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Abstract: Canine morphology is analysed at seven intervals along the crown in both anteroposterior and lateromedial perspective in seven species of large felids. The puma and the snow leopard have stout, rather conical canines, whereas those of lions, jaguars, and tigers bear substantial resemblance to each other, reflecting their phylogenetic relationships, and are less conical and large. The canines of the leopard are intermediate in morphology between those of the other species, probably reflecting its more generalized diet. The clouded leopard has very large and blade-like canines, which are different from the other analysed species. Canine bending strengths to estimated bite forces appear to differ less among the species than morphology, indicating that the evolution of canines has been constricted with respect to their strength in failure, probably owing to their being equally important for species fitness. However, the clouded leopard again stands out, having a high estimated bite force and rather weak canines in bending about the anteroposterior as well as lateromedial planes compared to the other species. Canine morphology to some extent reflects differences in killing mode, but also appears to be related to the phylogeny. The marked divergence of the clouded leopard is presently not understood.

# Canine morphology in the larger Felidae: implications for feeding ecology

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ADDITIONAL KEYWORDS: bite force – bending strengths – feeding behaviour – Felids.

## INTRODUCTION

Prominent, elongate canines are a major feature of carnivores (Wozencraft, 1989; Nowak, 1991), in particular large species such as large canids and felids. Although there does not appear to be taxon-specific differences in canine lengths between canids and felids of comparable body size (Van Valkenburgh & Ruff, 1987), the largest canines among the extant Carnivora are found in the large *Panthera* species (Turner & Antón, 1997; Christiansen & Adolfsson, 2005).

Canines are important tools for predatory carnivores, not only for dispatching prey, but are also frequently used in feeding (Schaller, 1972; Van Valkenburgh, 1989, 1996), and they appear frequently to have undergone sexual selection for intraspecific agonistic purposes (Gittleman & Van Valkenburgh, 1997). The importance of the canines in carnivore feeding ecology is graphically demonstrated by their frequent heavy wear, or even fracture (Van Valkenburgh, 1988;

Van Valkenburgh & Hertel, 1993; P. Christiansen, pers. observ.). To some extent, this appears to be related to diet because bone-cracking species appear to have higher frequencies of severe dental abrasion or even fractures (Van Valkenburgh, 1988).

In a series of seminal studies, Dayan and colleagues analysed sympatric predator skull morphology, and found strong evidence of character displacements (Brown & Wilson, 1956; Strong, Szyska & Simberloff, 1979) in canine size of small felids (Dayan *et al.*, 1990), canids (Dayan *et al.*, 1989a, 1993) and mustelids (Dayan *et al.*, 1989b; Dayan & Simberloff, 1994), indicating that canine size is a distinguishing factor among similar-sized, sympatric predators. It was suggested that selection acted directly on the important ecological trait, the canine size, because the canines are directly used for dispatching prey, whereas other, frequently cited examples of character displacement (e.g. skull or body sizes) are by-products of selection on canine size.

Extant felids (Felidae: Felinae) are frequently discussed using the vernacular term conical-toothed

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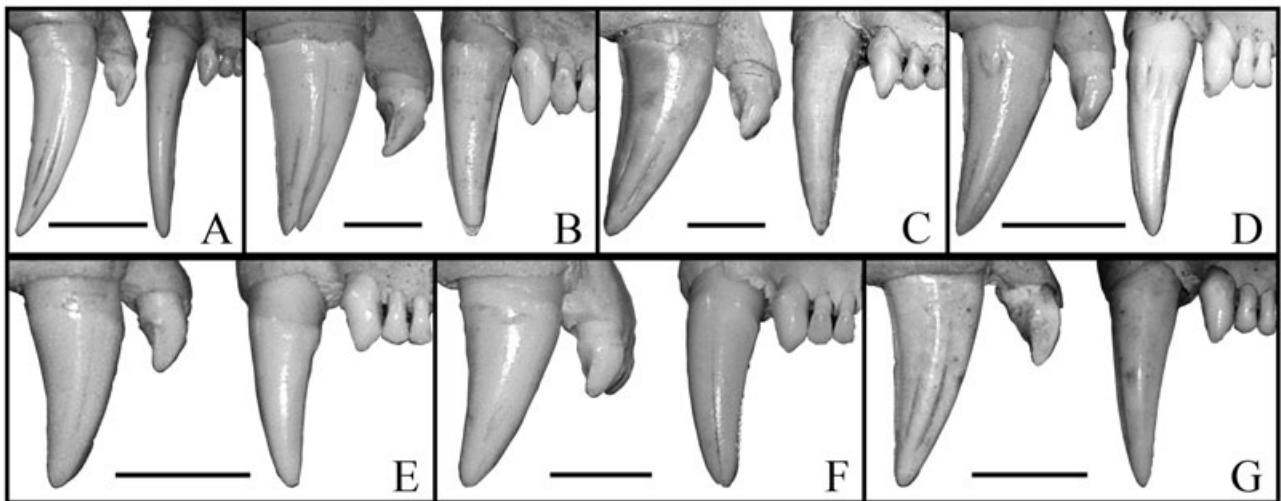
felids, as opposed to the extinct Machairodontinae, which included many sabertooth species (Turner & Antón, 1997). Feline canines are, however, not morphologically uniform, and differences in canine morphology could be expected to correlate with differences in feeding ecology, possibly making such studies an auxiliary tool for analyses of predator ecology. Canine shape in carnivores appears to reflect bite forces and killing mode, and there are marked differences between, for example, canids and felids (Van Valkenburgh & Ruff, 1987; Van Valkenburgh, 1989; Christiansen & Adolfssen, 2005). In the present study, evidence is presented for different canine morphotypes among seven large species of felids based not merely on alveolar dimensions, as traditionally used, but on 15 measurements per crown, reflecting the overall morphology of the tooth.

### MATERIAL AND METHODS

One hundred and forty-nine specimens of seven large extant felid species were analysed (Appendix 1; Fig. 1), 28 specimens of the puma (*Puma concolor* Linnaeus 1771), 18 clouded leopards (*Neofelis nebulosa* Griffiths 1821), 17 lions (*Panthera leo* Linnaeus 1758), 20 jaguars (*Panthera onca* Linnaeus 1758), 26 leopards (*Panthera pardus* Linnaeus 1758), of which 14 were from India (*Panthera pardus fusca*) and 12 were from sub-Saharan Africa (*Panthera pardus pardus*; Uphyrkina *et al.*, 2001), 28 tigers (*Panthera tigris* Linnaeus 1758) with specimens from six of the eight traditionally recognized subspecies (Mazák, 1981;

Nowak, 1991; but see also Kitchener, 1999), and 12 snow leopards (*Panthera uncia* Schreber, 1775). The present study required canines that were not broken, chipped or otherwise damaged, which is a frequent occurrence among larger carnivores (Van Valkenburgh, 1988; P. Christiansen, pers. observ.). The clouded leopard has recently been found to share a number of morphological traits with those of less derived sabertoothed felids (Christiansen, 2006), and, accordingly, four species of derived sabertoothed felids were included for comparative purposes only with the canine morphology of the former (Appendix 1).

Each specimen was photographed in direct lateral and anterior views with a scale ruler (mm) and the digital images were loaded into Adobe Photoshop (Adobe Inc.), where the dimensions of the canines were measured. The measurements used were: crown height in a straight line from the alveolar margin to the apex, and the anteroposterior and lateromedial diameters of the crown at the alveolar margin, and at 15%, 30%, 45%, 60%, 75% and 90% of crown height, respectively, counting from the alveolar margin. For comparative purposes, the canines of four specimens of derived species of extinct sabertoothed felids (Machairodontinae: *Homotherium serum*, *Megantreion cultridens*; *Smilodon fatalis* and *Smilodon populator*) were analysed for comparison with the clouded leopard because this animal has a number of skull features in common with machairodont felids to the exclusion of all other extant felids, including, among others, rather blade-like upper canines (Christiansen, 2006; Therrien, 2005).



**Figure 1.** Comparative morphology of felid canines in direct lateral and anterior perspectives, respectively, all scaled to approximately the same crown height. A, clouded leopard (*Neofelis nebulosa*) CN35; B, lion (*Panthera leo*) CN2113; C, Sumatran tiger (*Panthera tigris sumatrae*) BM39.335; D, snow leopard (*Panthera uncia*) CN4321; E, puma (*Puma concolor*) CN1451; F, jaguar (*Panthera onca*) CN5659; G, African leopard (*Panthera pardus pardus*) CN3980. Scale bars = 2 cm.

The bending strength of the canines was calculated in accordance with Van Valkenburgh & Ruff (1987). Each canine was modelled as a cantilever, a solid beam of homogenous material properties with an elliptical cross section fixed at one end (the alveolus). This model makes the assumption of modelling the canines as straight beams (Fig. 1). Additionally, the method assumes that the material properties among species are identical, which appears reasonable given the fairly uniform material properties of teeth (Waters, 1980). The maximum stress in a cross section of such a beam is:

$$\sigma_{\max} = M_y/I \quad (1)$$

where  $M$  is the bending moment at distance  $y$  from the neutral axis of the section to the exterior edge, and  $I$  is the second moment of area. The bending moment is equal to applied force times the distance from force application to the section in question and, thus, the bending moment will be highest around the tooth base because force is assumed to be applied at the tip when biting into an object. Accordingly, application of force perpendicular to the longitudinal axis of the canine implies that the bending moment will be equal to force times canine height. The second moments of area for bending about the anteroposterior (AP) and lateromedial (LM) axes are calculated as:

$$I_{AP} = (\pi * x * y^3) / 4 \quad (2)$$

$$I_{LM} = (\pi * y * x^3) / 4 \quad (3)$$

where  $x$  is the anteroposterior radius and  $y$  is the lateromedial radius of the canine, measured at the gumline. Peak bending strength is estimated as the inverse of peak stress, so the bending strength ( $S$ ) of the canines is calculated as:

$$S_{AP} = I_{AP} / hy \quad (4)$$

$$S_{LM} = I_{LM} / hx \quad (5)$$

where  $h$  is crown height. In Van Valkenburgh & Ruff (1987) and Christiansen & Adolfssen (2005),  $h$  equaled total crown height but, in the present study it is variable because the bending resistance is calculated at seven intervals along the canine long axis. The model only addresses bending stresses and ignores shearing stresses because studies have shown this factor to account for only a modest amount of overall stress (Van Valkenburgh & Ruff, 1987).

