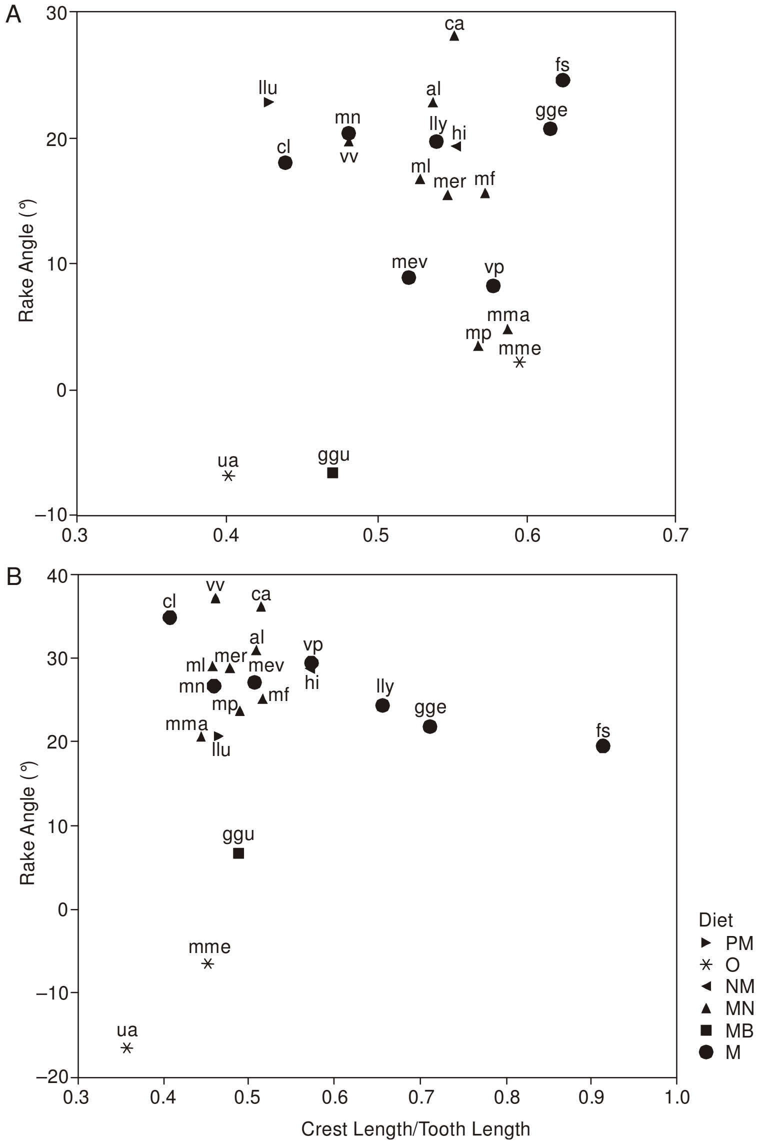

Figure 3. Relative crest length (2-dimensional crest length divided by tooth length) versus rake angle for 20 carnivoran species for the upper (A) and lower (B) carnassials. There is no association between relative crest length and rake angle. See Figure 2 for species and dietary abbreviations

When rake angle is plotted against crest length divided by tooth length, a measure of the relative length of the crest (Figure 3), the omnivores and meat/bone feeders tend to have low relative crest lengths for the upper and lower teeth, except for *M. meles* upper crest. *Felis silvestris* and *Genetta genetta* have the longest relative crest lengths and reasonably high rake angles, but the species with the highest rake angles tend to have shorter relative crest lengths, particularly in the lower crest, such as *V. vulpes*, *C. aureus* and *Canis lupus*. There was no significant correlation between relative crest length and rake angle ($R^2 < 0.1$, $p > 0.4$ for both upper and lower).

DISCUSSION

From these preliminary results, it appears that omnivores and meat/bone feeders have lower rake angles than the other feeding groups. This would substantially increase the amount of force and energy required for the tooth to divide food, most of these crests having very inefficient negative rake angles.

For *G. gulo*, the meat/bone feeder, it is likely that the consumption of strong foods has selected for a more robust tooth. This would lead to a compromised tooth shape that is less effective for cutting meat (due to the decreased rake angle) but able to withstand the higher stresses placed on the tooth when fracturing bone. Other characteristics of the teeth indicate less emphasis on meat cutting, such as the absence of a carnassial notch in the upper tooth.

The same constraints may apply to the omnivores, which consume stronger and more intractable foods such as seeds and vegetation. However, there may be much less selection for an efficient meat-cutting blade, and so the tooth function has been concentrated onto other factors that have compromised the meat-cutting function.

When the rake angle results are examined with respect to relative crest lengths, we can see that having a relatively short crest does not guarantee a low rake angle. In fact, the highest rake angles are found in those with short crests. Therefore, relative crest size does not dictate other functional characteristics of the tooth, such as rake angle, which may have been suspected from previous studies. The *F. silvestris* lower carnassial, with by far the longest relative crest length, has the moderate rake angle of 19.5º, with only the meat/bone feeder and omnivores lower. This would not have been expected based on previous analyses using only relative crest length, and may mean that the functional effectiveness of such long carnassials has been overestimated.

A specific example of the influence of crest length and rake angle can be seen in the comparison of felids and canids. The felids in this sample, *F. silvestris* and *Lynx lynx*, have some of the longest relative crest lengths, particularly in the lower crest. This is true in comparison to all of the canids (*Alopex lagopus, C. aureus*, *C. lupus* and *V. vulpes*), with relatively short crests. However, the rake angle of the canids is generally higher, this being especially the case for the lower crest. It seems, therefore, that the canids and felids have taken alternative routes to improving tooth function: felids have increased the relative length of the crest, seemingly to the detriment of rake angle, but the canids have kept their crests relatively short but achieved a high rake angle. This perhaps indicates conflicting constraints on tooth form that a very long crest with a high rake angle is not easily achieved. It also goes against conventional wisdom of felids having greatly superior meat-cutting carnassials than canids.

In a group of microchiropterans, the only other group of animals for which it has been measured, rake angle varied from about 25º in tractable (‘soft-feeding’) to about 5º in intractable (‘hard-feeding’) insectivorous bats (Evans and Sanson, 2005b). The carnivorans investigated here exhibited a greater range, but this is probably to be expected given their more diverse diets. It was also found to greatly decrease from light to heavy wear, changing from about 25º to about –35º (Evans, 2005). Rake angle would be expected to greatly change with wear in the carnivorans also.

CONCLUSIONS

The use of rake angle as a measure of the effectiveness of tooth shape reveals different patterns of function than would be expected from a simple analysis of relative crest length. It appears that teeth with short crests can have either efficient high rake angles, as high as 37º, or grossly inefficient negative rake angles, down to –16º. However, a very long crest (greater than 60% of the length of the tooth) does not have a very high rake angle, perhaps indicating a structural constraint in tooth construction. Diet is also seen to have an effect on rake angle, as it is very low or negative in meat/bone feeders and omnivores but not in other meat feeders. This preliminary analysis indicates that further work on this important functional measure is warranted.

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