THREE-DIMENSIONAL RECONSTRUCTION OF TOOTH RELATIONSHIPS DURING CARNIVORAN CHEWING

Alistair R. Evans and Mikael Fortelius

ABSTRACT

Contact between teeth during chewing has often been studied using the indirect evidence of cinematography during chewing and the wear facets on teeth. However, neither by itself gives the entire picture of the occlusal relationships between teeth. Here, we endeavoured to relate the two different lines of evidence using three-dimensional reconstructions of tooth-tooth contact in eight carnivoran species based on the shape of teeth and jaw joints. We found that jaw movement generates contacts between teeth that are consistent with attrition wear facets. This supports the long-held but not fully verified view that attrition facets are generated by tooth-tooth contact during chewing. The second major issue investigated was the shape of attrition facets on teeth. It has generally been assumed that such facets are planar. Here we establish that many attrition facets in carnivoran teeth are not planar. Non-planar attrition facets can, in fact, improve functional characteristics of the teeth such as relief behind occluding blades. We also show how the three-dimensional shape of facets affects the occlusal path of the teeth, which was found to be non-linear in carnivorans. Four morphological groups of carnivorans were examined. It was found that the degree of lateral movement in the chewing cycle was positively related to the number and complexity of the teeth in the tooth row.

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INTRODUCTION

The overarching function of most mammalian teeth is to mechanically process food, and, for a given food, tooth shape is a principal determinant of how effectively they carry out that function. One crucial aspect of the tooth-food interaction is how the teeth interact with each other when they meet, or occlude. However, a severe limitation on studying the fine-scale interactions between teeth during occlusion is that the act of coming into occlusion tends to obscure the very surfaces we are interested in. Occlusion also hides the food being fractured, and so impedes our ability to investigate this aspect.

This problem has been addressed by using proxies for tooth-tooth contact, mainly attrition facets on occluding teeth (Gregory 1920; Butler 1952; Mills 1955, 1967). The relative direction of tooth movement can also be determined by microfracture patterns (Gordon 1984) or dentine basin shape (Greaves 1973). Other techniques that have been used to estimate the position of non-contacting surfaces on opposing teeth include embedding and sectioning casts (Crompton and Hiiemae 1970) and simplified tooth occlusal reconstructions (Evans et al. 2001).

In a parallel set of studies, the jaw movement during mastication has been investigated using cinematographic, cineradiographic and electromyographic techniques (Crompton and Hiiemae 1970; Luschei and Goodwin 1974; Herring 1976; Gorniak and Gans 1980). These approaches have established the general pattern of jaw movement, but they do not allow visualisation of tooth-tooth contact between the postcanine teeth. This is because X-ray images cannot show proximity of teeth normal to the image, i.e., the third dimension is not resolved.

Here, we seek to relate dental occlusion studies to cinematographic studies and look more closely at the relationships between occluding tooth surfaces and the determinants of tooth movement. The current study will test whether observed jaw movements and the opposing tooth shapes themselves are capable of producing observed wear facets on teeth. Studies using dental paper have gone some way to establishing that this is true, but the application of this technique is greatly complicated when using small or highly complex teeth.

When considering jaw movement during mastication, Herring (1993) gave three possible determinants of power stroke direction:

1. the mandible being physically constrained, for example, by pre- and post-glenoid processes surrounding the mandible;

2. the mandible sliding along inclined planes formed either by the teeth or by the craniomandibular joint (CMJ); or

3. precise control of the power stroke by the muscles.

Our aim is to investigate fine-scale movements and relative position of tooth surfaces using three-dimensional reconstructions of jaw movement and tooth occlusion. This will allow us to explore the extent to which the first two factors constrain jaw movement, and therefore to what degree the movement is controlled by musculature only. Incorporating the shape of the jaw joint surfaces will identify whether pre- and post-glenoid processes significantly constrain mandible movement. This technique should achieve more accurate and revealing determinations of the trajectories of tooth movement than have previously been available using cinematography.

Evans and Sanson (2006) constructed models of several tooth forms found in carnivorans, including the carnassial and tribosphenic forms. These models assumed that the occlusal vector, the direction of movement of the lower tooth row with respect to the upper, did not change during an occlusal stroke, and therefore that the occlusal path, the path followed by the teeth during the stroke, was linear. Such tooth movement results in crests with attrition facets that are either planar (if the crest is linear) or like an extruded surface (see figure 4 in Evans and Sanson 2006). An extruded surface is one where a two-dimensional curve has been extended or 'extruded' at right angles to the plane of the curve to form a surface. Such surfaces can be likened to a plane that has been warped in only one direction, like corrugated iron or a curtain. The predominant view among dental workers, as demonstrated by Herring's (1993) description of inclined planes, implies that attrition facets are on the whole planar, and consequently that both the crests (viewed along the occlusal vector) and the occlusal path are linear. Our intention is to investigate the possible shapes of occluding attrition facets, and more specifically how facet shape affects jaw movement.

In this study we reconstruct the jaw and tooth movement in a sample of recent carnivoran species, incorporating tooth and jaw joint shape. We attempted to reconstruct chewing using only jaw rotation around the lateral axis of the condyles and lateral translation of the jaw. This system has been

developed in living mammals, with carnivorans being the principal example, but it is also applicable to fossil organisms.

