

Long in the tooth: evolution of sabertooth cat cranial shape

Graham J. Slater and Blaire Van Valkenburgh

Abstract.—Sabertooths exhibit one of the most extreme feeding adaptations seen in mammals. The functional consequences of accommodating extremely elongate upper canine teeth are severe, resulting in a well-documented suite of cranial modifications. We used geometric morphometric methods to study the evolution of overall shape in the skulls of extant and extinct feline and machairodontine felids, as well as extinct nimravids. Trends in skull evolution were evaluated by using relative warps analysis and tested for association with body size and canine tooth length. Primitive sabertooths from all lineages exhibit cranial shapes more similar to conical-toothed cats, despite the presence of moderately developed saberteeth. More-derived forms in both nimravids and felids diverge in skull morphospace to form two distinct sabertooth types (dirk-toothed and scimitar-toothed) that differ in canine shape. Skull shape in conical-toothed cats is strongly associated with body size, but not canine length. However, within each sabertooth lineage, skull shape is significantly correlated with canine length, suggesting that gape-related demands drove the evolution of sabertooth skull morphology.

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Introduction

Sabertooths are often the dominant large hypercarnivores in fossil mammal assemblages, filling the niche now occupied by large, pantherine felids (Van Valkenburgh 2001). All sabertooths appear catlike in their general morphology, with foreshortened skulls to facilitate large bite forces, reduced post-carnassial dentitions, and robust, dexterous forelimbs for grasping and manipulating prey (Martin 1980; Van Valkenburgh 1985, 1988; Holliday and Stepan 2004). The most striking feature of sabertoothed predators, however, is the elongation of the upper canine teeth that reach lengths of up to 210 mm in the lion-sized nimravid *Barbourofelis fricki* (Schultz et al. 1970). The canine teeth of sabertooths are also laterally compressed, or bladelike, in contrast with the stout, conical canine teeth of living cats (Van Valkenburgh and Ruff 1987).

A number of unique skull modifications are associated with the evolution of sabertooths, including ventral displacement of the jaw joint, a more vertical occipital plane, reduction of the coronoid process of the mandible, and upward rotation of the palate. These features are thought to relate to the need for both increased gape in order for the mandible to clear the tips of the canines, and reorganized jaw-

adducting musculature to avoid over-stretching of muscle fibers during wide gaping (Matthew 1910; Emerson and Radinsky 1980; Bryant 1996a; Martin 1998a). Furthermore, enlarged, ventrally displaced mastoid processes suggest that head-depressing cervical musculature, such as the m. obliquus capitis cranialis, played a substantial role in sabertooth predatory behavior (Akersten 1985; Antón et al. 2004b).

In spite of extensive study of sabertooth craniodental morphology, much of the existing literature remains qualitative. Quantitative studies have tended to focus on functional aspects of distinct features of the dentition (Van Valkenburgh and Ruff 1987; Biknevicius et al. 1996; Holliday and Stepan 2004) or the mandible (Therrien 2005), on isolated taxa, particularly *Smilodon fatalis* (Akersten 1985; Bryant 1996a), or on systematics (Matthew 1910; Martin 1980; Kurtén and Werdelin 1990). A notable exception is the study by Emerson and Radinsky (1980), who compared a series of cranial measurements from four lineages of sabertooths with those from their nearest non-sabertoothed relatives. They demonstrated that sabertooths differ from non-sabertooths in various craniodental features, and that these were independently derived in each sa-

bertooth lineage. However, they did not examine trends in sabertooth evolution within or among lineages. The lack of a detailed study of evolutionary trends has led to confusion as to whether the extreme cranial adaptations seen in derived sabertooths evolve as a tightly associated set of characters (e.g., Dawson et al. 1986) or in a mosaic fashion, with different character complexes appearing at different points in time (e.g., Antón et al. 2004a; Salesa et al. 2005).

Sabertooths evolved independently at least four times in Cenozoic mammals: once in marsupials and at least once in each of the Eutherian clades Creodonta, Nimravidae, and Felidae (Riggs 1934; Simpson 1941; Emerson and Radinsky 1980; Turner and Antón 1997; Van Valkenburgh 2007). Although the term "sabertooth" is used generally to describe any carnivore with elongated and laterally compressed canine teeth, two distinct forms have been recognized, and both have also evolved independently on multiple occasions (Kurtén 1968; Martin 1980). Dirk-toothed forms are characterized by extremely elongate upper canine teeth with few or no serrations, and short, robust limbs. Scimitar-toothed forms, in contrast, exhibit shorter canines that are normally coarsely serrated, and long, gracile limbs. The marked differences in gross morphology between the two forms have led some authors to suggest that they may have had different habitat preferences and hunting techniques (e.g., Rawn-Schatzinger 1992; Bryant 1996b). If this is true, then different functional demands may have shaped the evolution of cranial form in different sabertooth lineages, and lumping all sabertooths together is likely to confuse interpretation of evolutionary trends.

Multivariate analyses of morphological variables have yielded abundant information on the dietary and locomotor behavior of living and fossil carnivorans, including sabertooths (e.g., Van Valkenburgh 1988, 1989; Van Valkenburgh and Koepfli 1993; Anyonge 1996; Sacco and Van Valkenburgh 2004; Wesley-Hunt 2005; Friscia et al. 2006). In this paper we explore the evolution of sabertooth cranial adaptations by using geometric morphometrics. Geometric morphometric techniques have several

advantages over traditional morphometric methods (Zelditch et al. 2004). First, geometric methods provide an effective way of separating size and shape information, allowing patterns of shape variation to be studied alone or in relation to size variation. Second, deformation grids can be used to visualize shape changes along particular axes or intermediate forms. Finally, geometric methods make efficient use of available data, as a set of landmarks provides more shape information than a comparable number of linear measurements and angles.

A series of questions relating to the evolution of sabertooth cranial shape are addressed in this paper. Initially, we investigated trends in skull shape evolution among the conical-toothed feline cats. Although this was not the main aim of our study, we felt that documenting general patterns of cranial evolution within the extant clade would provide a useful comparison to their sabertoothed counterparts. We then investigated trends in the evolution of sabertooth cat skull shape. Here, three questions interested us in particular: First, Do independent sabertooth lineages overlap in shape space, providing a strong example of convergent evolution? Second, Do trends in skull shape evolution differ among sabertooth types; i.e., Do dirk- and scimitar-toothed cats cluster separately in shape space? Third, Do cranial features associated with sabertooths evolve gradually, as expected under pleiotropy, or in a more punctuated fashion as might be expected under a mosaic model of evolution? Finally, we investigated whether allometry or gape-related requirements best explain patterns of skull shape evolution within conical and sabertoothed cat lineages.

Our sabertooth sample is drawn from Nimravidae and Felidae. Both families are feliform carnivorans (Hunt 1987; Martin 1998a,b; Wesley-Hunt and Flynn 2005), and their phylogenetic relationships are shown in Figure 1. Together, these taxa constitute the majority of Cenozoic sabertooth diversity.

Nimravidae comprises two clades of mostly sabertoothed taxa. The late Eocene to late Oligocene (37–23 Ma) subfamily Nimravinae contains a number of scimitar and dirk-toothed forms, as well as at least two conical-

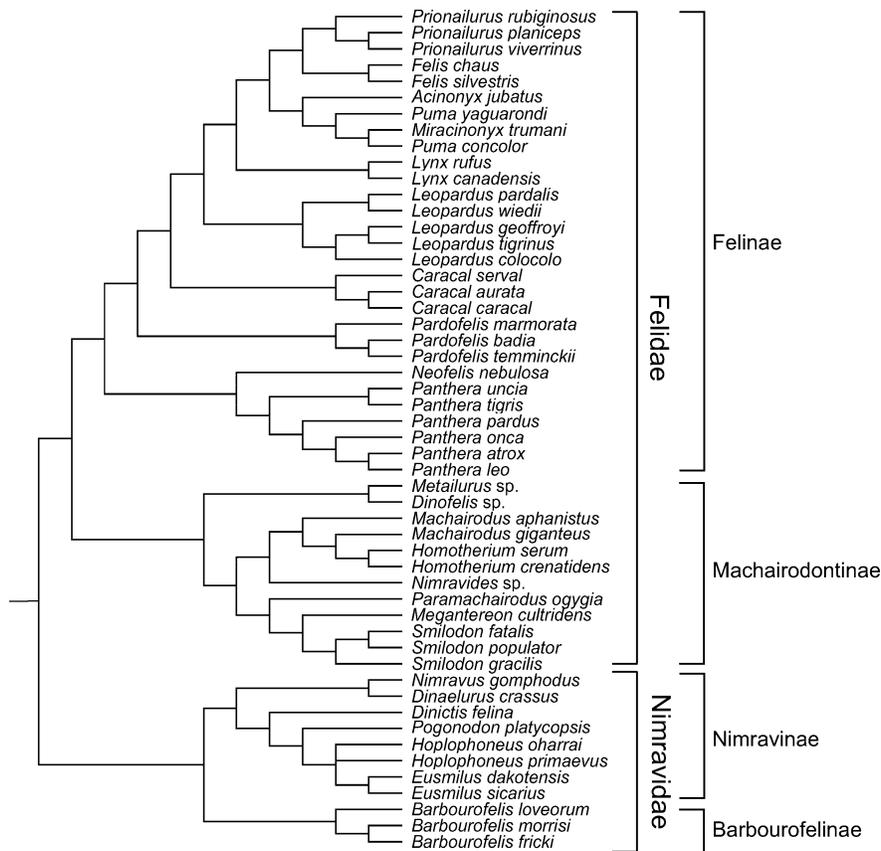


FIGURE 1. Composite phylogeny of taxa included in this study, and used in independent contrasts analyses (see "Methods"). Topology based on Bryant (1996b), Turner and Antón (1997), Antón et al. (2005b), Barnett et al. (2005), and Johnson et al. (2006).

toothed forms (Martin 1998a; Peigné 2001). Members of this subfamily were the dominant Paleogene catlike carnivorans and were distributed throughout the Old and New Worlds. The Miocene subfamily Barbourfelinae originated in Africa, spreading into Eurasia and, finally, North America where the largest and most derived forms, belonging to the genus *Barbourfelis*, existed between 11 and 6 Ma (Martin 1998a; Morlo 2006).