The model eqns 4 and 5 assume equal bite forces among all species, but this is of course not the case because some species are much larger than others. Incorporation of estimated bite forces into this model often changes the results obtained (Christiansen & Adolfssen, 2005). Christiansen (2007) calculated estimated bite forces (N) at the canines for 11 species of extant felids including, among others, the seven spe-

cies of large felids included in the present study. His averages were used in the present study to compare to the bending strengths along the seven points of the canine crown. It was assumed that the applied force traveled perpendicular through the crown long axis. Incorporation of estimated bite forces thus changes eqns 4 and 5 into the actual bending strength of the teeth (Van Valkenburgh & Ruff, 1987)

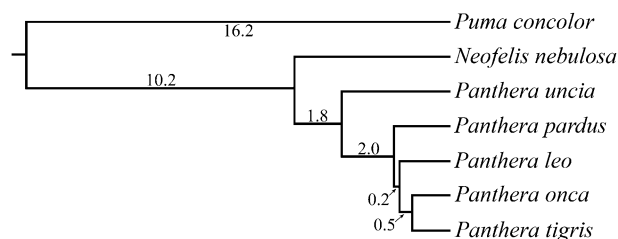
$$S_{AP} = I_{AP} / hyBF \quad (7)$$

$$S_{LM} = I_{LM} / hxBF \quad (8)$$

where  $BF$  is the estimated bite force.

The ratios of anteroposterior and lateromedial diameters, respectively, along the crown to crown height and to each other were compared among the species by means of one-way analysis of variance and post-hoc Tukey's HSD tests for non-equal sample sizes on arcsine (or angular) transformed values because this transformation procedure is appropriate for ratios (Sokal & Rohlf, 1995; Fowler, Cohen & Jarvis, 2003). The values measured from the digital images were also used in a multivariate principal components analysis (PCA).

Finally, the calculated bending strengths along the crown were regressed against estimated bite forces by means of phylogenetic independent contrasts, which corrects for phylogenetic bias (Garland *et al.*, 1993). This procedure calculates regressions through the origin and, accordingly, no intercept, and the results in the present study are given with 95% confidence limits for the slopes (Garland & Ives, 2000). Phylogenetic topology and inferred split ages between the taxa were taken from Mattern & McLennan (2000) and Bininda-Emonds *et al.* (1999) (Fig. 2). Prior to analyses, the contrasts must be standardized (i.e. brought to a common variance by dividing each contrast by the square root of the sum of the branch lengths that make up the contrast, implying that the common variance of the contrasts are independent of branch lengths). Evaluation of proper standardization was performed by generating plots of standardized contrasts to their standard deviations. This remains the best understood diagnostic of proper standardization (Garland, Harvey & Ives, 1992; Diaz-Uriarte & Garland, 1996) and plots



**Figure 2.** Topology of relationships with split ages in millions of years of the included species.

**Table 1.** Averages in mm and standard deviations, with the percentage of anteroposterior and lateromedial diameters of crown height in parentheses

CH	Alveole	15%	30%	45%
<b>Anteroposterior diameters</b>				
28.57 ± 4.25	12.85 ± 1.75 (45.10)	12.68 ± 1.74 (44.50)	11.70 ± 1.64 (41.01)	9.87 ± 1.49 (34.59)
32.77 ± 3.34	11.49 ± 1.58 (35.00)	11.07 ± 1.40 (33.77)	10.14 ± 1.27 (30.97)	9.01 ± 1.13 (27.50)
49.86 ± 5.95	23.30 ± 2.77 (46.77)	22.40 ± 2.59 (45.00)	20.37 ± 2.39 (40.91)	17.35 ± 2.17 (34.82)
41.63 ± 4.74	19.12 ± 2.46 (45.94)	18.55 ± 2.39 (44.59)	17.12 ± 2.09 (41.18)	14.72 ± 1.79 (35.42)
34.44 ± 4.07	14.72 ± 1.80 (42.78)	14.00 ± 1.66 (40.68)	12.89 ± 1.44 (37.50)	11.16 ± 1.17 (32.51)
50.82 ± 7.49	24.28 ± 3.41 (47.87)	23.41 ± 3.15 (46.18)	21.22 ± 2.74 (41.91)	18.67 ± 2.31 (36.92)
28.61 ± 2.77	11.85 ± 1.07 (41.48)	11.51 ± 1.12 (40.27)	10.48 ± 1.08 (36.67)	9.02 ± 0.92 (31.59)
72.97	34.56 (47.35)	32.63 (44.71)	28.96 (39.68)	23.75 (32.54)
93.77	24.60 (26.23)	23.63 (25.19)	22.53 (24.03)	20.22 (21.56)
143.85	44.22 (30.74)	40.73 (28.32)	35.23 (24.49)	33.39 (23.21)
159.60	42.83 (26.83)	45.21 (28.33)	43.01 (26.95)	37.34 (23.39)
<b>Lateromedial diameters</b>				
	11.70 ± 1.84 (41.07)	11.65 ± 1.83 (40.90)	10.71 ± 1.88 (37.52)	9.07 ± 1.77 (31.74)
	8.24 ± 0.98 (25.18)	8.01 ± 0.96 (24.47)	7.14 ± 0.82 (21.86)	6.17 ± 0.72 (18.92)
	18.29 ± 1.99 (36.88)	18.01 ± 2.05 (36.31)	16.23 ± 1.88 (32.65)	13.92 ± 1.68 (27.97)
	15.92 ± 1.98 (38.32)	15.70 ± 2.00 (37.79)	14.70 ± 2.04 (35.36)	12.46 ± 1.66 (29.98)
	12.44 ± 1.56 (36.26)	11.97 ± 1.50 (34.83)	10.39 ± 1.37 (30.20)	8.79 ± 1.07 (25.57)
	19.74 ± 2.45 (39.02)	19.39 ± 2.47 (38.33)	17.70 ± 2.56 (34.92)	14.97 ± 2.15 (29.56)
	11.06 ± 1.24 (38.70)	10.85 ± 1.20 (37.95)	9.51 ± 0.96 (33.28)	8.04 ± 0.87 (28.15)
	15.78 (21.63)	14.33 (19.64)	12.31 (16.87)	11.31 (15.49)
	13.52 (14.41)	13.35 (14.23)	11.80 (12.57)	10.42 (11.11)
	24.65 (17.14)	26.67 (18.53)	23.57 (16.38)	18.60 (12.93)
	19.03 (11.92)	20.52 (12.85)	18.44 (11.55)	16.06 (10.06)

CH, canine crown height.

should show no discernible structure and, accordingly, a very low correlation. Analyses were carried out with raw (i.e. unmodified) branch lengths and, in case of correlation ( $r = 0.05$ ), the branch lengths were transformed to square root, cube root or Pagel's arbitrary method (Pagel, 1992).

## RESULTS

The tiger has the largest canines of the analysed felids (Table 1; average 50.8 mm), followed closely by the lion (49.9 mm), the jaguar (41.6 mm), the leopard (34.4 mm), the clouded leopard (32.8 mm), and the snow leopard and puma (both 28.6 mm). The tiger has far larger ( $P < 0.001$ ) canines than any other felid, save the lion ( $P = 0.997$ ), and the lion likewise. The jaguar has far larger ( $P < 0.001$ ) canines than the leopard, clouded leopard, snow leopard, and puma. The leopard has significantly larger canines than the snow leopard ( $P = 0.018$ ) and the puma ( $P < 0.000$ ), but similar to those of the considerably smaller clouded leopard ( $P = 0.936$ ). Although distinctly longer on average, the canines of the clouded leopard are insignificantly larger than those of the puma ( $P = 0.091$ ) and the

snow leopard ( $P = 0.299$ ) and the averages in the two latter species are virtually identical ( $P > 0.999$ ).

Among extant large felids, the clouded leopard stands out, having canines which are relatively thin compared to crown height, in particular in the lateromedial plane (Table 1; Fig. 3A, B). Indeed, the clouded leopard has highly significantly thinner canines along their entire length than any other large felid, with most  $P$ -values being below 0.001 (Table 2). The values in the anteroposterior plane in the clouded leopard and the dirk-toothed sabertooths (*Megantereon*, *Smilodon*) appear broadly similar, but are only nonsignificantly different at the distalmost end (Table 2). The scimitar-toothed form (*Homothe-rium*), however, has anteroposterior diameters to crown height that do not appear to be particularly different from the large extant felids, but which are significantly higher than those of the clouded leopard. The lateromedial diameters of all the sabertooths are highly significantly different from both the clouded leopard and all other extant felids. Overall, the clouded leopard has distinctly long and slender canines but does not, however, share the proportions of derived sabertoothed cats.