METHODS

Eight carnivoran species were chosen to include a range of dental and jaw joint morphologies. They fall into four basic morphologies:

Group 1) upper – well-developed carnassial with a very small first molar; lower – only a well-developed carnassial (*Acinonyx jubatus* and *Crocuta crocuta*);

Group 2) upper – scimitar-shaped carnassial and a single molar; lower – carnassial and a single posterior molar (*Mustela lutreola* and *Vormela peregusna*);

Group 3) both upper and lower have a carnassial with two posterior molars (*Canis aureus* and *Alopex lagopus*); and

Group 4) upper – carnassial and two molars; lower – carnassial and a single posterior molar (*Genetta genetta* and *Herpestes ichneumon*).

Carnassial and post-carnassial upper and lower tooth rows of one side were scanned using a Nextec Hawk 3D laser scanner (Evans et al. 2007). These scans are viewable in the MorphoBrowser database, an online dental morphology database (http://morphobrowser.biocenter.helsinki.fi/). Left and right condyle and post-glenoid surfaces and incisor positions were also scanned, maintaining correct relative position and orientation between all features. Tooth surfaces were exported as text point files, interpolated using GIS software (Surfer for Windows v. 8.0, Golden Software, Colorado, USA), and then exported as VRML (Virtual Reality Modelling Language) files. Scans were exported as STL files and converted to VRML using Rhino for Windows v. 3.0 (McNeel, Washington, USA). Upper and lower teeth and joint surfaces were aligned in CosmoWorlds for Windows v. 2.0 (Silicon Graphics, Inc., California, USA), and CosmoWorlds was used for the jaw rotation and translation movements in the occlusal reconstructions.

To simulate the chewing cycle, the lower jaw was first placed at the end of the closing stroke, i.e., centric occlusion, with the condyles placed within the glenoid fossae, protocones within talonid basins (where present) and incisors in a closed position. Figure 1 shows the general setup for the simulations using model upper and lower jaws and teeth at Time 0 (centric occlusion), with four views

of the occluding jaws. The right tooth row was used in the simulation, and so the right side was the working side. The presence of the soft tissue of the joint capsule was accommodated by leaving a small space between the bone joint surfaces. The sagittal cross-section of the condyle was estimated as a circle, and the axis of rotation of the lower jaw passed through the centres of the left and right circles (Figure 1). As the first step in reconstructing the movement of the jaw, the lower jaw was moved in the opposite direction to the normal chewing stroke to allow easier manual alignment of the teeth and jaws. The jaw was rotated downwards to the position where the teeth would first come close to contacting each other. The condyles are held within the glenoid fossae. This leaves a lateral space between the teeth, and so the jaw was translated laterally until the teeth make contact (Figure 1, bottom right). Tooth-tooth contact was estimated to occur when small amounts of one surface passed through the contacting surface – automatic collision detection was not used. The jaw was rotated one or two degrees towards the closed position, and the jaw moved laterally again to maintain very slight contact between the teeth. This was repeated until centric occlusion was achieved. Small necessary adjustments were made to maintain contact between the occluding teeth as the rotation and translation progressed. Additional jaw positions were added to approximate the remaining portions of the chewing cycle, including jaw opening and the initial phase of jaw closing, where there is no tooth-tooth contact. Figure 2 shows the complete chewing cycle for the model jaws and teeth.

Two main measurements of the jaw movement were taken: the angle between initial tooth contact and centric occlusion, and the lateral movement of the jaw between initial tooth contact and centric occlusion. The second of these was standardised by the distance between the outer edges of the two glenoid fossae, termed the outer glenoid fossae distance.

The shape and curvature of the large attrition facets of *Acinonyx* and *Crocuta* were examined by comparing them to a plane in 3D space. Species in Group 1 were examined as they have the largest attrition facets and are the easiest to examine for this part of the study, but this means that the results may not be applicable to the other groups.