Felidae originated in the early Miocene (ca. 25 Ma) and also contains two subfamilies. Felinae is exclusively conical-toothed and contains all extant cats. The extinct Machairodontinae contains mostly sabertooths, although some taxa converge on a conical-toothed morphology (Werdelin and Lewis 2001). Three tribes are recognized within the Machairodontinae. Metalurini are primitive in morphology, showing only incipient development

of saber-like teeth. Homotheriini contains exclusively scimitar-toothed forms, and Smilodontini contains dirk-toothed forms (Turner and Antón 1997; Martin 1998b).

Materials and Methods

Sample.—We photographed skulls of 29 feline species, 11 machairodont species, and 4 nimravid species with a scale bar in direct lateral view using a Canon EOS-D60 digital SLR camera. Only adult specimens with fully closed basilar synchondroses were included. Sample sizes per species varied from one to 11, depending on availability. Where possible, we selected specimens randomly to avoid biasing our sample toward one sex or geographic locality. A limitation of using landmark methods with fossils is that well-preserved, undeformed, and complete specimens are required, and this in turn limited the number of

species we were initially able to include. To sample more broadly within the sabertooth lineages, we used some published images of fossil taxa, giving preference to published photographs of actual specimens. However, line drawings were also used in cases where this had potential to add significantly to our understanding of evolutionary trends. These alternative data might deviate from accurate representation of the morphology of taxa owing to the figuring of composite specimens or to error. In order to assess the robustness of this data source we conducted a test using published line drawings of taxa for which we had also photographed specimens. We only tested drawings by authors whose figures we wanted to use in this study, as follows: *Nimravus gomphodus* (Cope 1880); *Dinictis squalidens*, *Hoplophoneus primaevus*, and *Smilodon fatalis* (Matthew 1910; note that in this publication figure legends for *D. squalidens* and *H. primaevus* are erroneously switched); and *Barbourofelis morrisoni* (Schultz et al. 1970). In all cases, drawings clustered with photographed specimens of that species, suggesting that their inclusion here is acceptable. Inclusion of published images increased our sample to 12 machairodont species and 11 nimravid species. Species included in this study, sample sizes, and sources of published images are listed in Table 1.

Morphometrics.—We identified 13 morphological landmarks that could adequately describe skull shape in conical-toothed and sabertoothed cats (Fig. 2). Our choice of landmarks was influenced by features preserved in fossils, and by the need to describe overall skull shape adequately, and to capture features typically associated with sabertooths (Matthew 1910; Emerson and Radinsky 1980; Martin 1980; Turner and Antón 1997; Antón et al. 2004a; Salesa et al. 2005;). Although including more landmarks could have uncovered more shape variation, this would also have resulted in missing data or excluded specimens, as many fossils did not preserve all morphological details. We attempted to restrict landmarks to discrete juxtapositions of tissues, points of maximum curvature, or other local processes (Type 1 and 2 landmarks [Bookstein 1991]). Although landmarks 4 and

6 are not ideal when using these criteria, alternative types of landmark were not consistently assessable in these regions. These landmarks were chosen because they were easily and consistently assessable, and they provided necessary information on shape of the facial profile (landmark 4) and temporal fossa depth (landmark 6). Landmarks were digitized onto the images by using tpsDig v.1.40 (Rohlf 2004a).

Skull shape variation was assessed through relative warps analysis (RWA; Bookstein 1991; Rohlf 1993; Zelditch et al. 2004) using tpsRelw v.1.42 (Rohlf 2005). The uniform component of shape variation was included in the RWA, and α was set to 0. As with principal components analysis of linear measurements, relative warps are orthogonal combinations of shape variation, with the first warp describing the greatest amount of shape variation within the data, and consecutive warps describing decreasing amounts of variation. We chose to examine all axes accounting for more than 10% of shape variation. Although this cut-off ignores some aspects of skull shape variation, our focus in this study was on the larger patterns of skull shape change associated with the acquisition of saber-like canine teeth. The 10% cut-off was therefore deemed appropriate for this purpose. RW axes are sensitive to the taxa included in the analysis. Therefore, to assess whether patterns of skull shape variation differ among clades, we performed RWA three times; first using a sample of feline cats only, second using a sample of felines and machairodonts (Felidae), and third using Felidae and Nimravidae. Shape changes along each axis were visualized by using deformation grids.

To test the role of allometry in determining skull shape, we imported landmark coordinates into tpsRegr v.1.30 (Rohlf 2004b) for calculation of centroid sizes. Centroid size is the square root of the sum of squared distances of each landmark from the centroid of the landmark configuration (Bookstein 1991; Zelditch et al. 2004). We also wanted to determine whether canine length, and therefore minimum gape to clear the canines, played a role in driving skull evolution in conical-toothed and sabertoothed carnivores. We used ImageJ v.1.37 (Rasband 2006) to measure canine

TABLE 1. Species included in this study. Parentheses indicate canine morphology (C, conical; S, scimitar; D, dirk) and sample sizes. Taxonomy as follows: Felinae—Johnson et al. (2006); Machairodontinae—Ficarelli (1979), Turner and Antón (1997); Nimravidae—Bryant (1996b), Martin (1998a). Daggers indicate extinct taxa.

FELIDAE	
Felinae	Domestic Cat Lineage
Panthera Lineage	28. <i>Felis chaus</i> (C; 7)
1. <i>Neofelis nebulosa</i> (C; 11)	29. <i>Felis silvestris</i> (C; 9)
2. <i>Panthera uncia</i> (C; 8)	Machairodontinae
3. <i>Panthera tigris</i> (C; 10)	Metailurini
4. <i>Panthera pardus</i> (C; 10)	30. <i>Metailurus</i> sp.† (S; 1)
5. <i>Panthera onca</i> (C; 10)	31. <i>Dinofelis</i> sp.† (S; 2)
6. <i>Panthera leo</i> (C; 10)	Homotheriini
7. <i>Panthera atrox</i> † (C; 7)	32. <i>Nimravides</i> sp.† (S; 1)
Bay Cat Lineage	33. <i>Machairodus aphanistus</i> † (S; 1)
8. <i>Pardofelis marmorata</i> (C; 8)	34. <i>Machairodus giganteus</i> † (S; 1)
9. <i>Pardofelis temminckii</i> (C; 4)	35. <i>Homotherium crenatidens</i> † (S; 4)
10. <i>Pardofelis badia</i> (C; 2)	36. <i>Homotherium serum</i> † (S; 1)
Caracal Lineage	Smilodontini
11. <i>Caracal serval</i> (C; 10)	37. <i>Paramachairodus ogygia</i> † (D; 1)
12. <i>Caracal aurata</i> (C; 7)	38. <i>Megantereon cultridens</i> † (D; 2)
13. <i>Caracal caracal</i> (C; 10)	39. <i>Smilodon gracilis</i> † (D; 1)
Ocelot Lineage	40. <i>Smilodon fatalis</i> † (D; 10)
14. <i>Leopardus pardalis</i> (C; 4)	41. <i>Smilodon populator</i> † (D; 1)
15. <i>Leopardus wiedii</i> (C; 8)	NIMRAVIDAE
16. <i>Leopardus colocolo</i> (C; 7)	Nimravinae
17. <i>Leopardus geoffroyi</i> (C; 10)	42. <i>Dinaelurus crassus</i> † (C; 1)
18. <i>Leopardus tigrinus</i> (C; 8)	43. <i>Nimravus gomphodus</i> † (S; 1)
Lynx Lineage	44. <i>Dinictis felina</i> † (S/D?; 3)
19. <i>Lynx rufus</i> (C; 10)	45. <i>Pogonodon platycopsis</i> † (S; 1)
20. <i>Lynx canadensis</i> (C; 6)	46. <i>Hoplophoneus oharraii</i> † (D; 1)
Puma Lineage	47. <i>Hoplophoneus primaevus</i> † (D; 3)
21. <i>Acinonyx jubatus</i> (C; 10)	48. <i>Eusmilus sicarius</i> † (D; 1)
22. <i>Puma concolor</i> (C; 10)	49. <i>Eusmilus dakotensis</i> † (D; 1)
23. <i>Puma yaguarondi</i> (C; 6)	Barbourofelinae
24. <i>Miracinonyx trumani</i> † (C; 1)	50. <i>Barbourofelis loveorum</i> † (D; 1)
Leopard Cat Lineage	51. <i>Barbourofelis morrissi</i> † (D; 2)
25. <i>Prionailurus rubiginosus</i> (C; 4)	52. <i>Barbourofelis fricki</i> † (D; 1)
26. <i>Prionailurus planiceps</i> (C; 10)	
27. <i>Prionailurus viverrinus</i> (C; 5)	