60%	75%	90%	
8.20 ± 1.15 (28.79)	6.43 ± 0.87 (22.59)	4.20 ± 0.56 (14.79)	<i>Puma concolor</i>
7.78 ± 0.89 (23.76)	6.12 ± 0.68 (18.72)	3.78 ± 0.52 (11.54)	<i>Neofelis nebulosa</i>
14.63 ± 1.67 (29.40)	11.31 ± 1.39 (22.71)	7.45 ± 1.08 (14.97)	<i>Panthera leo</i>
12.35 ± 1.40 (29.71)	9.87 ± 1.04 (23.75)	6.56 ± 0.66 (15.81)	<i>Panthera onca</i>
9.51 ± 0.99 (27.68)	7.31 ± 0.89 (21.29)	4.58 ± 0.66 (13.36)	<i>Panthera pardus</i>
16.07 ± 2.36 (31.69)	12.56 ± 1.99 (24.75)	7.63 ± 0.98 (15.12)	<i>Panthera tigris</i>
7.63 ± 0.95 (26.73)	5.95 ± 0.59 (20.82)	3.90 ± 0.40 (13.65)	<i>Panthera uncia</i>
20.95 (28.70)	15.06 (20.63)	10.14 (13.89)	<i>Homotherium serum</i>
18.02 (19.22)	14.01 (14.94)	8.77 (9.35)	<i>Megantereon cultridens</i>
29.91 (20.79)	24.04 (16.71)	17.25 (11.99)	<i>Smilodon fatalis</i>
31.66 (19.84)	26.36 (16.51)	18.12 (11.35)	<i>Smilodon populator</i>
7.50 ± 1.35 (26.31)	5.96 ± 0.85 (20.97)	4.25 ± 0.51 (14.99)	<i>Puma concolor</i>
5.30 ± 0.72 (16.22)	4.31 ± 0.50 (13.20)	2.95 ± 0.28 (9.04)	<i>Neofelis nebulosa</i>
12.05 ± 1.33 (24.25)	9.77 ± 1.18 (19.70)	6.72 ± 0.74 (13.54)	<i>Panthera leo</i>
10.59 ± 1.34 (25.49)	8.80 ± 1.09 (21.18)	6.45 ± 0.62 (15.58)	<i>Panthera onca</i>
7.54 ± 0.96 (21.91)	6.05 ± 0.82 (17.56)	4.10 ± 0.49 (11.95)	<i>Panthera pardus</i>
12.62 ± 1.71 (24.93)	10.13 ± 1.25 (20.04)	6.74 ± 0.80 (13.35)	<i>Panthera tigris</i>
6.93 ± 0.78 (24.25)	5.76 ± 0.78 (20.13)	3.91 ± 0.50 (13.69)	<i>Panthera uncia</i>
9.52 (13.04)	7.67 (10.51)	5.37 (7.36)	<i>Homotherium serum</i>
9.13 (9.73)	7.66 (8.17)	5.34 (5.69)	<i>Megantereon cultridens</i>
16.90 (11.74)	14.88 (10.35)	12.25 (8.51)	<i>Smilodon fatalis</i>
14.42 (9.04)	11.60 (7.27)	9.07 (5.68)	<i>Smilodon populator</i>

The opposite extreme is represented by the jaguar, which has rather long canines, and the puma, which has rather short canines (Table 1; Fig. 3A, B). The puma frequently has proportionally stouter canines than even the lion and tiger, in particular along the mid part of the crown (Table 2), whereas the difference to the jaguar is only statistically significant at the lateromedial diameter at 15% of crown height, where the puma has a slightly (Table 2:  $P = 0.017$ ) higher average (Table 1). The stoutness of the pumas canines compared to the lion and tiger is, however, present along the lateromedial plane, whereas the values along the anteroposterior plane are broadly comparable (Tables 1, 2). The puma thus appears to have rather short, thick canines with a rather spike-like morphology, contrasting sharply with the knife-like canines of the clouded leopard.

Canine stoutness in the jaguar is broadly comparable to the values in the lion and tiger along both the anteroposterior and lateromedial axes (Tables 1, 2; Fig. 3A, B). These three species form a clade of their own (Fig. 2). By contrast, the leopard has distinctly more slender canines than the three large *Panthera* species, although the differences are usually more significant compared to corresponding values in the

jaguar and tiger than in the lion (Table 2). In anteroposterior aspect, the distal, although not the proximal part of the canine, is significantly stouter in the tiger than the lion (Tables 1, 2). The snow leopard has significantly more slender canines along the anteroposterior axis than the other *Panthera* species, save the leopard, but the differences along the lateromedial axis are less significant (Table 2).

The above pattern is broadly duplicated when analysing the cross-sectional geometry along the crown (the lateromedial to anteroposterior diameters; Table 3; Fig. 3C). The clouded leopard has far more blade-like canines than any of the other species, although highly significantly less so than the advanced sabertooth machairodont felids (Table 4). Although *Neofelis* has distinctly less bladelike upper canines than the derived machairodonts, its upper canines bear substantially closer resemblance to those of primitive machairodonts, such as *Paramachairodus* and *Nimravides* (Salesa *et al.*, 2005; Christiansen, 2006).

The puma and snow leopard have by far the least blade-like upper canines and, in these forms, the short upper canines have an almost round cross section along the entire crown (Table 3). In both species, the

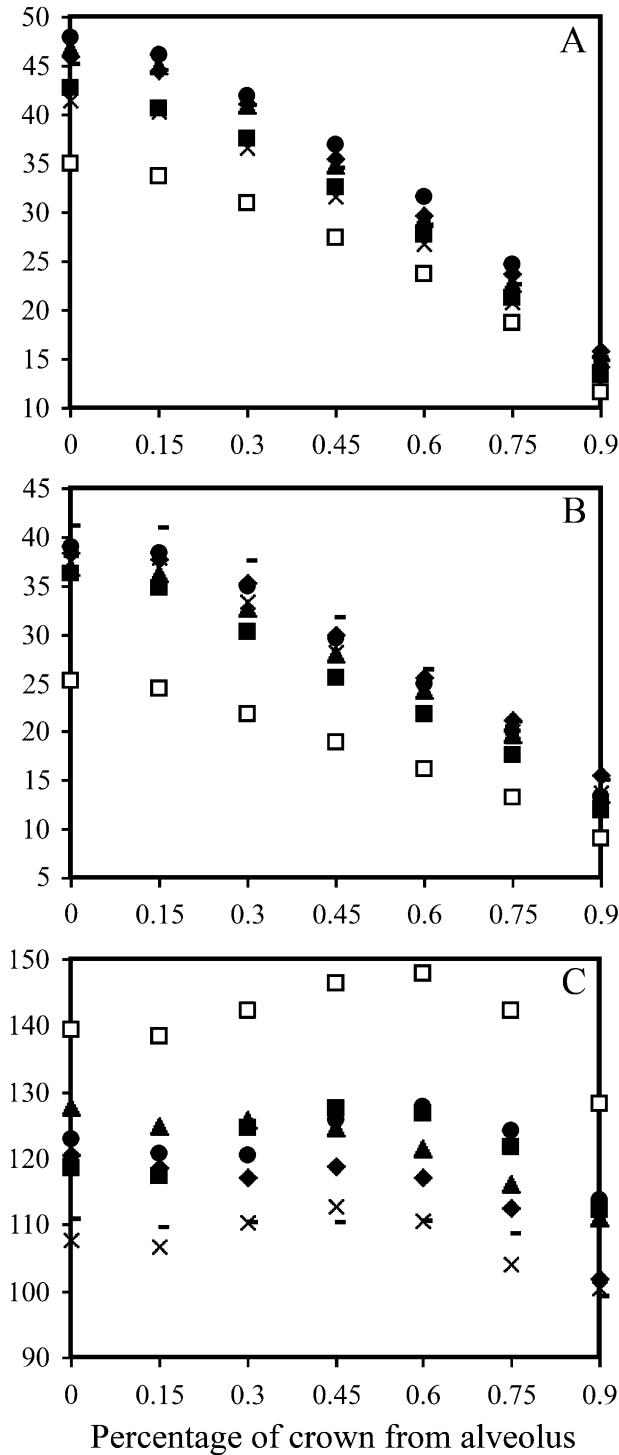
**Table 2.** One-way analysis of variance *F*-statistics and post-hoc Tukey's HSD comparisons of ratios of anteroposterior and lateromedial diameters, respectively, to crown height

Alveolus	Anteroposterior diameter							Lateromedial diameter						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	<i>F</i> = 61.556; <i>P</i> = 0.000							<i>F</i> = 52.444; <i>P</i> = 0.000						
1	1.000							1.000						
2	0.000	1.000						0.000	1.000					
3	0.305	0.000	1.000					0.001	0.000	1.000				
4	0.912	0.000	0.952	1.000				0.072	0.000	0.836	1.000			
5	0.011	0.000	0.000	0.000	1.000			0.000	0.000	0.997	0.346	1.000		
6	0.001	0.000	0.790	0.116	0.000	1.000		0.250	0.000	0.337	0.991	0.033	1.000	
7	0.000	0.000	0.000	0.000	0.747	0.000	1.000	0.381	0.000	0.759	1.000	0.333	1.000	1.000
	<i>F</i> = 67.556; <i>P</i> = 0.000							<i>F</i> = 59.589; <i>P</i> = 0.000						
1	1.000							1.000						
2	0.000	1.000						0.000	1.000					
3	0.994	0.000	1.000					0.000	0.000	1.000				
4	1.000	0.000	0.998	1.000				0.017	0.000	0.793	1.000			
5	0.000	0.000	0.000	0.000	1.000			0.000	0.000	0.752	0.029	1.000		
6	0.115	0.000	0.672	0.246	0.000	1.000		0.047	0.000	0.362	0.997	0.001	1.000	
7	0.000	0.000	0.000	0.000	0.999	0.000	1.000	0.113	0.000	0.810	1.000	0.070	1.000	1.000
	<i>F</i> = 64.195; <i>P</i> = 0.000							<i>F</i> = 67.157; <i>P</i> = 0.000						
1	1.000							1.000						
2	0.000	1.000						0.000	1.000					
3	1.000	0.000	1.000					0.000	0.000	1.000				
4	1.000	0.000	1.000	1.000				0.171	0.000	0.081	1.000			
5	0.000	0.000	0.000	0.000	1.000			0.000	0.000	0.096	0.000	1.000		
6	0.738	0.000	0.769	0.921	0.000	1.000		0.021	0.000	0.153	0.999	0.000	1.000	
7	0.000	0.000	0.000	0.000	0.928	0.000	1.000	0.001	0.000	0.997	0.482	0.036	0.683	1.000
	<i>F</i> = 43.532; <i>P</i> = 0.000							<i>F</i> = 54.003; <i>P</i> = 0.000						
1	1.000							1.000						
2	0.000	1.000						0.000	1.000					
3	1.000	0.000	1.000					0.000	0.000	1.000				
4	0.853	0.000	0.981	1.000				0.332	0.000	0.274	1.000			
5	0.007	0.000	0.010	0.000	1.000			0.000	0.000	0.058	0.000	1.000		
6	0.001	0.000	0.029	0.222	0.000	1.000		0.056	0.000	0.475	0.999	0.000	1.000	
7	0.001	0.000	0.001	0.000	0.875	0.000	1.000	0.003	0.000	1.000	0.524	0.078	0.744	1.000