RESULTS

The reconstructed tooth and jaw movements for one species of each of the four groups are shown in Figures 3-6. There are four views of the
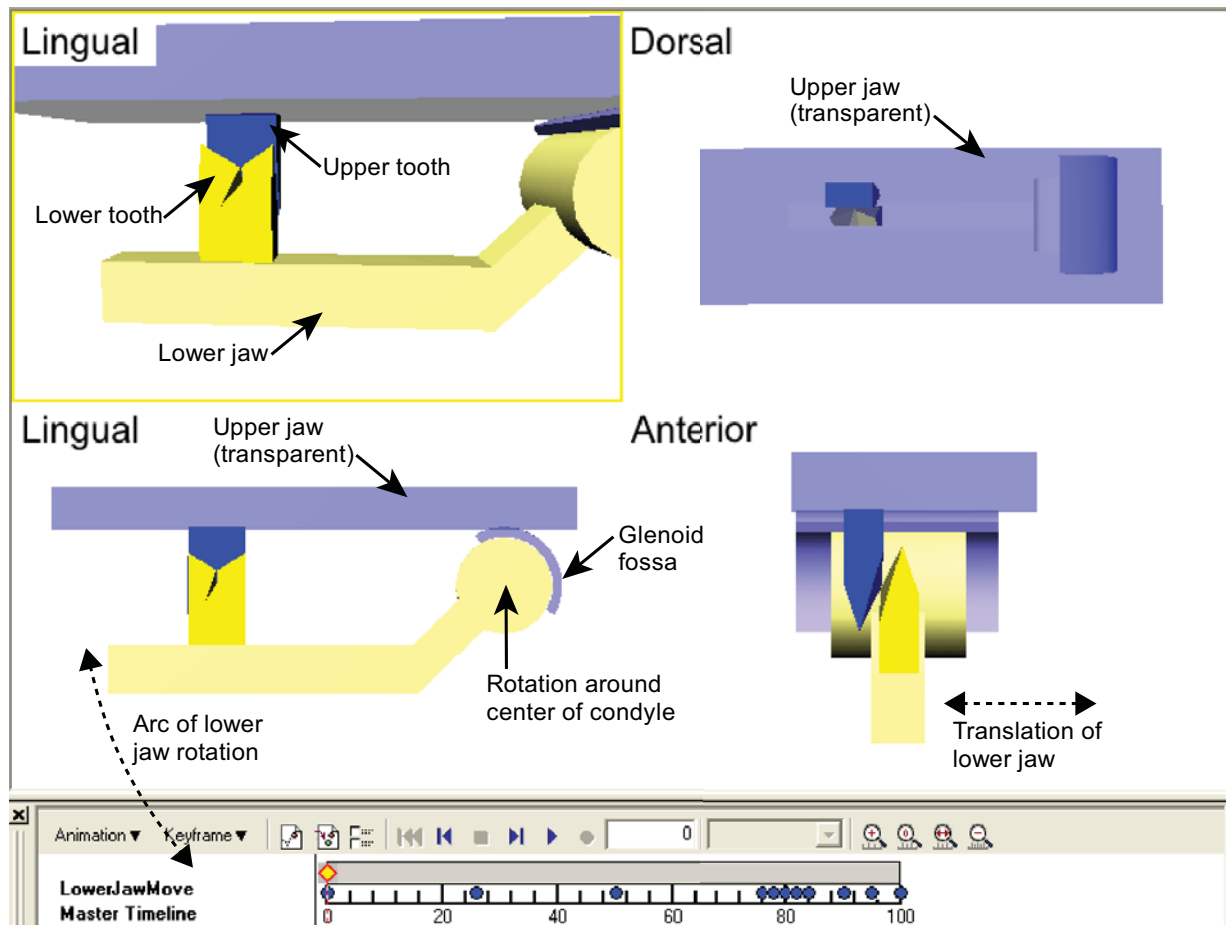
Figure 1. Setup and procedure for tooth movement reconstructions demonstrated using model upper and lower jaws, and model carnassial teeth from Evans and Sanson (2006). Four views of the reconstruction are given: a lingual view of the teeth; a dorsal view of the teeth; a lingual view showing both the teeth and the jaw joint surfaces; and an anterior view of the teeth and right jaw surfaces. Top two views are perspective views (which give a sense of depth and distance between objects), and bottom two views are orthogonal views (which aid in viewing the tooth and joint surfaces at the same time). Lower left shows arc of lower jaw rotation as the lower jaw rotates around the centre of the condyle. The condyle fits within the glenoid fossa of the upper jaw (size of condyle is enlarged for greater clarity). Lower right shows the path of translation of the lower jaw as it sits in the glenoid fossa. Upper teeth in dark blue, upper joint surfaces and jaw in light blue, lower teeth in yellow, lower joint surfaces and jaw in light yellow. Upper jaw is transparent to allow viewing teeth from dorsal.

occluding teeth and jaw joint surfaces shown in each figure. For the same four species, anterior and lateral views of the movement of the protoconid tip during a single chewing cycle are illustrated in Figure 7. After initial tooth contact (IC), the occlusal path tends to be slightly concave towards the beginning of that phase and straighter at the end of the closing phase until centric occlusion (CO). In all species, the main carnassial blades are no longer in contact at centric occlusion; for all but Group 1, other tooth elements are in contact at the end of the closing phase. Table 1 shows that the degree of lateral movement during occlusion was greater for Groups 3 and 4 than the other two groups. However, there was no discernable trend in occlusal closing angle (Table 1).

The large attrition facets of *Acinonyx* and *Crocuta* are not planar – they tend to be slightly convex, with greater curvature towards the tips, particularly for the lower teeth.

DISCUSSION

There are general differences in tooth and jaw movement among the groups examined here, with both the occlusal profile and the degree of lateral movement of the condyle showing that greater lateral excursion of the jaw and teeth occur in Groups
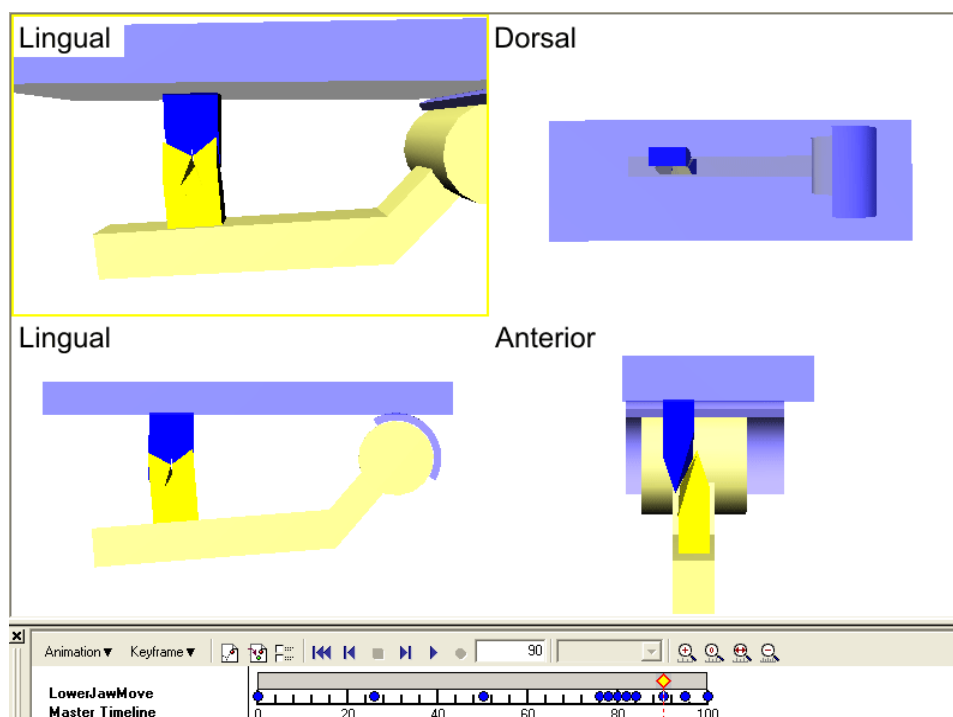
Figure 2. Jaw and postcanine tooth movement reconstruction for model in Figure 1. Teeth and jaws start at centric occlusion (Time 0 in time scale at bottom of figure); jaw then rotates downwards and then moves laterally while rotating (from Time 26) until end of opening stroke (Time 50). Jaw then rotates upwards until teeth meet (Time 76), then jaw rotates and translates while teeth are occluding until centric occlusion is reached (Time 100, identical to Time 0). See Figure 1 for labelling conventions.