Note: The following taxa were sampled from published images: 33: Antón et al. 2004a (Fig. 5 – line drawing); 34: Chang 1957 (Plate II, Fig. 1 – photograph); 42: Eaton 1922 (Fig. 4 – line drawing); 43: Matthew 1910 (Fig. 11 – line drawing); 45: Cope 1880 (Fig. 9 – line drawing); 46: Jepson 1933 (Plate I – photograph); 48: Bryant 1988 (Fig. 1B – photograph); 50: Bryant 1988 (Fig. 1A – photograph); 52: Schultz et al. 1970 (Fig. 2A – line drawing)

crown height for each specimen with a complete and unworn canine. The enamel-dentin junction is a more consistent landmark at which to measure canine dimensions than the alveolus, which can be subject to ontogenetic resorption or postmortem damage (Van Valkenburgh and Ruff 1987). However, it was not always possible to measure from the enamel-dentin junction because some fossils, casts, and line drawings did not preserve this feature. Instead we measured from the canine tip to a line drawn along the cingula of the premolars to the incisors, approximating the gin-

gival line. Canine crown height was divided by jaw length (here, the distance from the postglenoid process of the jaw joint to the center of the canine) to produce a relative canine length. Jaw length was chosen instead of an alternative measure of size, because jaw length determines the amount of canine clearance for a given angle of jaw opening (Kiltie 1984, 1988). We regressed average RW scores for each species on species averages for log-transformed centroid sizes and relative canine lengths to determine the degree to which either could predict skull shape in felines, ma-

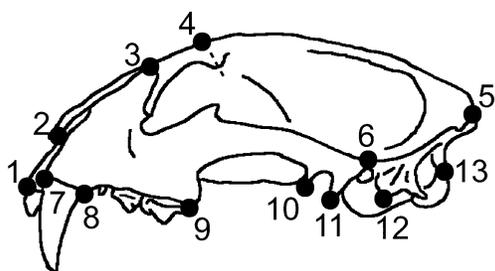


FIGURE 2. Landmarks used to describe cranial shape. 1, most anterior tip of premaxilla; 2, intersection of nasal and premaxilla in photographic plane; 3, maxillofrontal suture at dorsal outline of skull; 4, intersection of a line drawn through center of post orbital process with dorsal outline of skull; 5, most posteroventral point of occipital crest; 6, on the ventral border of temporal fossa, directly superior to the center of the external auditory meatus; 7, anterior border of canine at alveolus; 8, posterior border of canine at alveolus; 9, posterior of carnassial (fourth premolar) at alveolus; 10, ventral tip of preglenoid process; 11, ventral tip of postglenoid process; 12, anteroventral point of mastoid process; 13, intersection of occipital condyle and occiput.

chairodontines, and nimravids. We only used RW axes that appeared to correlate with the development of sabertooth cranial characteristics. Scores were taken from the RWA that included all taxa. Finally, to determine which metric provided the better predictor of skull shape along RW1, we calculated partial correlation coefficients for each, while controlling for the effect of the other.

The hierarchical nature of phylogeny means that similarities in morphology between taxa may be due to common ancestry rather than independent evolution of traits under selection (Felsenstein 1985). We used independent contrasts to determine the strength of the relationship between skull shape and log centroid size and relative canine length after taking phylogeny into account. Contrasts were computed in the PDAP module (Midford et al. 2005) of Mesquite (Maddison and Maddison 2006) using the composite tree topology shown in Figure 1.

Results

Shape changes along RWs 1 and 2, which were the only axes describing more than 10% of shape variation, were very similar in each analysis. We present the results of each analysis below, highlighting the trends in the newly added group in each section. For clarity of

presentation, species averages are shown in relative warp plots. Deformation grids are included at the extremes of each axis to illustrate significant components of shape variation.

Felinae.—The first two axes contained 47.28% and 18.10% of the variance respectively. Variance explained dropped to 8.94% on RW3 and no significant trends were present on inspection of other axes, which mainly highlighted a few individual taxa.

RW1 describes variation in facial shape and occipital angle (Fig. 3). Positive scores on RW1 are associated with more rounded facial profiles, short, down-turned rostra, and shallow occiputs. Negative scores on RW1 are associated with longer, sloping, and upwardly rotated rostra, larger anterior teeth, and more vertical occiputs. Small displacements are also present resulting in more procumbent incisors and an anteriorly displaced mastoid process. RW2 is associated primarily with variation in the shape of the dorsal profile of the face, but also with the height of the occiput. Positive scores on RW2 are associated with more domed profiles and lower occiputs, and negative scores with flatter dorsal profiles. A plot of RW1 against RW2 clearly separates the *Panthera* lineage (open triangles; 1–7). Pantherines are distinguishable by their long, dorsoventrally shallow rostra and high, vertical occiputs. *Acinonyx jubatus* (extant cheetah, 21) and *Miracinonyx* (extinct cheetah-like cat, 24) are clear outliers with fairly low, negative scores for RW1, comparable only to members of the *Panthera* lineage, and extremely high positive scores for RW2, resulting in somewhat longer, domed rostra and low occiputs. *Puma concolor* (puma, 22) falls closer to a cluster of small cats, although its RW1 score is more comparable to the smallest pantherine, *Neofelis nebulosa* (clouded leopard, 1). The remaining *Felinae* cluster to the right on RW1 because of their short rostra, but scatter along RW2.

Machairodontinae.—The first two axes of the analysis including feline and machairodontine felids described 55.27% and 16.03% of the variance, respectively. Variance explained dropped to 8.94% on RW3. RW1 described extremely similar shape changes as in the analysis of felines only, whereas RW2 described

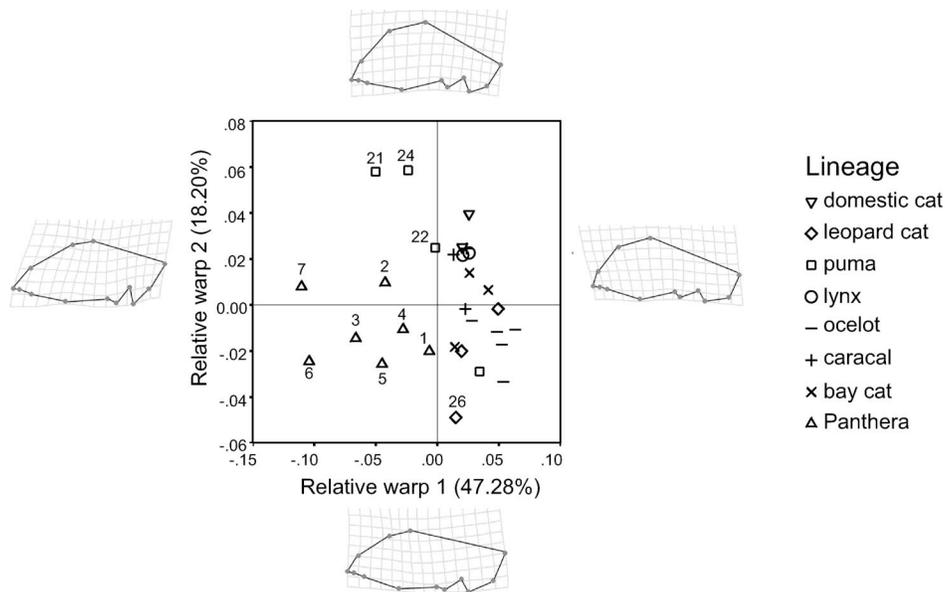


FIGURE 3. Plot of feline species mean scores for Relative Warp 1 against Relative Warp 2. Deformation grids show shape changes at the extremes of each axis. Numbers correspond to Table 1. In this plot, only taxa referred to in the “Results” section are numbered.

somewhat similar shape changes (Fig. 4). Derived sabertooths exhibit lower negative values along this axis than any extant felid. Negative scores along RW1 are associated with dramatic changes in skull geometry, including extremely vertical occiputs and corresponding shortening of the temporal fossa, anterior

displacement of the mastoid process, anteroventral displacement of the jaw joint, lengthening and upward rotation of the rostrum, flattening of the skull above the post-orbital constriction, elevation of the nasals (resulting in flattening of the facial profile dorsally), increased procumbency of the incisors, in-

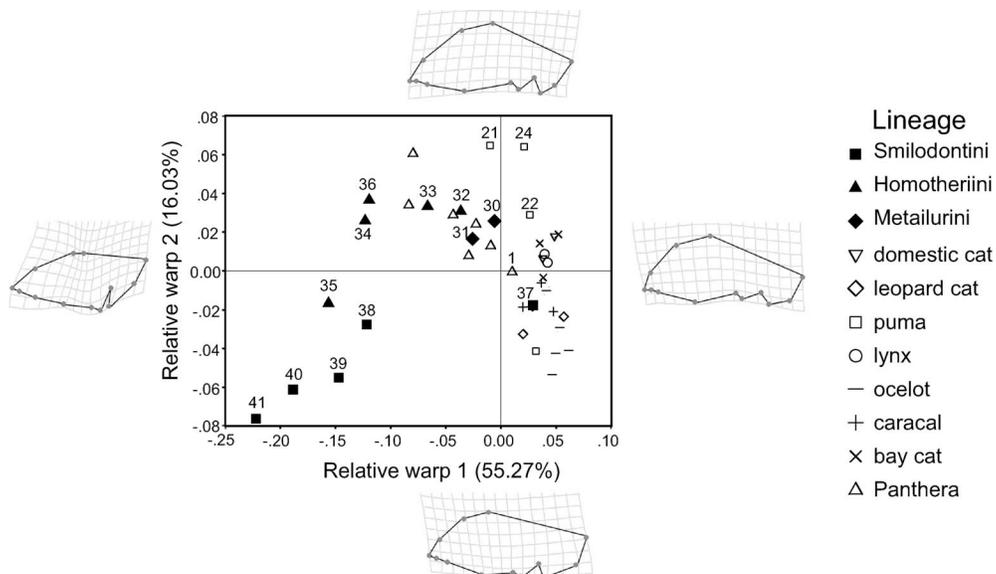


FIGURE 4. Plot of feline and machairodontine species mean scores for Relative Warp 1 against Relative Warp 2. Deformation grids show shape changes at the extremes of each axis. Numbers correspond to Table 1.

creased anteroposterior diameter of the canine, and posterior shortening of the palate. RW2 describes the profile of the face. Positive scores are associated with doming of the skull above the orbit, longer rostra, and sloped occiputs. Negative scores are associated with squared anterior facial profiles and shorter rostra, as well as more vertical occiputs, and anterior movement of the jaw joint and mastoid process.