60%	$F = 36.248; P = 0.000$							$F = 56.196; P = 0.000$						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	1.000	1.000	1.000					1.000	1.000					
	0.000	0.937	0.000					0.000	0.040	0.000	1.000			
	0.937	0.000	0.999	1.000				0.885	0.000	0.595	1.000			
	0.370	0.000	0.063	0.007	1.000			0.000	0.000	0.007	0.000	1.000		
	0.000	0.000	0.003	0.011	0.000	1.000		0.246	0.000	0.948	0.977	0.000	1.000	
	0.028	0.000	0.003	0.000	0.749	0.000	1.000	0.103	0.000	1.000	0.712	0.024	0.972	1.000
75%	$F = 30.999; P = 0.000$							$F = 59.315; P = 0.000$						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	1.000	1.000	1.000					1.000	1.000					
	0.000	1.000	1.000					0.000	1.000					
	1.000	0.000	1.000					0.200	0.000	1.000				
	0.202	0.000	0.486	1.000				0.999	0.000	0.116	1.000			
	0.057	0.000	0.080	0.000	1.000			0.000	0.000	0.001	0.000	1.000		
	0.000	0.000	0.002	0.426	0.000	1.000		0.434	0.000	0.993	0.270	0.000	1.000	
	0.030	0.006	0.037	0.000	0.983	0.000	1.000	0.808	0.000	0.993	0.634	0.000	1.000	1.000
90%	$F = 20.770; P = 0.000$							$F = 69.285; P = 0.000$						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	1.000	1.000	1.000					1.000	1.000					
	0.000	1.000	1.000					0.000	1.000					
	1.000	0.000	1.000					0.003	0.000	1.000				
	0.198	0.000	0.576	1.000				0.681	0.000	0.000	1.000			
	0.003	0.000	0.005	0.000	1.000			0.000	0.000	0.000	0.000	1.000		
	0.980	0.000	1.000	0.664	0.000	1.000		0.000	0.000	0.999	0.000	0.000	1.000	
	0.260	0.001	0.198	0.001	0.994	0.054	1.000	0.039	0.000	1.000	0.001	0.001	0.987	1.000
<i>Neofelis</i> and machairodont felids														
	Hs	Mc	Sf	Sp				Hs	Mc	Sf	Sp			
	Alveolus	0.000	0.000	0.000			Alveolus	0.000	0.000	0.000	0.000			
	15%	0.000	0.000	0.000			15%	0.000	0.000	0.000	0.000			
	30%	0.000	0.000	0.007	0.000		30%	0.000	0.000	0.000	0.000			
	45%	0.000	0.000	0.000	0.000		45%	0.000	0.000	0.000	0.000			
	60%	0.000	0.000	0.000	0.000		60%	0.000	0.000	0.000	0.000			
	75%	0.000	0.000	0.000	0.000		75%	0.000	0.000	0.000	0.000			
	90%	0.000	0.000	0.152	0.626		90%	0.000	0.000	0.000	0.000			

1, Puma (*Puma concolor*); 2, clouded leopard (*Neofelis nebulosa*); 3, lion (*Panthera leo*); 4, jaguar (*Panthera onca*); 5, leopard (*Panthera pardus*); 6, tiger (*Panthera tigris*); 7, snow leopard (*Panthera uncia*).  
Hs, *Homotherium serum*; Mc, *Megantereon cultridens*; Sf, *Smilodon fatalis*; Sp, *Smilodon populator*.





**Figure 3.** Average ratios in percentage at seven intervals along the canine crown. A, canine anteroposterior diameter to crown height; B, canine lateromedial ratios to crown height; C, canine anteroposterior diameter to lateromedial diameter.  $\square$ , puma (*Puma concolor*);  $\square$ , clouded leopard (*Neofelis nebulosa*);  $\blacktriangle$ , lion (*Panthera leo*);  $\blacklozenge$ , jaguar (*Panthera onca*);  $\blacksquare$ , leopard (*Panthera pardus*);  $\bullet$ , tiger (*Panthera tigris*);  $\times$ , snow leopard (*Panthera uncia*).

**Table 3.** Anteroposterior diameters divided by lateromedial diameters, expressed as percentages, along the canine crowns, along with standard deviations

Alveole	15%	30%	45%	60%	75%	90%	
	109.69 ± 10.27	110.39 ± 11.37	110.44 ± 12.86	110.61 ± 12.59	108.56 ± 11.12	99.24 ± 11.25	<i>Puma concolor</i>
	138.39 ± 8.88	142.22 ± 10.00	146.38 ± 13.49	147.85 ± 13.05	142.26 ± 8.69	128.14 ± 13.59	<i>Neofelis nebulosa</i>
	124.79 ± 10.93	125.75 ± 7.91	124.69 ± 5.97	121.54 ± 7.26	116.10 ± 10.26	110.93 ± 10.63	<i>Panthera leo</i>
	118.44 ± 8.93	117.17 ± 9.99	118.75 ± 10.90	116.99 ± 8.48	112.62 ± 8.54	101.92 ± 8.16	<i>Panthera onca</i>
	117.32 ± 8.00	124.51 ± 6.43	127.58 ± 9.29	126.68 ± 8.40	121.75 ± 12.06	112.24 ± 15.26	<i>Panthera pardus</i>
	122.95 ± 7.06	120.58 ± 10.02	125.70 ± 12.55	127.86 ± 13.63	124.15 ± 13.60	113.64 ± 11.25	<i>Panthera tigris</i>
	107.70 ± 8.15	110.43 ± 7.87	112.69 ± 11.28	110.58 ± 13.01	104.07 ± 10.16	100.47 ± 9.56	<i>Panthera uncia</i>
	218.92	235.16	210.01	220.13	196.36	188.62	<i>Homotherium serum</i>
	181.98	191.00	194.04	197.48	182.76	164.25	<i>Megantereon cultridens</i>
	179.38	149.49	179.50	176.98	161.50	140.82	<i>Smilodon fatalis</i>
	225.06	233.31	232.54	219.57	227.28	199.80	<i>Smilodon populator</i>

**Table 4.** One-way analysis of variance *F*-statistics and post-hoc Tukey's HSD comparisons of ratios of anteroposterior to lateromedial [(AP/LM) × 100] diameters in extant felids, and a one-sample *t*-test comparisons of *Neofelis* to four species to machairoidont felids

Alveolus	<i>F</i> = 23.195; <i>P</i> = 0.000			<i>F</i> = 24.758; <i>P</i> = 0.000			15%			<i>F</i> = 20.839; <i>P</i> = 0.000				
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
1	1.000							1	1.000					
2	0.000	1.000						2	0.000	1.000				
3	0.000	0.006	1.000					3	0.000	0.000	1.000			
4	0.005	0.000	0.233	1.000				4	0.009	0.000	0.326	1.000		
5	0.021	0.000	0.035	0.996	1.000			5	0.018	0.000	0.106	1.000	1.000	
6	0.000	0.000	0.690	0.964	0.605	1.000		6	0.000	0.000	0.779	0.972	0.786	1.000
7	0.964	0.000	0.000	0.002	0.010	0.000	1.000	7	0.945	0.000	0.000	0.003	0.006	1.000
30%	<i>F</i> = 24.706; <i>P</i> = 0.000			<i>F</i> = 20.839; <i>P</i> = 0.000			45%			<i>F</i> = 22.732; <i>P</i> = 0.000				
1	1.000							1	1.000					
2	0.000	1.000						2	0.000	1.000				
3	0.000	0.000	1.000					3	0.000	0.000	1.000			
4	0.143	0.000	0.083	1.000				4	0.122	0.000	0.669	1.000		
5	0.000	0.000	1.000	0.114	1.000			5	0.000	0.000	0.987	0.121	1.000	
6	0.001	0.000	0.555	0.881	0.709	1.000		6	0.000	0.000	1.000	0.375	0.996	1.000
7	1.000	0.000	0.000	0.424	0.000	0.028	1.000	7	0.996	0.000	0.062	0.744	0.003	1.000
60%	<i>F</i> = 23.858; <i>P</i> = 0.000			<i>F</i> = 22.732; <i>P</i> = 0.000			75%			<i>F</i> = 22.732; <i>P</i> = 0.000				
1	1.000							1	1.000					
2	0.000	1.000						2	0.000	1.000				
3	0.018	0.000	1.000					3	0.255	0.000	1.000			
4	0.388	0.000	0.879	1.000				4	0.842	0.000	0.965	1.000		
5	0.000	0.000	0.784	0.061	1.000			5	0.000	0.000	0.679	0.090	1.000	
6	0.000	0.000	0.593	0.022	1.000	1.000		6	0.000	0.000	0.241	0.009	0.988	1.000
7	1.000	0.000	0.104	0.654	0.001	0.000	1.000	7	0.890	0.000	0.048	0.293	0.000	1.000
90%	<i>F</i> = 14.060; <i>P</i> = 0.000			<i>F</i> = 14.060; <i>P</i> = 0.000			Neofelis and machairoidont felids			<i>F</i> = 14.060; <i>P</i> = 0.000				
1	1.000							Hs			Sp			
2	0.000	1.000						Alveolus			0.000			
3	0.016	0.001	1.000					15%			0.000			
4	0.980	0.000	0.229	1.000				30%			0.000			
5	0.001	0.000	1.000	0.059	1.000			45%			0.000			
6	0.000	0.002	0.991	0.012	0.999	1.000		60%			0.000			
7	1.000	0.000	0.203	1.000	0.068	0.019	1.000	75%			0.000			
								90%			0.001			

1, Puma (*Puma concolor*); 2, clouded leopard (*Neofelis nebulosa*); 3, lion (*Panthera leo*); 4, jaguar (*Panthera onca*); 5, leopard (*Panthera pardus*); 6, tiger (*Panthera tigris*); 7, snow leopard (*Panthera uncia*).  
Hs, *Homotherium serum*; Mc, *Megantereon cultridens*; Sf, *Smilodon fatalis*; Sp, *Smilodon populator*.

crown is significantly ( $P < 0.01$ ) more round in cross section than in other large felids, except the jaguar, which also has distinctly round canine proportions from around one quarter of the crown height from the alveolar margin to the canine apex (Tables 3, 4). Around the middle of the crown, the canine of the snow leopard becomes less rounded compared to that of the lion, often precluding assumptions of significance. With the exception of the alveolar margin ( $P = 0.035$ ), the leopard has canines of similar proportions to the lion and particularly the tiger. The values in the lion and tiger are broadly similar and none are significantly different (Table 4), but an interesting pattern is still present. At the proximal part of the crown, the tiger has slightly more rounded canines than the lion, whereas this is reversed along the distal part of the crown (Table 3; Fig. 3C).