3 and 4 compared to Groups 1 and 2. For none of the groups is the occlusal path of the protoconid linear, particularly towards the beginning of the occlusal phase after the teeth make contact, during which the carnassial blades are occluding. Therefore, the occlusal vector changes during the slow-closing phase.

The jaw movement simulated here for these species indicates that the jaw movement is associated with the number of teeth in the tooth row and the approximate complexity of the teeth. The more simple tooth rows (Groups 1 and 2) are those that show more vertical movement, and those with more lateral movement have a greater number of teeth and cusps (Groups 3 and 4). Groups 1 and 2 have fewer teeth (only one or two teeth in each jaw), and these teeth have only two or three main cusps, whereas groups 3 and 4 have a greater number of teeth (two or three in each jaw), which tend to have a larger number of cusps on them (see Figures 3-6). These general differences in complexity are also reflected in quantitative measurements of dental complexity such as orientation patch count (OPC; Evans et al. 2007): species in Groups 1 and 2 have an average OPC of 91 and

56.25 for the upper and lower tooth rows, respectively, while the corresponding values for Groups 3 and 4 are 163 and 115.25.

The domestic cat is the species that is the most applicable comparison with the current study, as it appears to be the only carnivoran in which a detailed study of jaw movement and electromyography during mastication has been carried out (Gorniak and Gans 1980). It is difficult to compare the reconstructions of jaw movement directly to the domestic cat as there is insufficient resolution at the end of the closing stroke using cinematographic methods to determine the fine-scale path of the tooth. However, the sequences generally show a lingual movement of the jaw at the very end of the sequence, which is consistent with these reconstructions.

During the slow-closing phase of these occlusal reconstructions, tooth-tooth contact between the upper and lower tooth rows occurs at the same approximate positions as the major attrition facets on the teeth. It is difficult to be precise about the areas of contact between the teeth in the reconstruction as very high resolution scans could not be used due to limitations of computer power.
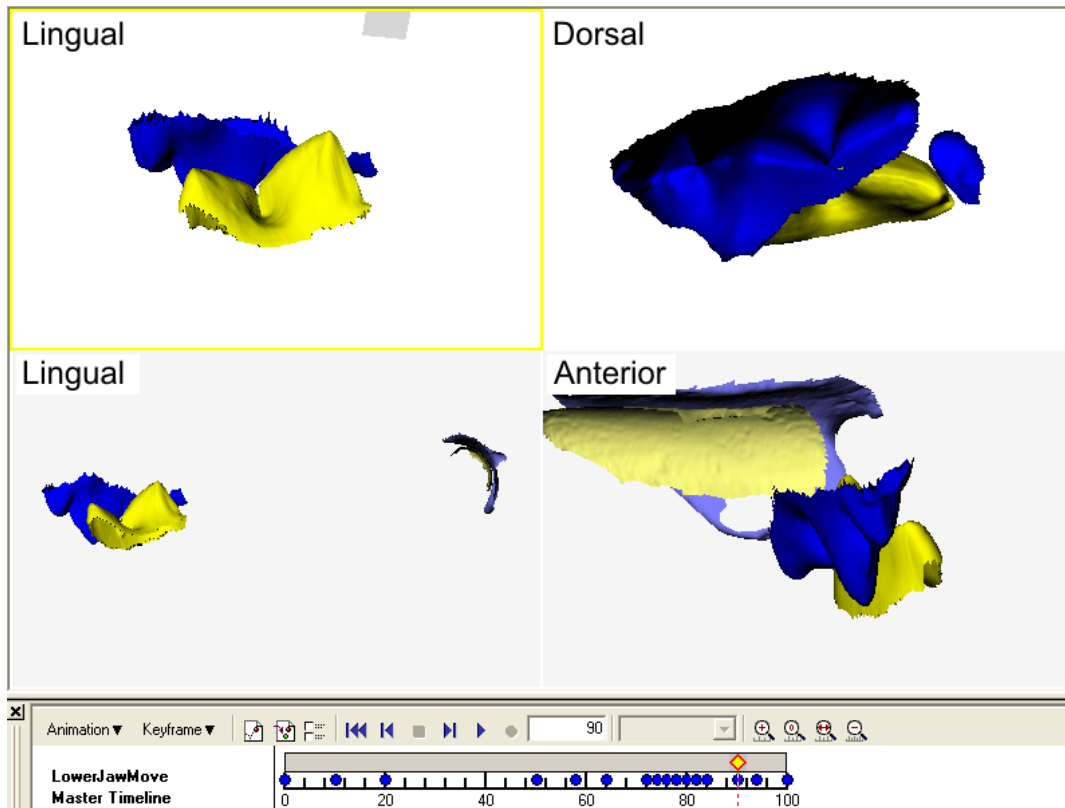
Figure 3. Postcanine tooth movement reconstruction for *Acinonyx jubatus*. Only upper teeth (dark blue), upper joint surfaces (light blue), lower teeth (yellow) and lower joint surfaces (light yellow) are illustrated. See Figures 1-2 for other labelling conventions.