In a plot of RW1 against RW2, small felines are separated from the *Panthera* lineage + cheetah along RW1. Despite having relatively long upper canine teeth, *N. nebulosa* (1) does not cluster with sabertooths, and instead occupies an intermediate position between small cats and *Panthera* (open triangles) + *A. jubatus*, close to the consensus configuration. The most basal machairodonts in our sample, *Metailurus* (30) and *Dinofelis* (31), both fall within the scatter of the pantherines in this plot. These taxa belong to the basal machairodont tribe, Metailurini (Turner and Antón 1997), and exhibit only slight sabertooth adaptation. Members of the other two lineages, the dirk-toothed Smilodontini and the scimitar-toothed Homotheriini, occupy different parts of this morphospace. The earliest known smilodontine, *Paramachairodus ogygia* (37) falls within the cluster of small felines in the lower right quadrant of Figure 4, indicating a short, squared rostrum in this taxon. The more derived members of this lineage, *Megantereon cultridens* (38) and the genus *Smilodon* (39–41), fall in the lower left quadrant, scoring progressively more negatively on both RW1 and RW2. The distribution of smilodontine taxa along these axes corresponds to their temporal appearance in the fossil record. This suggests that together they describe an evolutionary trajectory in morphospace, resulting from increasingly deeper rostra and more vertical occiputs. In contrast, the homotherine taxa fall mostly within the scatter of the pantherine felids (open triangles), resulting from longer but more sloped rostra. Again, the pattern appears to correspond to appearance in the fossil record, with the older *Nimravides* (32) and *Machairodus aphanistus* (33) falling closer to the consensus configuration than the later *M. giganteus* (34) or *Homotherium* (35, 36). The dis-

tribution of dirk- and scimitar-toothed forms on this plot strongly suggests diverging trajectories in skull shape evolution. An exception to this is *Homotherium crenatidens*, a scimitar-toothed machairodont from the Blancan/Irvingtonian of North America and Villafranchian of Eurasia, approximately 3.5–0.3 Ma (Ficarelli 1979; Jefferson and Tejada-Flores 1993). *H. crenatidens* (35) falls within the lower left quadrant of the morphospace, an area otherwise occupied solely by dirk-toothed cats.

Nimravidae.—The first two axes of this analysis explained 57.06% and 13.34% of the variance respectively and described extremely similar shape changes as in the previous analysis of feline and machairodontine felids (Fig. 5). Variation explained dropped to 7.33% on RW3.

All nimravids have negative scores on RW1, and *Barbourofelis fricki* (52) falls farther to the left on RW1 than any other taxon. RW2 separates taxa by canine morphology. *Dinaelurus* (42) and *Nimravus* (43) score positively on this axis and occupy pantherine/scimitar-tooth morphospace. *Pogonodon* (45) falls within this range along RW1, but is separated from other taxa by a high score on RW2. *Dinaelurus* is one of only two known conical-toothed nimravids (Eaton 1922; Martin 1998a; Peigné 2001), whereas *Nimravus* and *Pogonodon* are both scimitar-toothed. *Dinictis* (44), *Hoplophoneus* (46, 47), *Eusmilus* (48, 49), and *Barbourofelis* (50–52) score negatively and occupy dirk-tooth morphospace. All of these taxa have been described as dirk-toothed, with the exception of *Dinictis*, which is typically referred to as scimitar-toothed (Martin 1998a; Therrien 2005). The positions of the dirk-toothed nimravids in morphospace, particularly along RW1, correspond to stratigraphic and, to some extent, phylogenetic data (Bryant 1996b; Martin 1998a). *Dinictis*, *Hoplophoneus*, and *Eusmilus* appear as successively more derived nimravines, mirroring their chronological appearance in the fossil record. Similarly, the *Barbourofelis* species included fall along RW1 in order of temporal occurrence, with the youngest species exhibiting the lowest RW1 scores.

Allometric Trends.—We tested for allometric trends by using regressions of species RW1 scores on log centroid size and relative canine

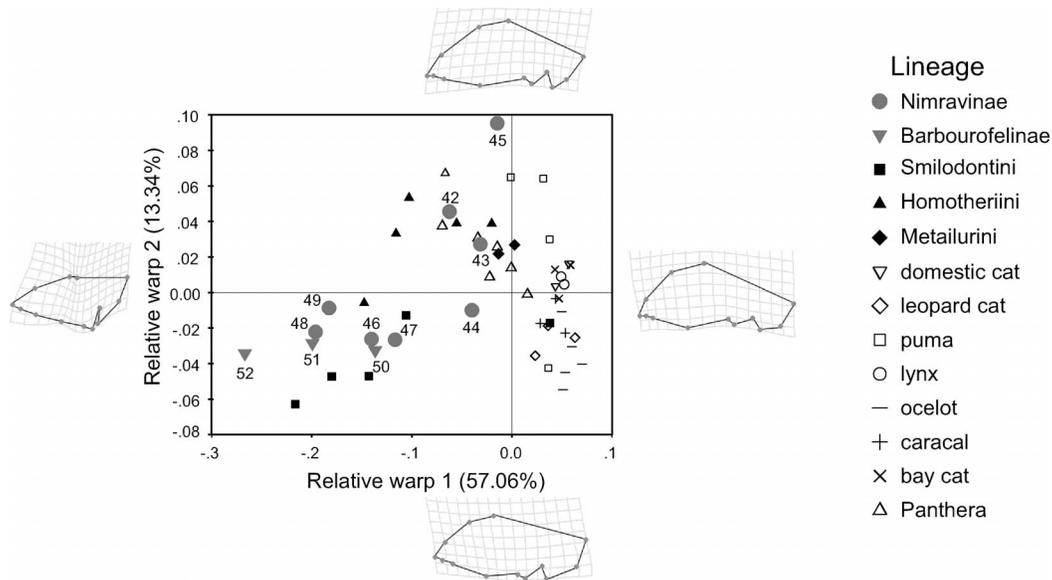


FIGURE 5. Plot of felid and nimravid species mean scores for Relative Warp 1 against Relative Warp 2. Deformation grids show shape changes at the extremes of each axis. Numbers correspond to Table 1.

length. Results of independent contrasts are only given where they contradict analyses using individual species as data points. Due to broken canines and uncertainty as to which species were represented in our sample, we omitted the two metailurine machairodonts, *Metailurus* and *Dinofelis*, from the analyses of relative canine length.

Log centroid size is a significant predictor

of skull shape variation described by RW1 for felines (Fig. 6; $r^2 = 0.89$, $F_{1,28} = 206.855$, $p < 0.001$) but not for machairodonts ($r^2 = 0.32$, $F_{1,11} = 4.787$, $p = 0.54$) or nimravids ($r^2 = 0.10$, $F_{1,8} = 0.08$, $p = 0.4$). To test goodness-of-fit for different predictors of shape between dirk- and scimitar-teeth, we ran separate regression analyses for Homotheriini, Smilodontini, and dirk-toothed nimravids (scimitar-toothed

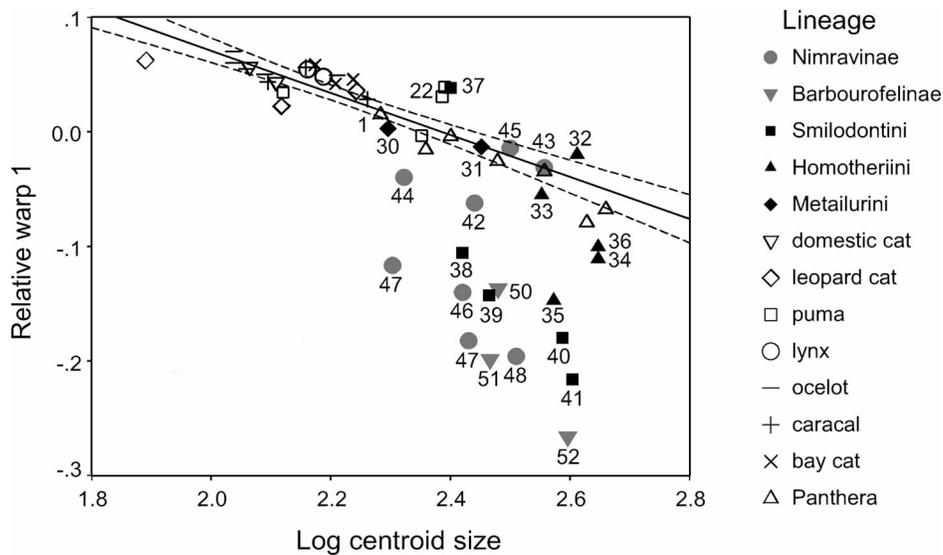


FIGURE 6. Regression of mean species RW1 scores on mean species log centroid sizes. Regression line and 95% confidence intervals are calculated for Felinae only.