Cross-sectional geometry in all species displays a nonlinear relationship along the crown (Fig. 3C), with the proximal and distal part of the canine being less blade-like and the central part more blade-like. This pattern is similar in both the clouded leopard and *Panthera*, but the puma has markedly a markedly uniform cross-sectional geometry along the crown, indicating that its canines are more spike-like than any other large felid. Toward the apex, the canine of the puma is almost perfectly round (Fig. 3C; Table 3), which is a common feature for the puma, jaguar, and snow leopard, although canine geometry along the crown is more similar in the latter two species to the other large felids.

PCA yielded good separation between the canine morphotypes. The eigenvalues (Table 5) indicated that two components would be sufficient for explanation of the variation in the data sample, which was confirmed by a Scree plot (Cattell, 1978), where factorial scree commences at PC1. PC1 explains in excess of 95% of the variation in the data (Table 5) and the uniformly distributed component loadings indicate that it is primarily a size component. PC2 explains a little less than 3% of the variation (cumulative variance = 97.8%) and there is a clear division between anteroposterior values, which all have positive component loadings, and lateromedial values, which all have negative component loadings.

Accordingly, species with very large canines are going to have predominately positive loadings on PC1, and species with smaller canines are going to have predominately negative loadings. Along the PC2 axis, species with long and lateromedially slender canines will have predominately positive loadings, and species with thick canines will have predominately negative loadings (Fig. 4). The clouded leopard is entirely distinct from all the other species, the jaguar, lion, and tiger cluster, together along the right hand side of the plot, and the puma and snow leopard cluster together

**Table 5.** Principal components, eigenvalues and corresponding variances for all canine measurements

	PC1	PC2
CL	0.945	0.243
AP <sub>Alv</sub>	0.986	0.104
AP <sub>15%</sub>	0.989	0.081
AP <sub>30%</sub>	0.990	0.097
AP <sub>45%</sub>	0.985	0.143
AP <sub>60%</sub>	0.977	0.184
AP <sub>75%</sub>	0.973	0.184
AP <sub>90%</sub>	0.964	0.131
LM <sub>Alv</sub>	0.978	-0.141
LM <sub>15%</sub>	0.979	-0.153
LM <sub>30%</sub>	0.977	-0.182
LM <sub>45%</sub>	0.974	-0.188
LM <sub>60%</sub>	0.982	-0.158
LM <sub>75%</sub>	0.979	-0.155
LM <sub>90%</sub>	0.956	-0.188
Variance explained by components (eigenvalues)	1 14.282	2 0.387
Percent of total variance explained	1 95.214	2 2.582

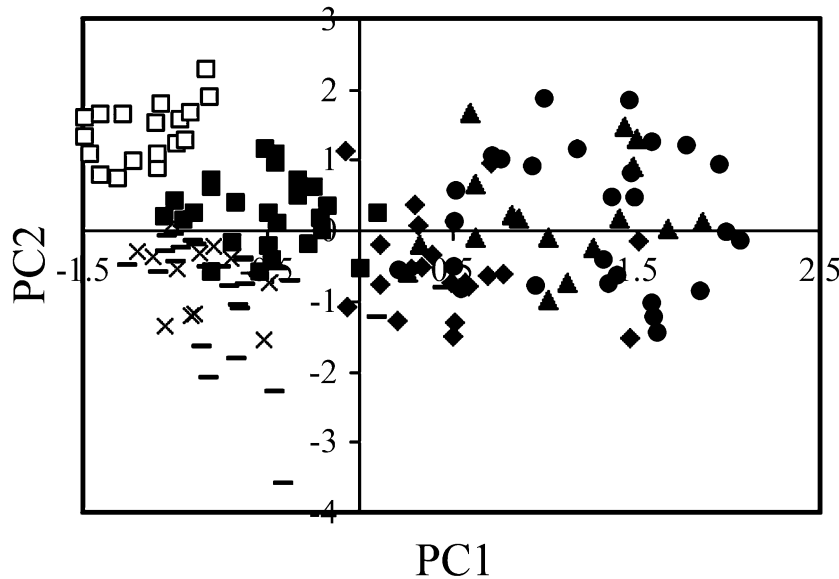
All measurements are in millimetres.

Alv, measurement at alveolar margin; AP, anteroposterior diameter; CL, canine length; LM, lateromedial diameter.

at the lower left hand side of the plot, with the leopard occupying a position along PC2 similar to the jaguar, lion and tiger, but its smaller canines overall makes it group in the vicinity of the clouded leopard, puma and snow leopard along PC1.

Canine bending strengths in the simple model (eqns 4 and 5) are strongly size-dependent, and are highest in the tiger, followed by the lion and then the jaguar (Table 6). The leopard and puma have approximately the same bending strengths followed by the snow leopard, and the clouded leopard has the lowest bending strengths. However, the actual strength of the canines will depend on the loads exerted upon them by the jaw adductors. Incorporation of bite forces often changes the interspecific relationships significantly from conclusions drawn when using the simple model (Christiansen & Adolfssen, 2005). The average bite forces at the canine tips computed by Christiansen (2007) are 499.6 N for the puma ( $n = 10$ ), 344.2 N for the clouded leopard ( $n = 12$ ), 1198.6 N for the lion ( $n = 10$ ), 879.5 N for the jaguar ( $n = 9$ ), 558.6 N for the leopard ( $n = 8$ ), 1234.3 N for the tiger ( $n = 14$ ), and 363.0 N for the snow leopard ( $n = 9$ ).

No sample could be analysed with unmodified branch lengths (Fig. 5). The regression slopes of bite forces to canine bending strengths are positively allometric (Table 7; Fig. 5), although small sample sizes frequently prevent assumptions of significance from



**Figure 4.** Principal components plot of felid canines dimensions. —, puma (*Puma concolor*); □, clouded leopard (*Neofelis nebulosa*); ▲, lion (*Panthera leo*); ◆, jaguar (*Panthera onca*); ■, leopard (*Panthera pardus*); ●, tiger (*Panthera tigris*); ×, snow leopard (*Panthera uncia*).

isometry. Overall, the canines become progressively stronger to bite forces with increasing body size and, thus, increasing bite forces and canine size. High correlation coefficients imply that canine strength to bite forces is highly constrained. Some of the slope allometry is evidently due to the low bending strength to estimated bite forces of the clouded leopard, as noted below.

Normalizing the bending strengths for estimated bite forces changes the pattern slightly. The tiger still appears to have the strongest canines of all species in bending about both planes (Fig. 6), but its canine strength is only consistently significantly higher than those of the clouded leopard and the leopard (Table 8). The tiger has stronger canines than the puma in bending about the lateromedial plane, whereas the two are often nonsignificantly different in bending about the anteroposterior plane. Only towards the apex does the bending strength of the tiger's canine significantly exceed that of the snow leopard in the lateromedial plane. The bending strengths in both planes are higher in the tiger than in the lion (Fig. 6), albeit nonsignificantly so (Table 8), and the more robust canines of the tiger are evidently somewhat compromised by its very high bite force. The bending strengths along the leopard canine are rather similar to those of the lion, snow leopard, and puma. Despite the bending strength of the seemingly massive teeth of the jaguar most often being above those of the other species, except the tiger (Fig. 6), its bending strengths in both planes are nonsignificantly different from those of the other pantherines and the puma (Table 8). Overall,

only the clouded leopard stands out, having markedly weaker canines, and, with the exception of this species, the big cats have broadly comparable canine bending strengths compared to estimated bite forces.

## DISCUSSION

Lumping large felids together using the vernacular name conical-toothed felids is an oversimplification, given the heterogeneity in canine proportions and bending strengths. The larger species show differences in canine proportions that clearly differentiate, for example, the puma or snow leopard from the jaguar, lion, and tiger, and the clouded leopard from any of them. However, with the exception of the latter, the bending strengths of the canines show a tendency towards less variation than canine morphology, indicating that the evolution of the canines is constricted, probably owing to their importance in feeding ecology. It is often suggested that the safety factors of biological structures should reflect to their importance in fitness (Alexander, 1981, 1984) and, as such, the risk of failure of the canines in carnivores may be regarded as being broadly similar interspecifically. Given this, it appears peculiar that the clouded leopard has weaker canines than the puma and the pantherines.

One possibility is that canines are built with approximately the same safety factors with respect to predictably encountered loads, which, in the present study, imply inferred maximal, static bite force, although other predictable loads, much less easily quantifiable, could be the thickness of prey skin and

**Table 6.** Bending strength of felid canines in anteroposterior (AP) and lateromedial (LM) planes, along with standard deviations

Alveolus		15%		30%		45%	
AP	LM	AP	LM	AP	LM	AP	LM
6.1824 ± 1.954	6.7493 ± 1.933	7.1289 ± 2.289	7.7108 ± 2.228	6.7715 ± 2.449	7.3255 ± 2.280	5.2546 ± 2.270	5.6456 ± 2.072
2.3860 ± 0.668	3.3319 ± 0.988	2.5554 ± 0.699	3.5316 ± 0.989	2.2626 ± 0.605	3.2129 ± 0.887	1.9106 ± 0.514	2.7818 ± 0.753
15.5958 ± 3.666	19.8286 ± 4.615	17.1189 ± 4.072	21.2273 ± 4.871	15.3426 ± 3.704	19.2343 ± 4.626	12.2605 ± 3.187	15.2814 ± 3.964
11.6513 ± 3.351	13.9835 ± 4.059	12.9539 ± 3.854	15.2906 ± 4.531	12.7580 ± 4.006	14.8023 ± 4.399	9.9949 ± 2.917	11.7780 ± 3.374
6.6253 ± 1.774	7.8119 ± 1.923	6.8457 ± 1.789	7.9827 ± 1.942	5.7819 ± 1.612	7.1455 ± 1.798	4.5339 ± 1.114	5.7412 ± 1.281
18.5693 ± 4.559	22.8789 ± 5.896	20.3408 ± 5.016	24.5533 ± 6.151	18.6740 ± 5.060	22.3150 ± 5.575	14.9294 ± 3.833	18.5412 ± 4.204
5.0303 ± 1.078	5.3699 ± 0.982	5.5298 ± 1.202	5.8525 ± 1.160	4.6915 ± 0.982	5.1703 ± 1.088	3.6745 ± 0.830	4.1185 ± 0.863