This supports the contention that observed jaw movements are capable of producing the observed wear facets, and therefore, that an examination of these wear facets will reveal a significant amount regarding occlusal relations. Therefore, the incorporation of the three-dimensional position and orientation of both the overall tooth shapes and the attrition facets will bring a much greater understanding to this endeavour.

In this simulated occlusion experiment, it was found that the contact between teeth occurred at the attrition facets on the teeth. Therefore, attrition facet shape greatly influences the occlusal path of the teeth. We also found that the occlusal path is not perfectly linear, and at least some of the attrition facets are not planar. We can examine the possible shapes of occluding facets and their effect on occlusal path and blade occlusion by considering three basic shapes of facets, illustrated for a simple carnassial blade – planar, concave and convex (Figure 8). In order for the blades of one tooth to be able to contact the blade of another during the occlusal stroke, the convex curvature of one surface must be higher than any concave curvature of the opposing surface. Figure 8 shows the four basic combinations of occluding facet shapes that fulfill this criterion and allow contact between the occluding blades – planar-planar, planar-convex, concave-convex and convex-convex (other combinations do not allow contact between occluding blades). For these shapes, only the planar-planar combination of facets gives a linear occlusal path, as shown by the dashed line; the other three combinations result in a curved occlusal path (Figure 8).

For the planar-planar and convex-convex shapes, continual contact will be maintained between the upper and lower blades through the occlusal stroke, giving effective cutting between the blades. However, for the other two combinations illustrated (convex-planar and convex-concave), the blades will be separated at the beginning and/or end of the stroke, depending on the exact shape of the facets. This will presumably lead to inefficient blade-on-blade cutting by these two combinations.
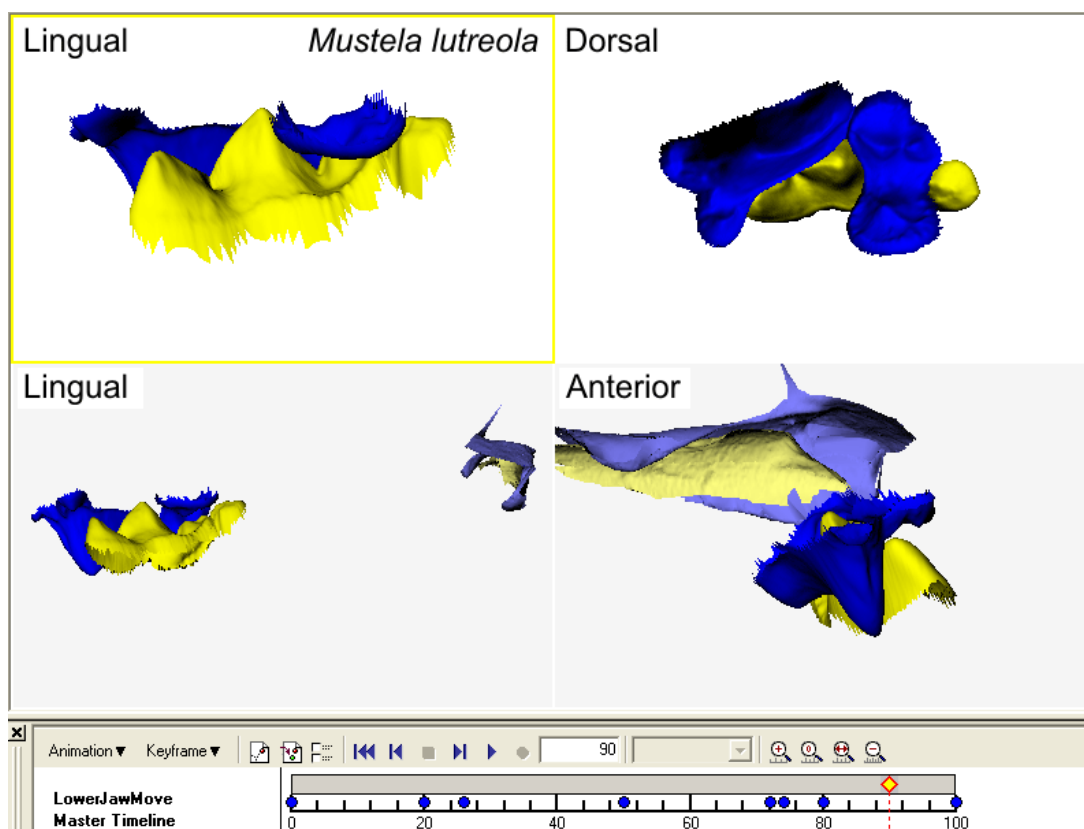
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Figure 4. Tooth movement reconstruction for *Mustela lutreola*. See Figures 1-3 for labelling conventions.

Attrition facets indicate tooth-tooth contact and therefore that there is no relief or space between the trailing surfaces of the blades at that point. In newly-erupted carnivoran teeth, attrition facets are absent. This generally means that there is relief behind the blades, which is functionally desirable as it will reduce jamming or friction between the blades (Evans and Sanson 2003; Evans 2005).