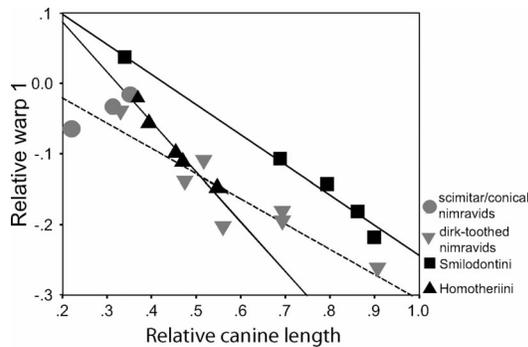


FIGURE 7. Regression of species mean RW1 scores on species mean relative canine length for sabertoothed taxa. Solid regression lines are for Homotheriini and Smilodontini; broken regression line is for dirk-toothed nimravids.

nimravids were not included in the regression analyses because of a small sample size [$n = 3$]). However, log centroid size was not found to be a significant predictor of shape for sabertooths at these levels either.

Regression of relative canine length on RW1 score was also significant for Felinae ($r^2 = 0.25$, $F_{1,28} = 9.174$, $p = 0.005$), and this fit improved when the aberrant *N. nebulosa* was removed ($r^2 = 0.39$, $F_{1,27} = 16.59$, $p < 0.001$). However, this result was not recovered when independent contrasts were performed ($r^2 = 0.004$, $F_{1,27} = 0.114$, $p = 0.73$). Regressions for sabertoothed taxa were significant for relative canine length (Machairodontinae: $r^2 = 0.73$, $F_{1,9} = 22.029$, $p = 0.002$; Nimravidae: $r^2 = 0.85$, $F_{1,8} = 40.058$, $p < 0.001$), and improved in analyses using dirk- or scimitar-teeth only (Fig. 7; Smilodontini: $r^2 = 0.98$, $F_{1,4} = 190.108$, $p = 0.001$; Homotheriini: $r^2 = 0.096$, $F_{1,4} = 69.322$, $p = 0.004$; dirk-toothed Nimravids: $r^2 = 0.88$, $F_{1,5} = 27.967$, $p = 0.006$). An F -test for

homogeneity of slopes (Sokal and Rohlf 1995) reveals that the homotherine and smilodontine lines differ significantly from each other ($F_{1,6} = 27.291$, $p < 0.001$), with Homotheriini showing greater shape change for a given increase in canine length.

Partial correlation coefficients were calculated to control for the effect of one variable while allowing the other to vary. They indicate that log centroid size is the better predictor of RW1 score for Felinae (Table 2). Both log centroid size and relative canine length are significant predictors of shape along RW1 for Machairodontinae as a whole, but only relative canine length is significant for the Homotheriini, Smilodontini, and Nimravidae.

Discussion

Geometric morphometric techniques succeeded in uncovering patterns of skull shape variation and evolution in both conical and sabertoothed cats. Cranial morphology of the Felinae is homogeneous compared to the diversity seen in other carnivoran families such as canids or viverrids (Martin 1980; Radinsky 1981; Van Valkenburgh and Koepfli 1993), and this probably reflects their extreme adaptations to hypercarnivory (Van Valkenburgh 1988; Holliday and Steppan 2004). However, a large amount of variation is present along RW1 (Fig. 3). Members of the large-bodied *Panthera* lineage cluster to the left on RW1 with more negative scores than other felines except *Acinonyx* and *Miracinonyx*, the two largest non-pantherines in our sample. These larger felines tend to have longer, slightly upturned rostra and taller, more vertical occiputs than the smaller felines. Additional shape var-

TABLE 2. Partial correlation coefficients for relative warp one scores with log centroid size (CS) and relative canine length (RCL). Asterisks indicate significant correlations.

Lineage	RW1 vs. Log CS		RW1 vs. RCL		DF
	Controlling for RCL	p	Controlling for Log CS	p	
Felinae	-0.9195	<0.001*	-0.0356	0.857	26
Felinae (minus <i>Neofelis</i>)	-0.9006	<0.001*	-0.0563	0.780	25
Machairodontinae	-0.7818	0.013*	-0.737	0.023*	7
Homotheriini	-0.5125	0.488	-0.9842	0.016*	2
Smilodontini	-0.3429	0.657	-0.9783	0.022*	2
Nimravidae	0.0272	0.941	-0.9173	<0.001*	8
Dirk-toothed nimravids	-0.618	0.139	-0.8109	0.027*	5

iation is present along RW2 and separates *Acinonyx* and *Miracinonyx* from other taxa by virtue of domed facial shapes. This morphology is associated with enlarged nasal passages in the extant cheetah, which is a high-speed cursor (Ewer 1973; Sunquist and Sunquist 2002). The independent acquisition of this morphology in *Miracinonyx* provides some support for a similar locomotor behavior in the North American Pleistocene taxon, as previously inferred from post-cranial anatomy (Adams 1979; Van Valkenburgh et al. 1990)

The dramatically enlarged canine teeth and extreme cranial modifications observed in sabertoothed carnivores suggest that they should cluster away from conical-toothed felids in morphospace. The most derived sabertoothed taxa, such as *Smilodon* and *Barbourofelis*, do fall well outside the scatter of feline cats, owing to extremely low scores on RW1 (Figs. 4, 5). Elongation of the upper canines is more extreme in even moderately derived sabertooths than in the largest felines, and it is therefore not surprising that the degree of cranial modification seen in these taxa is greater. Inspection of deformation grids for the lowest scores on RW1 reveals that most of the shape changes described on this axis are, unsurprisingly, associated with increasing gape while maintaining or enhancing bite force. Elongation of the upper canines results in more extreme elongation and upward rotation of the face and ventral depression of the jaw joint, both of which increase maximum possible gape. These shape changes are correlated with anteroventral displacement of the mastoid process, which enhances the leverage of the head-depressing musculature, in particular the *m. obliquus capitis cranialis* (Antón et al. 2004b). Akersten (1985) argued that this complex would have been used to drive a shallow canine shear bite as the jaw-adducting musculature became weaker through gape-related modification (Wroe et al. 2005; McHenry et al. 2007). Our finding that these shape changes correlate strongly with canine length lends additional support to his model. However, domestic cats have been observed to use dorsoventral cranial movements during feeding (Gorniak and Gans 1980), indicating that these muscles might play a significant role in

biting and feeding in non-sabertoothed taxa as well.

Rotation of the occipital plane and shortening of the temporal fossa are common to all sabertoothed taxa included here, as well as the larger, pantherine felids, and might have served both to facilitate gape and to maintain bite force. Martin (1980) suggested that the vertical occiput of *Barbourofelis* might have allowed greater dorsiflexion of the head during wide gaping. Alternatively, Bryant (1996a) has shown that the reduced coronoid process of the mandible in sabertooths (which reduces stretching of the jaw-adducting musculature during wide gaping [Herring 1975]), results in a more anteriorly oriented lever arm for the temporalis muscle compared with feline cats. The occiput of sabertoothed taxa is rotated vertically, resulting in a shorter and more anteriorly positioned temporal fossa than in feline cats (Figs. 3–5), and a corresponding re-orientation of the line of action of the temporalis musculature to more anterior and vertical. This would have allowed the temporalis of sabertooths to generate torque about the jaw joint comparable to that of feline cats at large gapes, despite the reduced lever arm (Bryant 1996a).

The inclusion of basal taxa from each sabertoothed lineage reveals an intriguing pattern. Sabertooth cranial adaptations appear to develop primarily along the axis of variation described by RW1, which is very similar in separate analyses of conical-toothed felines and sabertooths. Early sabertooths, such as *Machairodus*, *Paramachairodus*, and *Dinictis*, fall among or close to large felines along RW1 (Figs. 4, 5), rather than farther to the left with the more derived taxa. The relative positions of sabertooths along RW1 reflect their appearance in the fossil record, with older taxa having higher scores and younger taxa falling progressively farther away with lower scores. Moreover, this pattern occurs iteratively in different sabertoothed lineages, regardless of phylogenetic affinity or canine morphology. Although the most derived sabertooths reach a portion of morphospace that conical-toothed felids do not, the overlap of basal sabertooths with felines suggests that skull shape evolution has proceeded in similar ways and direc-

tions in both. Derived sabertooth cranial shapes are, in many regards, simply more extreme versions of feline cat skull shapes. The patterns of repeated, parallel convergence along RW1, without an increase in overall similarity, correspond to the Type 3 convergence described by Stayton (2006).