**Table 7.** Independent contrasts least squares regression equations and 95% confidence limits

	Anteroposterior diameters				Lateromedial diameters			
	$b \pm 95\% \text{ CI}$	$r$	$F$	$P$	$b \pm 95\% \text{ CI}$	$r$	$F$	$P$
Alveolus	1.229 ± 0.568	0.928	30.928	0.003	1.298 ± 0.286*	0.982	136.814	0.000
15%	1.254 ± 0.603	0.922	28.558	0.003	1.197 ± 0.311	0.979	114.875	0.000
30%	1.293 ± 0.564	0.935	34.753	0.002	1.285 ± 0.319	0.977	107.252	0.000
45%	1.295 ± 0.556	0.937	35.858	0.002	1.291 ± 0.279*	0.983	140.967	0.000
60%	1.269 ± 0.420	0.961	60.334	0.001	1.298 ± 0.273*	0.984	149.838	0.000
75%	1.216 ± 0.486	0.945	41.392	0.001	1.259 ± 0.306	0.978	111.423	0.000
90%	1.218 ± 0.723	0.889	18.749	0.007	1.227 ± 0.515	0.939	37.577	0.002

In all cases, the bite forces (N) constitute the independent variable ( $X$ ); whereas the dependent variable ( $Y$ ) is canine bending strengths along the crown.

\*95% CI for slope excludes 1.00.

the preferred killing mode. However, structures can be estimated primarily to fail under maximal loads or, alternatively, and perhaps more likely, accidental and/or unpredictable loads, such as struggling prey or accidentally striking bone in the case of canine injuries in carnivores. This seems to be a likely explanation because bone-cracking species frequently have greater percentages of heavy dental wear and/or fractures than species which do not ingest bone (e.g. the lion vs. the cheetah; Van Valkenburgh, 1988). Traumatic injuries, such as being kicked forcefully from large prey, do not appear to be uncommon in large felids (Van Valkenburgh, 1988; Turner & Antón, 1997), but it would probably be difficult to adapt canine safety factors to such erratic loads.

By this token, the clouded leopard would accidentally encounter bone when delivering the killing bite much less frequently than the other large felids, or its prey would be largely immobile during the killing bite as has been suggested (Therrien, 2005), which both seem unlikely, although its feeding ecology is virtually unknown. The available evidence suggests that the clouded leopard primarily employs a nape bite to dis-

patch larger prey (Rabinowitz, Andau & Chai, 1987) and also each other (Seager & Demorest, 1978), which is not in accordance with the above suggestion. Whether it is able to pacify prey with its proportionally very short and powerful limbs and large paws (Gonyea, 1976; Nowak, 1991; Turner & Antón, 1997; Sunquist & Sunquist, 2002) to any greater extent than other felids is presently unknown, but appears unlikely (*contra* Therrien, 2005). Also, compared to its body size, the clouded leopard appears to have a powerful bite (Christiansen & Adolfsen, 2005; Wroe, McHenry & Thomason, 2005), which is partly responsible for compromising its canine strength. Presently, the hypertrophied, gracile canines of the clouded leopard remain an interesting conundrum.

Most large felids frequently employ a throttling throat bite when subduing large prey (Sunquist & Sunquist, 2002), but there appear, however, to be interspecific differences with respects to preferred killing mode and frequency of the various killing bites. The puma hunts a variety of prey species of widely different sizes but deer appear to constitute the main bulk of the diet (Robinette, Gashwiler &

60%		75%		90%		
AP	LM	AP	LM	AP	LM	
4.0847 ± 1.530	4.4144 ± 1.415	3.2004 ± 0.906	3.4410 ± 0.924	2.6482 ± 0.615	2.6178 ± 0.654	<i>Puma concolor</i>
1.6823 ± 0.511	2.4514 ± 0.661	1.3942 ± 0.346	1.9754 ± 0.480	1.0012 ± 0.253	1.2903 ± 0.370	<i>Neofelis nebulosa</i>
10.6138 ± 2.504	12.8818 ± 2.977	8.6731 ± 2.336	10.0042 ± 2.530	6.7469 ± 1.791	7.5168 ± 2.248	<i>Panthera leo</i>
8.3071 ± 2.277	9.6574 ± 2.486	7.3155 ± 1.825	8.1775 ± 1.879	6.5082 ± 1.271	6.6055 ± 1.262	<i>Panthera onca</i>
3.9092 ± 0.981	4.9144 ± 1.099	3.1008 ± 0.834	3.7451 ± 0.960	2.2235 ± 0.548	2.5013 ± 0.729	<i>Panthera pardus</i>
12.5339 ± 3.119	15.9691 ± 4.178	10.0809 ± 2.380	12.5570 ± 3.513	6.7785 ± 1.459	7.6904 ± 1.758	<i>Panthera tigris</i>
3.1855 ± 0.812	3.5194 ± 0.921	2.7586 ± 0.840	2.8309 ± 0.711	2.0860 ± 0.579	2.0694 ± 0.523	<i>Panthera uncia</i>

Morris, 1959; Anderson, 1983; Currier, 1983). In temperate regions, prey is often of comparable size to the puma itself, typically 45–50 kg, but, in tropical South America, the diet often includes smaller (< 15 kg) prey, such as small deer, pacas, agoutis, and armadillos (Iriarte *et al.*, 1990). Red deer (*Cervus elaphus*) is frequently taken, preferably older males and calves (Hornocker, 1970). The throat bite is the preferred killing mode of large prey, whereas smaller prey is frequently dispatched with a nape bite (Hansen, 1992; Sunquist & Sunquist, 2002). The latter method is, however, also often employed for large prey, frequently after leaping onto the back of the prey from a higher place (Hibben, 1937; Young & Goldman, 1946). This is not entirely congruent with the puma's rather small canines, although their stoutness appears well suited for this mode of attack, given that large prey often struggles when being subdued by a nape bite.

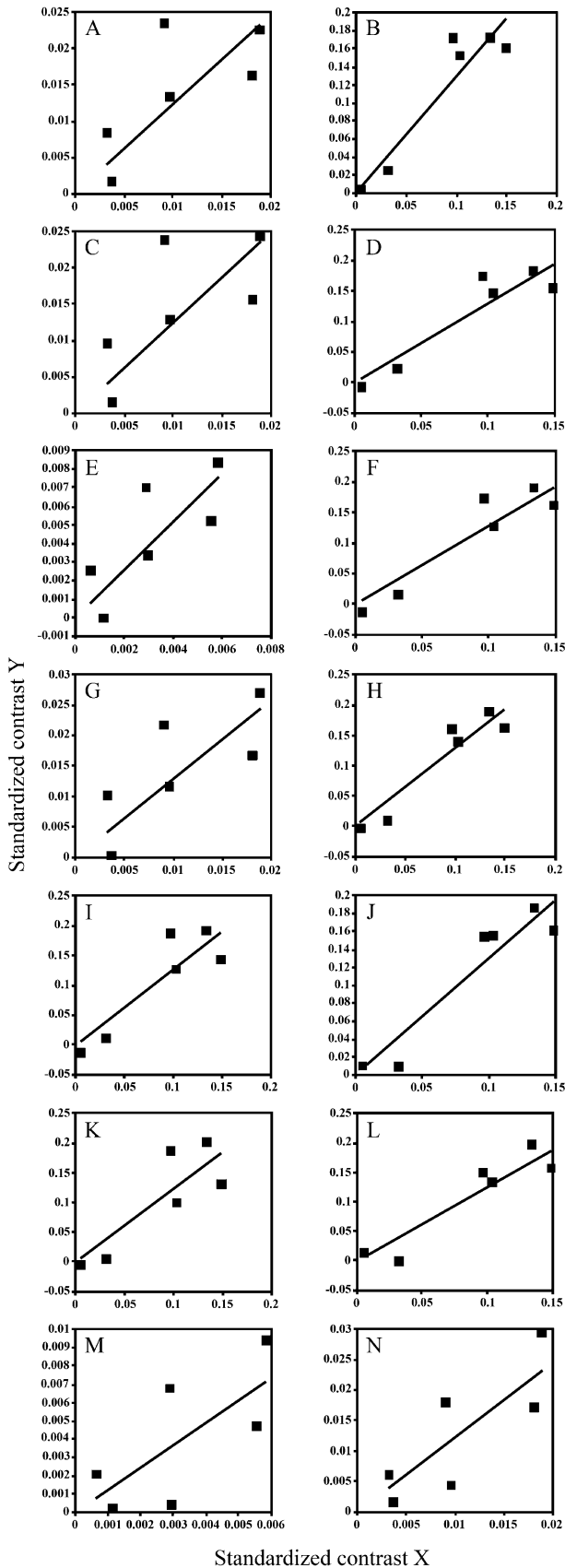
The leopard is known to feed on a wide variety of prey, from large insects to buffalo (*Syncerus caffer*) and eland (*Taurotragus* sp.; Kingdon, 1977), and over 90 prey species have hitherto been recorded from its diet (Bailey, 1993). Large prey is most frequently dispatched with a throat bite, and smaller prey with a nape bite, although nose bites are also used (Ilany, 1990). Where sympatric with lions and tigers, direct competition is often avoided by a difference in preferred prey size (Seidensticker, 1976; Karanth & Sunquist, 2000; Sunquist & Sunquist, 2002). The more generalized appearance of the leopard's canines, not as blade-like as those of the clouded leopard and not as stout as those of jaguars or tigers, and proportionally larger and less conical than those of snow leopards and pumas, could be a reflection of its more generalized predatory lifestyle.