We found that the lower molars in the Group 1 species had a higher facet curvature towards the tips of the cusps. This could aid in initial alignment of the carnassials at the beginning of the stroke. If the attrition facets at the tip of the cusp tended to be flat, very precise alignment would be required to ensure that the opposing blades came into contact close to the tip of the cusps, i.e., the area of the lower tooth that the upper tooth could contact, which we could term the 'target area', is quite small. However, a higher curvature towards the tips of the cusps increases the 'target area' for one blade to align with the other at the beginning of the stroke. This will give a greater tolerance for initial alignment. After that, alignment can be controlled by the opposing facet shapes.The models of car-

nassial tooth shape constructed by Evans and Sanson (2006) have a linear occlusal path, the blades are two-dimensional in that they lie in a plane, and relief behind the blades is generated by curving the relief surface out of the plane in which the blade lies. Substantial tooth-tooth wear on the relief surface of such a tooth (and little wear on the rake or leading surface) would generate a large attrition facet (see figure 7 in Evans 2005). This will be disadvantageous to the function of the tooth, allowing food to be trapped between the relief surfaces, and requiring more force to maintain contact between occluding blades than when there is relief space behind the cutting edge. Many of the specimens examined in this study have large attrition facets (particularly *Acinonyx* and *Crocuta*), implying that there are large areas of tooth-tooth contact, potentially reducing the effectiveness of the teeth. However, the attrition facets for these two species are convex (non-planar), and as the tooth-tooth contact proceeds during the virtual chew, only a small amount of the attrition facet is in contact between the teeth at any one time. This means that the instantaneous facet contact is much lower than the actual facet size, like the convex-convex
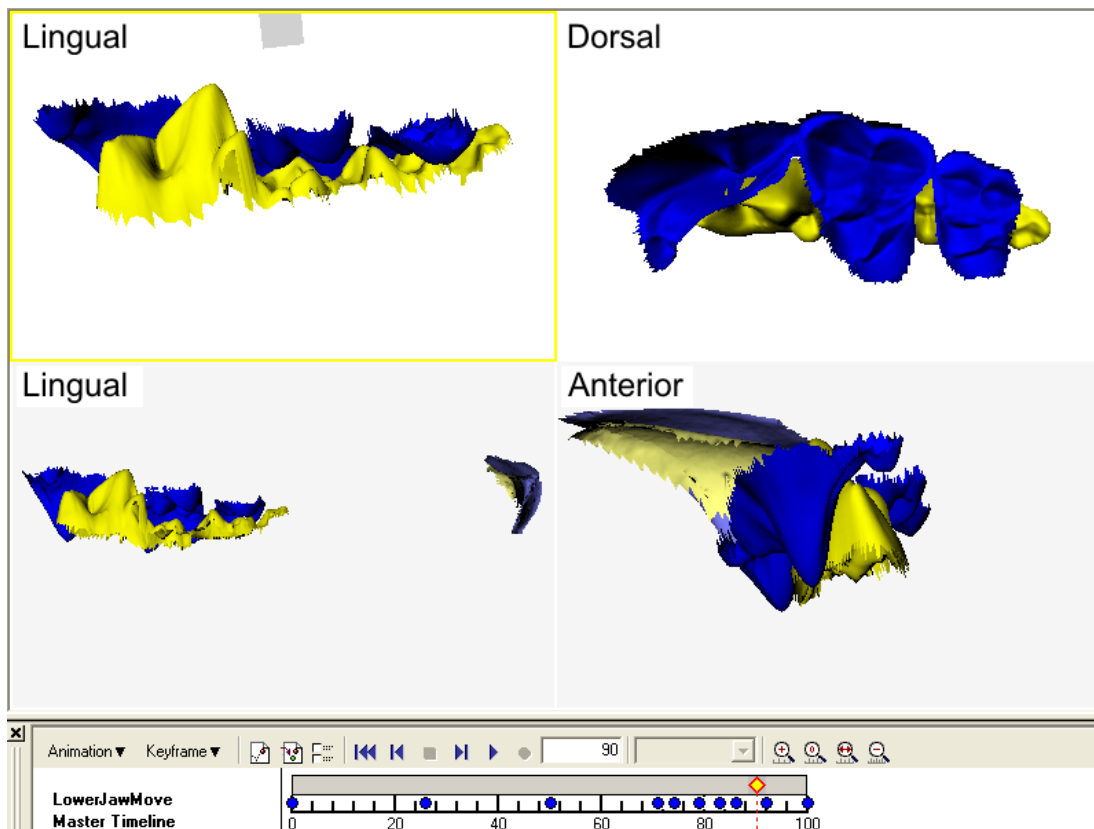
Figure 5. Tooth movement reconstruction for *Canis aureus*. See Figures 1-3 for labelling conventions.

combination in Figure 8. Relief behind the cutting edge is, therefore, maintained due to the reciprocally curved geometry of the attrition facets and the occlusal movement of the teeth. Relief would be present in the convex-planar and convex-concave combinations when the blades are in contact, but on average will be greatest for the convex-convex combination. The facts that the attrition facets for some of these species are not planar, and the occlusal path is not linear, are consistent with one another: non-planar (non-extruded curve) facets would indicate a non-linear occlusal path and vice versa.