It should be mentioned here that our analysis failed to find much similarity between the extant *Neofelis nebulosa* and sabertoothed carnivores (contra Christiansen 2006, 2008). *N. nebulosa* possesses extremely long upper canine teeth, similar in relative crown height to basal sabertooths such as *Dinictis* and *Paramachairodus*. However, they are conical in cross-section, in contrast with the laterally compressed upper canine teeth of sabertooths (Martin 1980; Van Valkenburgh and Ruff 1987; Salesa et al. 2005; Werdelin and Sardella 2006). Christiansen (2008) used a geometric morphometric approach to show that craniomandibular shape of *N. nebulosa* is more similar to the basal smilodontine *P. ogygia* than to other pantherine felids. In our study, which included an additional 23 species of small felines as well as many other sabertoothed taxa, *N. nebulosa* consistently fell between the pantherine and small felines (Figs. 3–5). Because basal sabertooths from all lineages have similar scores along RW1 to felines, some features of cranial shape are common to both. However, given that the clouded leopard scores close to zero on RW1, it cannot be considered to exhibit any sabertooth characteristics; rather *P. ogygia* and other basal sabertooths might better be described as having a skull shape more similar to conical-toothed felids than to derived sabertooths. Furthermore, all other *Panthera* exhibit more sabertooth-like cranial shapes than *N. nebulosa*. This finding emphasizes that long upper canines are not always associated with the same suite of cranial morphologies.

Both families of sabertoothed carnivores included in our study produced dirk- and scimitar-toothed taxa (Table 1) (Kurtén 1968; Martin 1980). Although sabertooth evolution proceeds along RW1 in general, our results show that dirk- and scimitar-toothed forms diverge in morphospace (Figs. 4, 5). Scimitar-toothed forms cluster close to pantherine felids, which is unsurprising given their relatively short ca-

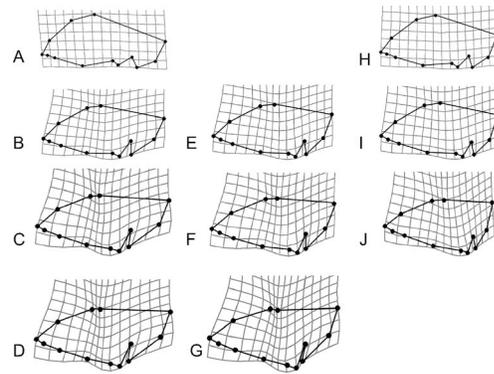


FIGURE 8. Deformation grids showing similarity in patterns of skull shape variation among three lineages of dirk-toothed carnivores: A–D, Smilodontini; E–G, Barbourofelinae; H–J, Nimravinae. Species: A, *Paramachairodus ogygia*; B, *Megantereon cultridens*; C, *Smilodon fatalis*; D, *S. populator*; E, *Barbourofelis loveorum*; F, *B. morrissi*; G, *B. fricki*; H, *Dinictis felina*; I, *Hoplophoneus primaevus*; J, *Eusmilus* sp.

nine teeth. However, scimitar-tooths do show a gradual increase in relative canine length throughout their evolutionary histories, particularly in the Homotheriini, and this results in progressive increases in gape-related adaptation (Fig. 7). Dirk-tooths occupy a unique portion of morphospace, owing to low scores on both RW1 and RW2 (Figs. 4, 5). This likely reflects the combined demands of facilitating gape (RW1) and accommodating the roots of long canine teeth within a deeper face (RW2). When dirk- or scimitar-toothed forms from all three lineages are compared, they overlap extensively in morphospace, with scimitar-tooths also overlapping pantherine felids. Occupation of the same area of morphospace is evidence of traditional, or Type 1 convergence (as opposed to incomplete, or Type 2, convergence, where taxa only trend toward the same area of morphospace [Stayton 2006]). Because the relative positions of sabertoothed taxa also correspond to their appearance in the fossil record (Figs. 4, 5), we interpret these patterns as representing evolutionary trajectories in morphospace. Trajectories for independent lineages also overlap, providing strong evidence for repeated convergent evolution of sabertoothed carnivores. Patterns of Type 1 convergence are particularly striking when the three dirk-toothed lineages are compared (Fig. 8). The four smilodontine taxa span a

range of progressively more derived cranial shapes, from feline-like (*Paramachairodus*, Fig. 8A) to an extreme sabertooth (*Smilodon populator*, Fig. 8D). The Barbourofelinae (Fig. 8E–G) contains forms that are extremely similar to the latest three smilodontines. The three taxa that we were able to sample in this study are New World barbourofelines, and they represent the youngest and most derived forms in the lineage. Less derived barbourofelines, such as *Sansanosmilus*, are known from the Old World (Morlo 2006), and we predict that they exhibit cranial shapes more similar to those of *Paramachairodus* or *Dinictis*. The Nimravinae (Fig. 8H–J) contains forms that are very similar to the three earliest smilodontines. It is unclear why there was not a more derived nimravine than *Eusmilus*. Our sample, which contained only New World taxa, may have affected this result, although available evidence for this is equivocal (Peigné 2003). Other possible reasons include patterns of prey availability or clade age, but all require further investigation. Regardless, the similarity in the evolutionary pathways seen in nimravid and felid sabertooths is striking and suggests that the transition to this extreme morphology makes functional demands that can be met in a limited number of ways.

Dirk- and scimitar-toothed forms also differ in their postcranial anatomy and are often found sympatrically in fossil assemblages. This has led some to argue for ecological separation through different habitat and prey preferences (Bryant 1996b; Turner and Antón 1997; Antón et al. 2005; Salesa et al. 2006). Isotopic evidence from two sympatric machairodonts from the lower Pleistocene of Europe supports the notion that the two forms utilized different prey types (Palmqvist et al. 2003). The amount of cranial shape change for a given increase in canine length differs between dirk- and scimitar-tooths (Fig. 7), and further suggests that different functional demands drove the evolution of these two forms.

Regression of species RW1 scores onto both log centroid size and relative canine length suggests that different factors may drive skull shape evolution in conical and sabertoothed cats, despite similar trends along that axis. Skull shape variation on RW1 for felines is

best predicted by size, but is unrelated to canine length. This suggests that the largest amount of skull shape variation in felines (47.28%) is driven by allometry, rather than functional or phylogenetic factors. Werdelin (1983) also noted size related differences in skull shape between small and large felines. Interestingly, he further pointed out that *Puma concolor* appeared to retain cranial proportions of small cats despite reaching large body size. The RW1 score for *P. concolor* (22) is extremely high for a cat of its body size, falling well outside the 95% confidence intervals of the regression (Fig. 6), supporting Werdelin's (1983) assertion that *P. concolor*'s skull shape is more akin to that of an isometrically enlarged small cat than that of a large cat. The RW1 score for the similarly sized *N. nebulosa* is as predicted for a feline of its body size.

Skull shape along RW1 in sabertoothed taxa is best predicted by canine length, rather than body size. Sabertooths do exhibit phyletic increases in body size throughout their history, as indicated by the significant partial correlation coefficient for log centroid size for the Machairodontinae (Table 2). Such a trend is expected within a lineage of specialized hypercarnivores (Van Valkenburgh et al. 2004). However, relative canine length is a better predictor of this component of skull shape variation within sabertoothed lineages (Table 2, Fig. 7). Clearing the tips of the canine teeth appears to have exerted such strong morphological demands on the skull that it over-rode allometric shape determination in these taxa. Significantly, meeting these demands was, in part, accomplished by exaggerating the pattern of allometric skull shape variation seen in conical-toothed cats.

The presence of elongate upper canines combined with the lack of sabertooth cranial features in basal machairodonts and *N. nebulosa* has led some authors to suggest that sabertooth characteristics may arise through mosaic evolution (Antón et al. 2004a; Salesa et al. 2005, 2006). Mosaic evolution occurs when characters differ in their rates of evolution, and it results in taxa that display a mix of primitive and derived features (Futuyma 1986). We would expect sabertoothed taxa not to overlap at all with conical-toothed taxa in

morphospace if sabertooth adaptations instead arose pleiotropically, as a developmentally, functionally, or genetically linked suite of characteristics (e.g., Dawson et al. 1986). Although we do observe trends in cranial modification associated with elongation of the canines, it is important to note that saber-like canine teeth always predate the appearance of derived cranial morphologies as expected under a mosaic model of evolution. This is not surprising; clades often exhibit mosaics of phenotypic traits close to their origin (e.g., Qiang et al. 1999; Rae 1999). Early sabertooths overlap extensively with conical-toothed cats in morphospace, despite the presence of longer, saber-like canines. Gape-related adaptations are completely lacking in *Paramachairodus ogygia*, for example, which scores higher on RW1 than any other sabertoothed taxon and well within the range of felines. Although the suggestion of mosaic evolution has been based only on evidence from machairodont felids (Antón et al. 2004a; Salesa et al. 2005), this pattern is repeated in the nimravids, where *Dinictis*, *Pogonodon*, and *Nimravus* all fall within the range of feline scores on RW1, despite well-developed saberteeth.

The lack of derived features in early sabertooths suggests that the initial shift to laterally flattened and elongate canines probably did not require much change in prey killing behavior, compared to feline cats. While this is understandable under a mosaic model of evolution, it does not help us understand what functional advantage saber-like canine teeth might have provided. Visual signals play an important role in communication among carnivores (Ewer 1973), and it seems plausible that this may explain the evolution of elongate canines. The canine teeth are extremely conspicuous and are used in display and agonistic encounters in extant species, as well as during predation. Sexual selection should favor enlarged canines in social systems where males compete intensely for access to females, and Gittleman and Van Valkenburgh (1997) have shown that within Carnivora, uni-male, group-living species exhibit the greatest canine dimorphism. However, sabertooths appear to exhibit only moderate amounts of dimorphism in canine proportions, suggesting

that sexual selection is unlikely to be responsible for canine enlargement in these taxa (Van Valkenburgh and Sacco 2002; Salesa et al. 2006). Felids display bared-teeth expressions in all agonistic encounters, including those between species (Schaller 1972; Ewer 1973; Leyhausen 1979), and an alternative explanation for the evolution of saber teeth is that they could have been used in interference competition. Kleptoparasitism may be favored when the cost of killing a prey item is higher than the cost of driving another predator from its kill. A carcass requires less energy to acquire than live prey, and the risk of sustaining a hunting injury is also reduced (Creel 2001). Any feature that enhances a predator's threat display would increase its chances of driving another predator from a kill, or of defending its own kill from scavengers. However, given that gape-related features of the skull reduce bite force (Wroe et al. 2005) and that saberteeth are inherently more likely to break under unpredictable loading (Van Valkenburgh and Ruff 1987), it seems unlikely that interference competition alone would have driven the evolution of sabertoothed carnivores.