The size of the jaguar varies greatly throughout its geographical range and, although inhabiting a wide range of habitats, mainly subtropical or tropical forests, it is most often associated with large bodies of fresh water (Seymour, 1989; Nowak, 1991; Sunquist &

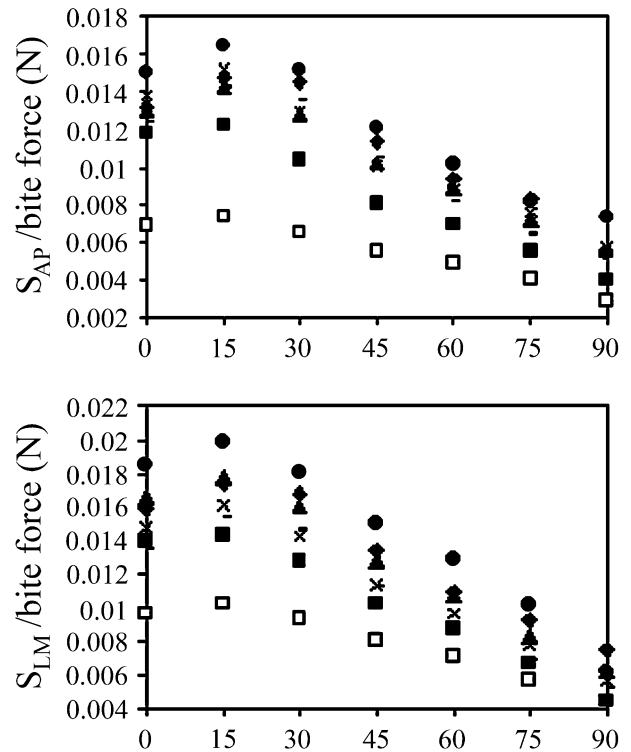
Sunquist, 2002). The list of prey species is extensive (Leopold, 1959; Seymour, 1989), but preferred prey appear to be peccaries, capybaras, pacas, agoutis, and armadillos, along with caimans, fish, and turtles (Seymour, 1989; Hoogesteijn, Hoogesteijn & Mondolfi, 1993). There is dispute as to the frequency with which the jaguar hunts deer and tapir (Seymour, 1989; Schaller & Vasconcelos, 1978; Hoogesteijn *et al.*, 1993; Taber *et al.*, 1997). The jaguar frequently takes domestic livestock, even cattle weighing 500 kg (Hoogesteijn *et al.*, 1993). It appears to mainly kill large prey with a throat bite (Sunquist & Sunquist, 2002; although Seymour (1989) states that throat bites are uncommon) and with a nape bite, which often results in severe damage to the cervicals (Brock, 1963). Large prey are often attacked from the back or side, by gripping the head with the forepaws and toppling it over (Seymour, 1989), sometimes breaking its neck in the fall. The nape bite, thus, does not in itself break the neck (de Almeida, 1976; Mondolfi & Hoogesteijn, 1986). The jaguar also frequently employs a special killing bite, especially for capybaras, by biting through the skull between the ears (Schaller & Vasconcelos, 1978; Seymour, 1989; Sunquist & Sunquist, 2002). This is also frequently employed even to large prey, such as cattle (Hoogesteijn & Mondolfi, 1996; Hoogesteijn *et al.*, 1993). The above is in full accord with its very high bite force and large, massive canines.

The lion and tiger frequently take very large prey species (Kruuk & Turner, 1967; Schaller, 1972). The lion primarily hunts large ungulates (Kruuk & Turner, 1967; Schaller, 1972; Ruggiero, 1991; Mills & Biggs, 1993), employing a variety of hunting styles dependent on the prey species (Schaller, 1972; Sunquist & Sunquist, 2002). Small prey are often knocked over and dispatched with a nape or throat bite, and large prey are either knocked over or grabbed with the forepaws and then strangulated by a throat bite (most commonly), or a nose bite (Turner & Antón, 1997).

The tiger is the largest and most powerful extant felid. In warm parts of Asia, various deer are the most



**Figure 5.** Regression plots of independent contrasts, along with branch length transformation modes and resulting correlation coefficients in parentheses. In all cases the bite forces (N) constitute the independent variable (X); whereas the dependent variable (Y) is canine bending strengths. A, anteroposterior (AP)-diameter at alveolus ( $\sqrt[3]{}$ ;  $r = 0.0041$ ); B, lateromedial (LM)-diameter at alveolus (Pagel;  $r = 0.0304$ ); C, AP-diameter at 15% ( $\sqrt[3]{}$ ;  $r = 0.0008$ ); D, LM-diameter at 15% (Pagel;  $r = 0.0192$ ); E, AP-diameter at 30% ( $\sqrt{}$ ;  $r = 0.0086$ ); F, LM-diameter at 30% (Pagel;  $r = 0.0007$ ); G, AP-diameter at 45% ( $\sqrt[3]{}$ ;  $r = 0.0004$ ); H, LM-diameter at 45% (Pagel;  $r = 0.0131$ ); I, AP-diameter at 60% (Pagel;  $r = 0.0001$ ); J, LM-diameter at 60% (Pagel;  $r = 0.0310$ ); K, AP-diameter at 75% (Pagel;  $r = 0.0046$ ); L, LM-diameter at 75% (Pagel;  $r = 0.0071$ ); M, AP-diameter at 90% ( $\sqrt{}$ ;  $r = 0.0016$ ); N, LM-diameter at 90% ( $\sqrt[3]{}$ ;  $r = 0.0092$ ).



**Figure 6.** Bending strengths about the anteroposterior ( $S_{AP}$ ) and lateromedial ( $S_{LM}$ ) axes, respectively, to estimated bite forces along the canine crown. —, puma (*Puma concolor*); □, clouded leopard (*Neofelis nebulosa*); ▲, lion (*Panthera leo*); ◆, jaguar (*Panthera onca*); ■, leopard (*Panthera pardus*); ●, tiger (*Panthera tigris*); ×, snow leopard (*Panthera uncia*).

**Table 8.** One-way analysis of variance *F*-statistics and post-hoc Tukey's HSD comparisons of ratios of bending strengths about the anteroposterior and lateromedial axis, respectively, to estimated bite forces (N)

	Anteroposterior diameter							Lateromedial diameter						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
Alveolus	<i>F</i> = 14.162; <i>P</i> = 0.000							<i>F</i> = 11.961; <i>P</i> = 0.000						
	1	1.000						1	1.000					
	2	0.000	1.000					2	0.004	1.000				
	3	0.991	0.000	1.000				3	0.128	0.000	1.000			
	4	0.967	0.000	1.000	1.000			4	0.343	0.000	0.998	1.000		
	5	0.999	0.000	0.912	1.000	1.000		5	0.999	0.001	0.342	0.666	1.000	
	6	0.048	0.000	0.511	0.570	1.000	1.000	6	0.000	0.000	0.747	0.309	0.001	1.000
	7	0.813	0.000	0.994	0.998	0.577	0.970	7	0.931	0.001	0.923	0.994	0.993	0.141
15%	<i>F</i> = 15.312; <i>P</i> = 0.000							<i>F</i> = 12.527; <i>P</i> = 0.000						
	1	1.000						1	1.000					
	2	0.000	1.000					2	0.000	1.000				
	3	1.000	0.000	1.000				3	0.529	0.000	1.000			
	4	0.999	0.000	1.000	1.000			4	0.693	0.000	1.000	1.000		
	5	0.447	0.000	0.534	0.272	1.000		5	0.953	0.005	0.104	0.167	1.000	
	6	0.279	0.000	0.536	0.701	1.000	1.000	6	0.002	0.000	0.717	0.440	0.000	1.000
	7	0.978	0.000	0.993	0.999	0.210	0.978	7	0.997	0.000	0.964	0.992	0.821	0.190
30%	<i>F</i> = 16.172; <i>P</i> = 0.000							<i>F</i> = 12.784; <i>P</i> = 0.000						
	1	1.000						1	1.000					
	2	0.000	1.000					2	0.000	1.000				
	3	0.999	0.000	1.000				3	0.887	0.000	1.000			
	4	0.967	0.000	0.850	1.000			4	0.498	0.000	0.998	1.000		
	5	0.021	0.001	0.233	0.002	1.000		5	0.574	0.012	0.088	0.010	1.000	
	6	0.634	0.000	0.437	0.997	1.000	1.000	6	0.022	0.000	0.701	0.940	0.000	1.000
	7	1.000	0.000	1.000	0.945	0.283	0.682	7	1.000	0.002	0.903	0.623	0.903	0.102
45%	<i>F</i> = 14.114; <i>P</i> = 0.000							<i>F</i> = 12.125; <i>P</i> = 0.000						
	1	1.000						1	1.000					
	2	0.000	1.000					2	0.004	1.000				
	3	1.000	0.000	1.000				3	0.675	0.000	1.000			
	4	0.904	0.000	0.918	1.000			4	0.210	0.000	0.997	1.000		
	5	0.059	0.007	0.187	0.003	1.000		5	0.935	0.101	0.149	0.016	1.000	
	6	0.300	0.000	0.413	0.982	0.000	1.000	6	0.000	0.000	0.262	0.619	0.000	1.000
	7	1.000	0.000	1.000	0.938	0.337	0.529	7	1.000	0.024	0.923	0.616	0.942	0.021