The obvious difference between the simplified attrition facets in Figure 8 and those of the real teeth are that there is rotation around a condyle rather than a direct translation up the page, as shown in the figure. Rotation around a condyle would still give a planar surface for a straight crest or a 'fan-shaped' plane for another shape. The curvature of this fan would depend on the distance from the centre of rotation. The occlusion reconstructions demonstrate that if the only rotation allowed is around the lateral axis, then lateral movement of the jaw within the glenoid fossa is required. For those species that appear to show large degrees of lateral jaw movement in these reconstructions, rotation around a second axis, such as the dorso-ventral or mandibular axes, may also occur. Tooth occlusion could then take place without as much lateral translation of the condyles along the glenoid fossae, and this will affect the resulting facet shape. The degree of fusion of the symphysis and mobility at the CMJ will influence how much rotation in other axes is possible. The shape of the jaw joint surfaces could be used to estimate the position and degree of rotation of the jaw. For species with cylindrical joint surfaces, such as Group 1, it is unlikely that much rotation around the vertical or mandibular axis occurs, but for those where the fit between the joint surfaces is not as tight, this is more likely.

A number of limitations in the design of this study should be borne in mind. The tooth and joint positions were scanned from a dry skull, and so post-mortem warping of the skull and mandible means that the positions and orientations of these may have changed. However, the very good fit of most of the teeth during the occlusion stroke suggests that this is not substantial. The necessity of estimating the gap between the jaw joint surfaces to account for the joint capsule also limits the accu-
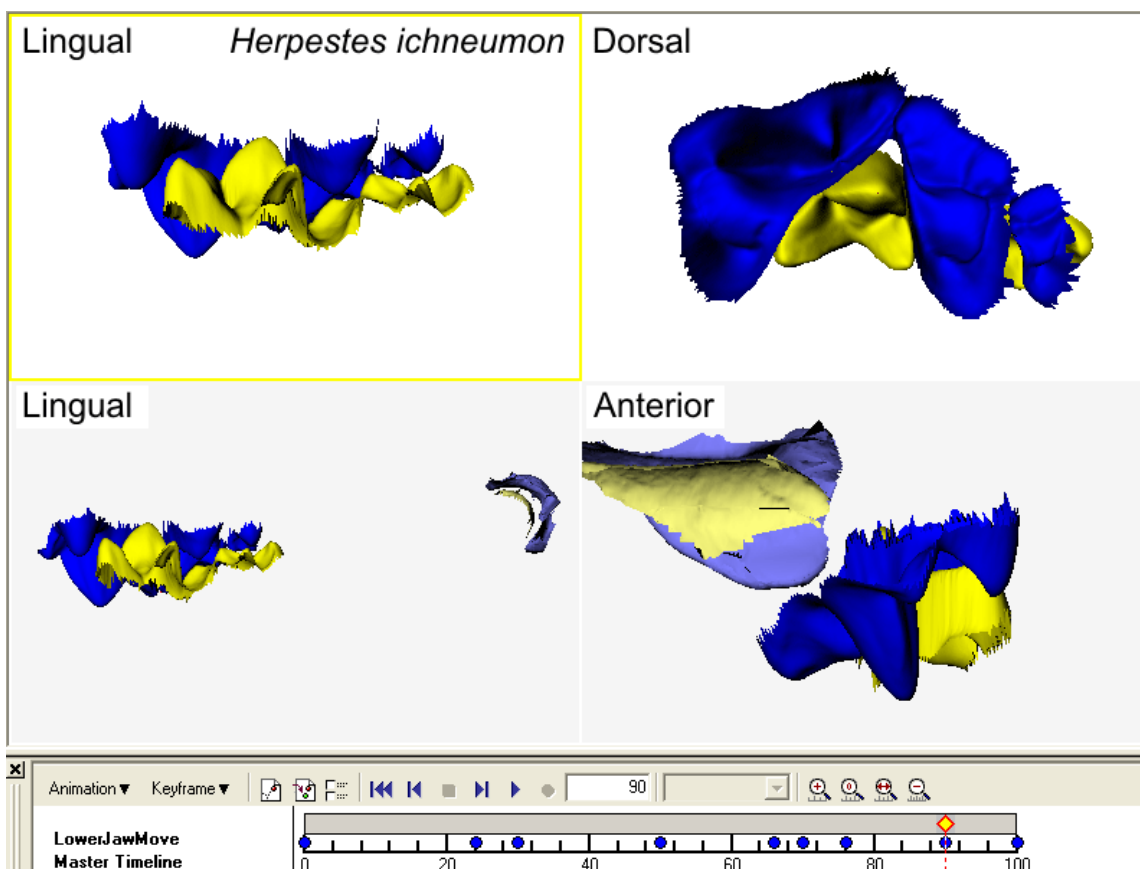
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Figure 6. Tooth movement reconstruction for *Herpestes ichneumon*. See Figures 1-3 for labelling conventions.

racy with which the occlusion in the functioning skull can be simulated. Furthermore, the position and contact between occluding canines has not been modelled in this study. In a number of carnivoran species (as well as in certain primates, suiforms, and representatives of other living and extinct groups), the canine teeth appear to aid guiding the postcanine teeth into occlusion, and limit the lateral excursion of the jaw. Since the main focus of this study was to model how the teeth and jaw move once the postcanine teeth have come into occlusion, this omission should not affect the general findings of the study.

This reconstruction of occlusal dynamics in several carnivoran species has established that both the tooth and jaw joint surfaces provide constraints on occlusion, which were Herring's (1993) first two determinants of power stroke direction, and that they are sufficient to give an occlusal path consistent with that described in previous investigations. However, for some species at least, it is apparent that the tooth facets do not form strict inclined planes, but rather surfaces that are slightly curved, which can often be advantageous for tooth function. More detailed analyses of the three-dimensional shape and movement of the mandible and jaw joints *in vivo* will go further in establishing the fine-scale control and functional consequences of dental occlusion in mammals.