Shape changes associated with reorientation of jaw and neck musculature support the view that sabertooth adaptations are functional and relate to predatory behavior (Emerson and Radinsky 1980; Akersten 1985; Bryant 1998a; McHenry et al. 2007). If this is the case, how did the predatory behavior of sabertooths differ from that of large living cats? Freeman and Leman (2006) have recently shown that canines with anterior and posterior edges, such as those of sabertoothed taxa, are better suited than conical canines for piercing tough but ductile materials. This is because edges concentrate stress and propagate cracks in a predictable and efficient fashion (Gordon 1978). As a result, less force is required to penetrate vertebrate flesh with an edged canine (Freeman and Leman 2006). Large felines rarely penetrate the skin of their prey with the canines. Instead, suffocation through a throat or muzzle bite is the most common method for dispatching large prey (Schaller 1972; Bailey 1993). This can be a lengthy process, however. For example, Schaller (1972) observed that it took ten minutes for

a pride of lions (*Panthera leo*) to kill a wounded and exhausted adult buffalo (*Syncerus caffer*). A piercing bite, such as the canine shear bite (Akersten 1985) could have allowed saber-tooths to kill prey faster than conical-toothed cats could, limiting their risk of injury during the kill (Salesa et al. 2006). Moreover, fossil carnivore guilds tend to contain more large species than modern faunas (Van Valkenburgh 1988, 1989, 1995, 1999) and competition for access to carcasses was probably intense. A quicker kill may have resulted in less noise from a struggling prey item, giving the saber-tooth more time to feed before scavengers arrived. Evolution of this extreme predator type might therefore be best understood in the context of high levels of competition in past carnivore faunas (e.g., Van Valkenburgh and Hertel 1993; Leonard et al. 2007).

In summary, the evolution of saber-like canine teeth is accompanied by massive reorganization of the skull to accommodate wide gaping and to compensate for stretching muscles while maintaining bite force. Using a geometric morphometric approach, we have been able to gain a better understanding of the evolutionary trends in sabertooth skull evolution. Our analysis refutes earlier ideas that the evolution of sabertooth cranial morphology was under strong pleiotropic control. Instead, we find support for the recent suggestion that early sabertooths arose through mosaic evolution, with saber-like teeth appearing in concert with relatively unspecialized cranial morphologies. Subsequent elongation of the canine teeth resulted in compensatory changes in cranial shape, eventually producing the extreme morphologies seen in derived sabertoothed taxa. The level of convergence between independent sabertooth lineages, as well as with larger, conical-toothed cats, suggests that wide gaping makes extreme demands on the skulls of carnivores, and that there is a limited number of ways that these demands can be met.

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Literature Cited

- Adams, D. B. 1979. The cheetah: native American. *Science* 205: 1155–1158.
- Akersten, W. A. 1985. Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae). *Los Angeles County Museum Contributions in Science* 356:1–22.
- Antón, M., A. Galobart, and A. Turner. 2005. Co-existence of scimitar-toothed cats, lions and hominins in the European Pleistocene: implications of the post-cranial anatomy of *Homotherium latidens* (Owen) for comparative palaeoecology. *Quaternary Science Review* 24:1287–1301.
- Antón, M., M. J. Salesa, J. Morales, and A. Turner. 2004a. First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus* (Felidae, Carnivora) from the Spanish Late Miocene site of Batallones-1. *Journal of Vertebrate Paleontology* 24:957–969.
- Antón, M., M. J. Salesa, J. F. Pastor, I. M. Sanchez, S. Fraile, and J. Morales. 2004b. Implications of the mastoid anatomy of larger extant felids for the evolution and predatory behaviour of sabretoothed cats (Mammalia, Carnivora, Felidae). *Zoological Journal of the Linnean Society* 140:207–221.
- Anyonge, W. 1996. Locomotor behaviour in Plio-Pleistocene sabre-toothed cats: a biomechanical analysis. *Journal of Zoology* 238:395–413.
- Bailey, T. N. 1993. *The African leopard: ecology and behavior of a solitary felid*. Columbia University Press, New York.
- Barnett, R., I. Barnes, M. J. Phillips, L. D. Martin, C. R. Harington, J. A. Leonard, and A. Cooper. 2005. Evolution of the extinct sabretooths and the American cheetah-like cat. *Current Biology* 15:R589–R590.
- Biknevicius, A. R., B. Van Valkenburgh, and J. Walker. 1996. Incisor size and shape: implications for feeding behavior in sabertoothed “cats.” *Journal of Vertebrate Paleontology* 16:510–521.
- Bookstein, F. L. 1991. *Morphometric tools for landmark data*. Cambridge University Press, Cambridge.
- Bryant, H. N. 1988. Delayed eruption of the deciduous upper canine in the sabertoothed carnivore *Barbourofelis lovei* (Carnivora, Nimravidae). *Journal of Vertebrate Paleontology* 8: 295–306.
- . 1996a. Force generation by the jaw adductor musculature at different gapes in the Pleistocene sabertoothed felid *Smilodon*. Pp. 283–299 in K. M. Stewart and K. L. Seymour, eds. *Palaeoecology and palaeoenvironments of Late Cenozoic mammals—tributes to the career of C. S. (Rufus) Churcher*. University of Toronto Press, Toronto.
- . 1996b. Nimravidae. Pp. 453–475 in D. R. Prothero and R. J. Emry, eds. *The terrestrial Eocene-Oligocene transition in North America*. Cambridge University Press, Cambridge.
- Chang, H.-C. 1957. On new material of some machairodonts of Pontian age from Shansi. *Vertebrata Palasiatica* 1:193–200.