Table 8. Continued

		Anteroposterior diameter							Lateromedial diameter							
60%		$F = 13.965; P = 0.000$							$F = 12.383; P = 0.000$							
	1	1.000							1	1.000						
	2	0.000	1.000						2	0.192	1.000					
	3	0.913	0.000	1.000					3	0.148	0.000	1.000				
	4	0.411	0.000	0.992	1.000				4	0.051	0.000	1.000	1.000			
	5	0.557	0.005	0.100	0.006	1.000			5	1.000	0.184	0.181	0.068	1.000		
	6	0.019	0.000	0.620	0.959	0.000	1.000		6	0.000	0.000	0.165	0.230	0.000	1.000	
	7	0.970	0.000	1.000	0.990	0.244	0.673	1.000	7	0.941	0.052	0.928	0.823	0.955	0.011	1.000
	75%		$F = 16.984; P = 0.000$							$F = 13.416; P = 0.000$						
		1	1.000							1	1.000					
		2	0.000	1.000						2	0.365	1.000				
		3	0.722	0.000	1.000					3	0.202	0.001	1.000			
		4	0.006	0.000	0.577	1.000				4	0.001	0.000	0.811	1.000		
		5	0.503	0.018	0.028	0.000	1.000			5	1.000	0.588	0.108	0.000	1.000	
6		0.005	0.000	0.657	1.000	0.000	1.000		6	0.000	0.000	0.111	0.884	0.000	1.000	
7		0.468	0.000	0.999	0.937	0.014	0.971	1.000	7	0.813	0.048	0.993	0.441	0.659	0.030	1.000
90%			$F = 28.771; P = 0.000$							$F = 16.767; P = 0.000$						
		1	1.000							1	1.000					
		2	0.000	1.000						2	0.001	1.000				
		3	0.984	0.000	1.000					3	0.261	0.000	1.000			
		4	0.000	0.000	0.001	1.000				4	0.000	0.000	0.136	1.000		
		5	0.000	0.008	0.000	0.000	1.000			5	0.295	0.437	0.001	0.000	1.000	
	6	0.997	0.000	0.999	0.000	0.000	1.000		6	0.120	0.000	0.999	0.061	0.000	1.000	
	7	0.961	0.000	1.000	0.011	0.000	0.999	1.000	7	0.961	0.001	0.962	0.016	0.105	0.939	1.000

1, Puma (*Puma concolor*); 2, clouded leopard (*Neofelis nebulosa*); 3, lion (*Panthera leo*); 4, jaguar (*Panthera onca*); 5, leopard (*Panthera pardus*); 6, tiger (*Panthera tigris*); 7, snow leopard (*Panthera uncia*).

important prey (Schaller, 1967; Sunquist, 1981; Sunquist & Sunquist, 2002), and, in Russia, it is wild pigs (*Sus scrofa*) and red deer (*Cervus elaphus*) (Miquelle *et al.*, 1996). Tigers mainly employ two killing techniques, largely based on prey size (Mazák, 1981; Sunquist & Sunquist, 2002). Smaller prey, up to approximately one half of the tiger's body mass, are frequently killed with a powerful nape bite, often causing severe damage to the cervicals (Sunquist, 1981; Seidensticker & McGougal, 1993), and large prey are dispatched with a throat bite. The above appears congruent with the tiger's very high bite force (Christiansen & Adolfssen, 2005; Wroe *et al.*, 2005; Christiansen, 2007) and very large and strong canines. Overall, the lion appears slightly less extreme in both respects, and this could be owing to it preying on the same size-classes of animals in groups, rather than individually.

The killing behaviour of the snow leopard has not been well studied but the available evidence suggests that they frequently employ stalking by using steep cliffs and hillsides to approach prey prior to attack (Hemmer, 1972; Sunquist & Sunquist, 2002). Wild goats and sheep appear to be preferred prey (Sunquist & Sunquist, 2002), although they also feed on, for example, musk deer, wild ass, suids, and a variety of smaller mammals and birds. They also frequently kill livestock, but individuals doing so often possess physical injuries (Fox & Chundawat, 1988). A diet of medium-sized prey appears to be in accordance with its moderate canine size, although the reasons for the canine stoutness do not appear discernible from either the preferred prey or killing mode, which appears to be the throat bite, as in other pantherines (Sunquist & Sunquist, 2002).

In summary, canine morphology appears, at least to some extent, to reflect killing behaviour. There do not seem to be great differences in frequency of canine breakage between, for example, the jaguar and the leopard (Van Valkenburgh, 1988), despite clear differences in canine morphology, suggesting that bite forces, canine strengths, and killing modes are correlated. Canine morphology also appears to be influenced by genealogy to some extent because the phylogenetically most distant extant member of *Panthera*, the snow leopard (Johnson *et al.*, 2006; but see also Yu & Zhang, 2005) has the most divergent canine morphology of the genus, the somewhat generalized leopard has a more generalized canine morphology, and the three closely related species (i.e. lion, jaguar, and tiger) have canines that appear to be more similar to each other than to the two other species. However, they are also large, and physical size could constrain canine morphology, given the correlation of bite forces and morphology. The puma's cone-like, stout canines in some respects resemble those of smaller felids,

reflecting the debate of its true phylogenetic placing (Hemmer, 1978; Mattern & McLennan, 2000; Sunquist & Sunquist, 2002; Johnson *et al.*, 2006). The clouded leopard, however, stands out, and its proportionally high bite force and very large, blade-like and gracile canines would suggest a rather different function than that seen in other big cats.

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## APPENDIX 1

Specimens used in the analyses, with crown height in millimetres in parentheses. BM, Natural History Museum, London; CN, Zoological Museum, University of Copenhagen; LACMHC, George C. Page Museum, Hancock Collection; SE, Naturhistorisches Museum, Basel; TMM, Texas Memorial Museum.

## FELINAE

*Puma concolor*

BM1926.1.12.3 (22.6); BM1903.9.4.37 (24.1); BM1850.11.22.46 (25.2); BM1917.1.25.70 (25.2); CN1673 (25.4); BM59.14 (25.5); BM1913.10.24.26 (26.1); BM1913.10.24.27 (26.2); BM79.1633 (26.5); BM34.9.10.66 (26.6); BM1901.3.21.15 (26.7); BM1858.5.4.6.1 (26.7); BM1901.11.14.2 (26.8); BM1934.9.10.65 (27.2); BM40.692 (27.3); CN1674 (27.9); BM1894.12.18.2 (28.7); CN1451 (29.0); BM1934.9.2.39 (29.5); BM1837.3.15.7 (29.5); BM1858.5.4.6.2 (29.9); BM67.4.12 (30.1); CN841 (30.5); BM1926.1.12.2 (31.2); BM50.11.22.45 (31.9); BM11.2.21.1 (32.1); BM1901.11.14.21 (38.5); BM40.359 (43.3).

*Neofelis nebulosa*

BM57.4.3.1 (27.7); BM30.3.3.4 (29.3); BM1903.4.9.2 (29.7); BM30.3.3.5 (29.9); BM30.3.3.6 (30.5);

BM39.336 (30.6); BM43.65 (31.0); BM1938.11.30.22 (31.2); CN1351 (31.7); BM47.685 (32.6); BM55.1644 (33.1); BM1977.17 (33.3); BM1938.11.30.25 (34.0); BM1938.11.30.24 (34.7); BM40.374 (34.9); BM39.1656 (36.6); BM1938.11.30.23 (38.5); CN35 (40.5).

*Panthera leo*

CN2114 (41.0); CN887 (41.8); CN7364 (44.6); CN704 (45.0); CN5227 (45.6); CN5844 (46.5); CN6043 (47.5); BM1938.10.18.8 (48.3); BM58.227 (48.4); CN2113 (49.2); BM58.211 (49.2); BM55.225 (52.0); CN3794 (56.2); CN7231 (56.9); BM58.221 (57.0); CN3503 (57.3); BM45.168 (61.3).

*Panthera onca*

CN5707 (34.6); CN5659 (36.0); BM1934.9.10.64 (36.6); BM1870.3.10.19 (37.2); CN4348 (37.8); CN842 (38.5); CN5660 (39.5); CN6221 (39.5); BM1935.3.6.2 (40.2); BM39.537 (40.3); BM1845.8.25.21 (40.6); BM1851.8.25.12 (41.8); CN39 (42.8); BM87.236 (43.4); BM1884.2.8.1 (43.7); BM1871.4.8.2 (43.8); BM1845.8.25.22 (45.9); BM1990.542 (47.4); BM77.857 (50.3); CN843 (52.7).

*Panthera pardus*

*Panthera pardus fusca*: BM29.9.26.2 (27.5); BM34.8.17.7 (28.0); BM32.8.24.3 (28.1); BM31.9.21.3 (30.5); BM26.10.8.22 (30.9); BM1851.5.5.5 (34.0); BM1937.4.8.13 (34.5); BM26.10.8.19 (35.3); BM1937.4.8.12 (35.4); BM33.2.4.1 (37.1); BM25.6.13.1 (37.5); BM30.11.4.1 (37.9); BM34.8.17.5 (38.0); BM27.2.14.25 (38.1); *Panthera pardus pardus*: BM61.988 (27.8); BM32.9.1.40 (31.6); CN3980 (32.2);

BM27.2.11.13 (32.6); BM66.796 (32.7); BM36.2.28.22 (33.9); BM27.2.11.9 (36.5); CN3981 (37.6); BM65.2678 (37.8); BM27.2.9.6 (38.1); BM1934.4.4.1 (39.4); BM31.1.2.7 (42.9).

*Panthera tigris*

*Panthera tigris altaica*: CN5697 (59.0); CN6049 (59.4). *Panthera tigris balica*: BM1938.3.14.6 (41.6); BM1938.3.14.5 (49.1); BM1937.12.1.2 (49.6). *Panthera tigris corbetti*: BM10.3.10.9 (42.6); BM10.3.10.8 (56.7). *Panthera tigris sondaica*: BM67.4.12.200 (49.0); BM67.4.12.199 (49.5); BM20.11.14.2 (52.7); BM67.4.12.192 (54.6); BM1937.12.1.1 (55.1); BM67.4.12.198 (55.7); BM67.4.12.194 (59.8). *Panthera tigris sumatrae*: BM35.4.6.1 (38.8); BM35.4.6.2 (39.4); BM35.4.6.3 (42.9); BM39.335 (47.2); BM47.449 (47.3); BM39.334 (50.4). *Panthera tigris tigris*: CN969 (40.5); CN883 (45.4); BM30.1.4.1 (46.0); CN1454 (50.7); BM56.5.6.54 (55.6); CN3446 (55.9); CN5667 (57.3); CN4552 (71.4).

*Panthera uncia*

BM47.37 (24.4); CN1367 (25.5); BM1938.6.28.3 (26.1); BM32.8.21.1 (27.7); CN6046 (27.9); BM81.1498 (28.2); BM67.3.20.1 (28.8); CN5216 (29.0); CN1394 (29.5); BM41.208 (30.5); CN4321 (30.9); CN6047 (34.9).

MACHAIRODONTINAE

*Homotherium serum* TMM3582 (73.0); *Megantereon cultridens* SE311 (93.8); *Smilodon fatalis* LACMHC2001-173 (143.9); *Smilodon populator* CN52 (159.6).