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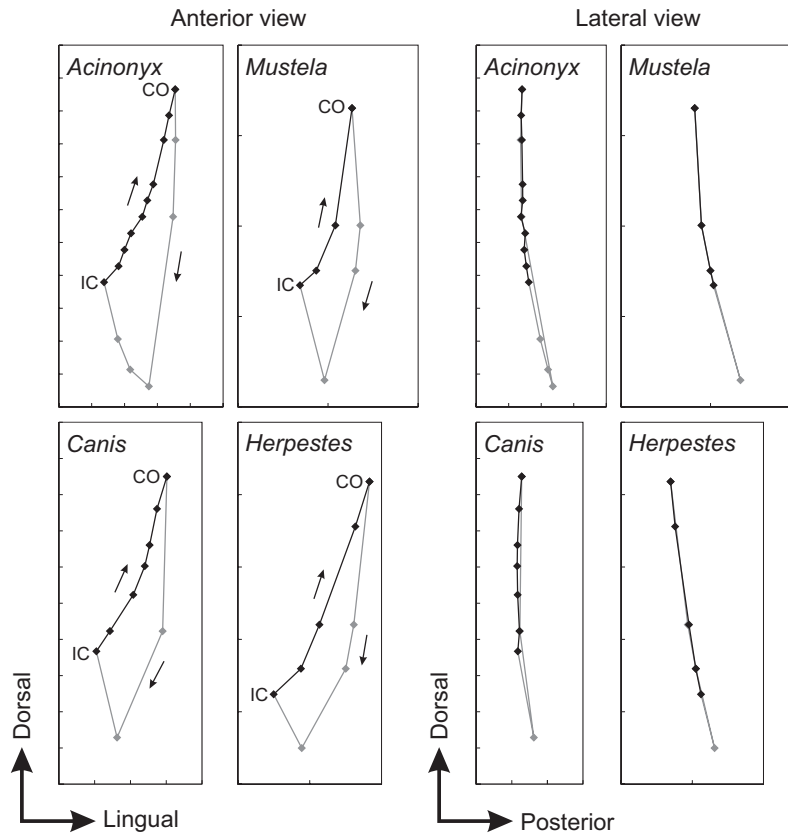
Figure 7. Trace plots of protoconid position for anterior (left) and lateral (right) views of four species for a single cycle of jaw movement. Occlusal path reconstructed when teeth are in occlusion is shown as a black line; jaw positions inserted merely to complete the chewing cycle are shown in grey. Small arrows indicate direction of movement for anterior views. Tick marks are 2 mm apart for all plots. Dorsal, lingual and posterior directions are indicated.

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Table 1. Statistics for occlusal reconstructions of the eight species of Carnivora. Lateral movement is the distance that the jaw moves from initial tooth contact (IC) to centric occlusion (CO), also shown as a proportion of the outer glenoid fossae distance (OGFD). Occlusal closing angle is the angle of rotation of the jaw between IC and OC.

| Group	Species	Lateral movement of jaw (mm)	OGFD (mm)	Lateral movement (%)	Occlusal closing angle (°)
1	*Acinonyx jubatus*	4.33	108.6	3.99	-12.57
	Crocuta crocuta	4.19	123.0	3.40	-19.48
2	*Mustela lutreola*	1.16	34.7	3.33	-12.39
	Vormela peregusna	0.98	28.9	3.39	-12.95
3	*Alopex lagopus*	2.85	56.2	5.07	-13.60
	Canis aureus	3.94	70.0	5.63	-11.55
4	*Genetta genetta*	1.96	34.9	5.62	-10.05
	Herpestes ichneumon	2.67	41.7	6.40	-14.06
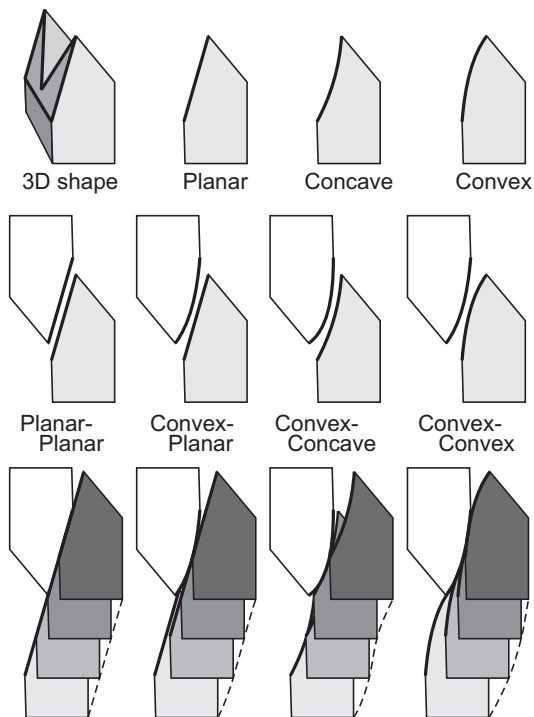
Figure 8. The interaction between facet shape and occlusal path. The attrition facet is outlined by thick line on the '3D shape', and shown as a thick line when viewed side-on in the remainder of the figures. Three basic facet shapes are illustrated – planar, concave and convex. The four allowable combinations of occluding facets are illustrated. The movement of the lower with respect to the upper is shown at the bottom, with successive positions of the lower shown in a darker shade. All combinations other than the planar-planar combination give a curved occlusal path (dashed line). The convex-convex combination gives the highest relief between the blades.