- Christiansen, P. 2006. Sabertooth characters in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). *Journal of Morphology* 267:1186–1198.
- . 2008. Evolutionary convergence of primitive sabertooth craniomandibular morphology: the clouded leopard (*Neofelis nebulosa*) and *Paramachairodus ogygia* compared. *Journal of Mammalian Evolution*. doi 10.1007/s10914-007-9069-z
- Cope, E. D. 1880. On the extinct cats of North America. *American Naturalist* 14:833–858.
- Creel, S. 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology* 15:271–274.
- Dawson, M. R., R. K. Stucky, L. Krishtalka, and C. C. Black. 1986. *Machaeroides simpsoni*, new species, oldest known sabertooth creodont (Mammalia), of Lost Cabin Eocene. *Contributions to Geology, University of Wyoming, Special Paper* 3: 177–182.
- Eaton, G. F. 1922. John Day Felidae in the Marsh Collection. *American Journal of Science* 204:425–452.
- Emerson, S. B., and L. Radinsky. 1980. Functional analysis of sabertooth cranial morphology. *Paleobiology* 6:295–312.
- Ewer, R. F. 1973. The carnivores. Weidenfeld and Nicolson, London.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Ficarella, G. 1979. The Villafranchian machairodonts of Tuscany. *Palaontographia Italica* 71:17–26.
- Freeman, P. W., and C. Lemen. 2006. Puncturing ability of idealized canine teeth: edged and non-edged shanks. *Journal of Zoology* 269:51–56.
- Frischia, A. R., B. Van Valkenburgh, and A. R. Biknevicius. 2006. An ecomorphological analysis of extant small carnivores. *Journal of Zoology* 272:82–100.
- Futuyma, D. J. 1986. *Evolutionary biology*, 2d ed. Sinauer, Sunderland, Mass.
- Gittleman, J. L., and B. Van Valkenburgh. 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology* 242: 97–117.
- Gordon, J. E. 1978. *Structures, or why things don't fall down*. Da Capo Press, New York.
- Gorniak, G. C., and C. Gans. 1980. Quantitative assay of electromyograms during mastication in domestic cats (*Felis catus*). *Journal of Morphology* 163:253–281.
- Herring, S. W. 1975. Adaptations for gape in the hippopotamus and its relatives. *Forma et Functio* 8:85–100.
- Holliday, J. A., and S. J. Steppan. 2004. Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. *Paleobiology* 30:108–128.
- Hunt, R. M., Jr. 1987. Evolution of the aeluroid Carnivora: significance of auditory structure in the nimravid cat *Dinictis*. *American Museum Novitates* 2886:1–74.
- Jefferson, G. T., and A. E. Tejada-Flores. 1993. The Late Pleistocene record of *Homotherium* (Felidae: Machairodontinae) in the Southwestern United States. *PaleoBios* 15:37–46.
- Jepson, G. L. 1933. American eusmiloid sabre-tooth cats of the Oligocene epoch. *Proceedings of the American Philosophical Society* 72:355–369.
- Johnson, W. E., E. Eizirik, J. Pecon-Slatery, W. J. Murphy, A. Antunes, E. Teeling, and S. J. O'Brien. 2006. The Late Miocene radiation of modern Felidae: a genetic assessment. *Science* 311:73–77.
- Kiltie, R. A. 1984. Size ratios among sympatric neotropical cats. *Oecologia* 61:411–416.
- . 1988. Interspecific size regularities in tropical felid assemblages. *Oecologia* 76:97–105.
- Kurtén, B. 1968. Pleistocene mammals of Europe. Aldine, Chicago.
- Kurtén, B., and L. Werdelin. 1990. Relationships between North and South American *Smilodon*. *Journal of Vertebrate Paleontology* 10:158–169.
- Leonard, J. A., C. Vila, K. Fox-Dobbs, P. L. Koch, R. K. Wayne, and B. Van Valkenburgh. 2007. Megafaunal extinctions and the disappearance of a specialized wolf ecomorph. *Current Biology* 17:1146–1150.
- Leyhausen, P. 1979. *Cat behavior: the predatory and social behavior of domestic and wild cats*. Garland STPM Press, New York.
- Maddison, W. P., and D. R. Maddison. 2006. Mesquite: a modular system for evolutionary analysis, Version 1.12. <http://mesquiteproject.org>.
- Martin, L. D. 1980. Functional morphology and the evolution of cats. *Transactions of the Nebraska Academy of Sciences* 8: 141–154.
- . 1998a. Nimravidae. Pp. 228–235 in C. M. Janis, K. M. Scott, and L. L. Jacobs, eds. *Evolution of Tertiary mammals of North America, Vol. 1. Terrestrial carnivores, ungulates and ungulate-like mammals*. Cambridge University Press, Cambridge.
- . 1998b. Felidae. Pp. 236–242 in C. M. Janis, K. M. Scott, and L. L. Jacobs, eds. *Evolution of Tertiary mammals of North America, Vol. 1. Terrestrial carnivores, ungulates and ungulate-like mammals*. Cambridge University Press, Cambridge.
- Matthew, W. D. 1910. The phylogeny of the Felidae. *Bulletin of the American Museum of Natural History* 27:289–316.
- McHenry, C. R., S. Wroe, P. D. Clausen, K. Moreno, and E. Cunningham. 2007. Supermodeled sabercat, predatory behavior in *Smilodon fatalis* revealed by high-resolution 3D computer simulation. *Proceedings of the National Academy of Sciences USA* 104:16010–16015.
- Midford, P. E., T. Garland Jr., and W. P. Maddison. 2005. PDAP Package of Mesquite. Version 1.07. http://mesquiteproject.org/pdap_mesquite/index.html
- Morlo, M. 2006. New remains of Barbourfelidae (Mammalia, Carnivora) from the Miocene of Southern Germany: implications for the history of barbourfelid migrations. *Beiträge zur Paläontologie* 30:339–346.
- Palmqvist, P., D. R. Grocke, A. Arribas, and R. A. Farina. 2003. Paleoeological reconstruction of a lower Pleistocene large mammal community using biogeochemical ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, Sr: Zn) and ecomorphological approaches. *Paleobiology* 29:205–229.
- Peigné, S. 2001. A primitive nimravine skull from the Quercy fissures, France: implications for the origin and evolution of Nimravidae (Carnivora). *Zoological Journal of the Linnean Society* 132:401–410.
- . 2003. Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Paleogene Nimravidae. *Zoologica Scripta* 32:199–229.
- Qiang, J., L. Zhexi, and J. Shu-an. 1999. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature* 398:326–330.
- Radinsky, L. 1981. Evolution of skull shape in carnivores. 1. Representative modern carnivores. *Biological Journal of the Linnean Society* 15:369–388.
- Rae, T. C. 1999. Mosaic evolution in the origin of the Hominoidea. *Folia Primatologica* 70:125–135.
- Rasband, W. S. 2006. ImageJ, v.1.37. U.S. National Institutes of Health, Bethesda, Md. <http://rsb.info.nih.gov/ij/>
- Rawn-Schatzinger, V. 1992. The scimitar cat *Homotherium serum* Cope: osteology, functional morphology, and predatory behavior. *Illinois State Museum Reports of Investigations* 47:1–80.
- Riggs, E. S. 1934. A new marsupial saber-tooth from the Pliocene of Argentina and its relationships to other South Amer-

- ican predacious marsupials. *Transactions of the American Philosophical Society* 24:1–32.
- Rohlf, F. J. 1993. Relative-warp analysis and an example of its application to mosquito wings. Pp. 131–159 in L. F. Marcus, E. Bello, and A. García-Valdecasas, eds. *Contributions to morphometrics*, Vol. 8. Museo Nacional de Ciencias Naturales, Madrid.
- . 2004a. tpsDig, digitize landmarks and outlines, Version 1.40. Department of Ecology and Evolution, State University of New York at Stony Brook.
- . 2004b. tpsRegr, shape regression, Version 1.30. Department of Ecology and Evolution, State University of New York at Stony Brook.
- . 2005. tpsRelw, relative warps analysis, Version 1.42. Department of Ecology and Evolution, State University of New York at Stony Brook.
- Sacco, T., and B. Van Valkenburgh. 2004. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). *Journal of Zoology* 263:41–54.
- Salesa, M. J., M. Antón, A. Turner, and J. Morales. 2005. Aspects of the functional morphology in the cranial and cervical skeleton of the sabretoothed cat *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) from the Late Miocene of Spain: implications for the origins of the machairodont killing bite. *Zoological Journal of the Linnean Society* 144:363–377.
- . 2006. Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain. *Journal of Zoology* 268:243–254.
- Schaller, G. B. 1972. *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press, Chicago.
- Schultz, C. B., M. R. Schultz, and L. D. Martin. 1970. A new tribe of sabertoothed cats (Barbourofelini) from the Pliocene of North America. *Bulletin of the Nebraska State Museum* 9:1–31.
- Simpson, G. G. 1941. The function of saber-like canines in carnivorous mammals. *American Museum Novitates* 1130:1–12.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*, 3d ed. W. H. Freeman, New York.
- Stayton, C. T. 2006. Testing hypotheses of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. *Evolution* 60:824–841.
- Sunquist, M. E., and F. Sunquist. 2002. *Wild cats of the world*. University of Chicago Press, Chicago.
- Therrien, F. 2005. Feeding behaviour and bite force of sabretoothed predators. *Zoological Journal of the Linnean Society* 145:393–426.
- Turner, A. and M. Antón. 1997. *The big cats and their fossil relatives: an illustrated guide to their evolution and natural history*. Columbia University Press, New York.
- Van Valkenburgh, B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* 11:406–428.
- . 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology* 14:155–173.
- . 1989. Carnivore dental adaptations and diet: a study of trophic diversity within guilds. Pp. 410–436 in J. L. Gittleman, ed. *Carnivore behavior, ecology, and evolution*, Vol. 1. Cornell University Press, Ithaca, N.Y.
- . 1995. Tracking ecology over geological time: evolution within guilds of vertebrates. *Trends in Ecology and Evolution* 10:71–76.
- . 1999. Major patterns in the history of carnivorous mammals. *Annual Review of Earth and Planetary Sciences* 27:463–93.
- . 2001. Predation in sabre-tooth cats. Pp. 420–423 in D. E. G. Briggs and P. R. Crowther, eds. *Paleobiology II*. Blackwell Science, Oxford.
- . 2007. Déjà vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology* 47:147–163.
- Van Valkenburgh, B., F. Grady, and B. Kurtén. 1990. The Pliocene cheetah-like cat *Miracinonyx inexpectatus* of North America. *Journal of Vertebrate Paleontology* 10:434–454.
- Van Valkenburgh, B., and F. Hertel. 1993. Tough times at La Brea: tooth breakage in large carnivores of the late Pleistocene. *Science* 261:456–459.
- Van Valkenburgh, B., and K.-P. Koepfli. 1993. Cranial and dental adaptations to predation in canids. *Symposium of the Zoological Society of London* 65:15–37.
- Van Valkenburgh, B., and C. B. Ruff. 1987. Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology* 222:379–397.
- Van Valkenburgh, B., and T. Sacco. 2002. Sexual dimorphism and intra-sexual competition in large Pleistocene carnivores. *Journal of Vertebrate Paleontology* 22:164–169.
- Van Valkenburgh, B., X. Wang, and J. Damuth. 2004. Cope's rule, hypercarnivory, and extinction in North American canids. *Science* 306:101–104.
- Werdelin, L. 1983. Morphological patterns in the skulls of cats. *Biological Journal of the Linnean Society* 19:375–391.
- Werdelin, L., and M. E. Lewis. 2001. A revision of the genus *Dinofelis* (Mammalia, Felidae). *Zoological Journal of the Linnean Society* 132:147–258.
- Werdelin, L., and R. Sardella. 2006. The “*Homotherium*” from Langebaanweg, South Africa and the origin of *Homotherium*. *Palaeontographica, Abteilung A* 277:123–130.
- Wesley-Hunt, G. D. 2005. The morphological diversification of carnivores in North America. *Paleobiology* 31:35–55.
- Wesley-Hunt, G. D., and J. J. Flynn. 2005. Phylogeny of the Carnivora: basal relationships among carnivoramorphans, and assessment of the position of ‘Miacoidae’ relative to Carnivora. *Journal of Systematic Palaeontology* 3:1–28.
- Wroe, S., C. McHenry, and J. Thomason. 2005. Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society of London B* 272:619–625.
- Zelditch, M. L., D. L. Swinderski, H. D. Sheets, and W. L. Fink. 2004. *Geometric morphometrics for biologists: a primer*. Elsevier Academic Press, San Diego.