Evolution of Skull and Mandible Shape in Cats (Carnivora: Felidae)

Per Christiansen*

Department of Vertibrates, Zoological Museum, Copenhagen, Denmark

Abstract

The felid family consists of two major subgroups, the sabretoothed and the feline cats, to which all extant species belong, and are the most anatomically derived of all carnivores for predation on large prey with a precision killing bite. There has been much controversy and uncertainty about why the skulls and mandibles of sabretoothed and feline cats evolved to become so anatomically divergent, but previous models have focused on single characters and no unifying hypothesis of evolutionary shape changes has been formulated. Here I show that the shape of the skull and mandible in derived sabretoothed cats occupy entirely different positions within overall morphospace from feline cats, and that the evolution of skull and mandible shape has followed very different paths in the two subgroups. When normalised for body-size differences, evolution of bite forces differ markedly in the two groups, and are much lower in derived sabretoothed cats, and they show a significant relationship with size and cranial shape, whereas no such relationship is present in feline cats. Evolution of skull and mandible shape in modern cats has been governed by the need for uniform powerful biting irrespective of body size, whereas in sabretoothed cats, shape evolution was governed by selective pressures for efficient predation with hypertrophied upper canines at high gape angles, and bite forces were secondary and became progressively weaker during sabretooth evolution. The current study emphasises combinations of new techniques for morphological shape analysis and biomechanical studies to formulate evolutionary hypotheses for difficult groups.

Results

Based on warp analysis of 22 cranial and 17 mandibular landmarks (Fig. 1), it is evident that the entire shape of the skull and mandible in derived sabretoothed cats became dramatically different from those of extant cats during the course of evolution, and they collectively occupy an entirely separate portion of overall morphospace from any extant felid (Fig. 2A,B). Derived sabretoothed cat mandibles are possible within a relatively narrow group of mammals, in this case a family of carnivorans.
and differences within derived sabre-cats appear related to the length of the upper canines, since dirk-toothed Smilodon sp. group separately with lower relative warp scores from other derived sabre-cats, such as scimitar-toothed Homotherium sp. and Epimachairodus. Relative warp 2 is primarily related to dorsoventral skull shape, and specimens with lower warp scores have a dorsoventrally much taller and anteroposteriorly more compact skull, ventrally deflected glenoid fossa, greatly curved and anteroventrally compressed and dorsoventrally tall zygomatic arch, elevated facial portion of the skull, and abbreviated mid-section of the skull. They also have enlarged external nares and distinct posterior retraction of the infraorbital foramen, posteroventral deflection of the ventral orbital rim, and slightly smaller and dorsally deflected occipital condyles. In contrast, primitive sabre-cats such as pumasized Paramachairodus and jaguar-sized Dinofelis group with the extant clouded leopard and Diard’s clouded leopard (genus Neofelis), a taxon which, uniquely among extant felids, is known to have numerous characters in common with primitive sabre-cats [14,22,23]. This demonstrates that it is not in accord with evolutionary morphology to divide the cats into two groups which are inferred to differ markedly in cranio-mandibular morphology, because some members of the sabretooth group converge morphologically. The enormous divergence of later sabretooths was a result of distinct evolutionary selective forces operating within the group, and not an inherent characteristic of the group.

In contrast to derived sabre-cats, modern cats differ primarily in skull shape along relative warp 1, with very large species (lion, tiger) having low warp scores, implying an elongate snout region, anteroposteriorly compressed mid-part of the skull, elongate and straighter posterior part of the skull, more dorsoventrally elongate orbital aperture, more powerfully built zygomatic arch, and slightly lowered glenoid fossa. It has previously been suggested that skull morphology in modern cats will divide these into two groups; large species, encompassing the Panthera cats (lion, jaguar, leopard, tiger, and snow leopard), and small cats, respectively, with some taxa (puma, Neofelis) occupying intermediate positions between the two [24]; this would imply different evolutionary selective forces for skull shape in small and large cats. However, traditional approaches do not actually study shape [25], and the current analysis of skull shape does not support such a dichotomy. Rather, the shape of the skull along relative warp 1 represents a continuum which covaries highly significantly with overall skull size, whereas relative warp 2 does
not (Table 1). There is no discernible division between large and small cats, and among *Panthera*, the smaller species (leopard, jaguar, snow leopard) have higher relative warp 1 scores than the lion and tiger, and among so-called small cats, larger species (e.g., *Lynx* sp. fishing cat; puma) have higher warp scores than smaller species (e.g., Geoffroy’s cat; leopard cat; margay; see also Supplementary Information). Thus, the utility of felid skull shape characters in systematic analyses [26] is questionable, owing to the differences between scimitar-toothed and dirk-toothed forms. Thus, among modern cats, the uniformity of skull shape when correcting for size indicates similar evolutionary selective forces; as will be shown below, these were most likely mechanical reasons.

It has been suggested that one difference between sabretoothed cats and modern cats is that in sabretooths, skull shape is primarily related to skull size, whereas shape is more closely related to upper canine size among sabretooths [27]. This is corroborated to some extent by this study, but most derived sabretooths are larger than primitive ones, clouding this image. Additionally, among extant cats, the upper canine also becomes longer relative to condylobasal skull length with increasing size (r = 0.612; 0.30 < p < 0.50) [28]. It has been shown that human skulls, with increasing size (r = 0.481), but owing to small sample size (n = 8) and great heterogeneity of proportional canine size between the dirk-toothed (*Megatherium* sp., *Smilodon*) and scimitar-toothed (*Epimachairodus* sp., *Homo*), the regression equation is non-significant (p = 0.156). No curvilinearity is present in this sample, as indicated by a non-significantly different correlation coefficient with application of polynomial regression. Among sabretoothed felids, the ratio of upper canine length to condylobasal skull length also increases with increasing size (r = 1.504; 0.251; r = 0.352), but owing to small sample size (n = 5).

### Table 1. Interspecific Reduced Major Axis regression lines for analyses of skull size (log10 condylobasal length in mm [CBL]), relative upper canine height to CBL (C/CBL; arc sine transformed ratio), Bite Force Quotients at the canine (BFQ; in Newtons), and associated skull shape (Relative warps 1 and 2, [Relw1] and [Relw2], respectively); mandible size (log10 mandible length in mm [MAN]), and associated mandible shape (Relative warps 1 and 2, [Relw1] and [Relw2], respectively) along with correlation coefficients (r), standard errors of the estimate (SEE), and significance of the regression.

| Sample | n  | X       | Y       | α ± 95% CI | β ± 95% CI | r      | SEE | F    | p    |
|--------|----|---------|---------|------------|------------|--------|-----|------|------|
| Extant cats | 24  | CBL  | Relw1  | 0.635 ± 0.112 | −0.283 ± 0.053 | 0.907 | 0.020 | 101.604 | <0.001 |
| Sabretooth cats | 8  | CBL  | Relw1  | 1.352 ± 0.632 | −0.591 ± 0.260 | 0.898 | 0.026 | 24.986 | 0.002 |
| Extant cats | 24  | CBL  | Relw2  | 0.383 ± 0.166 | −0.178 ± 0.078 | 0.089 | 0.030 | 0.177 | 0.678 ns |
| Sabretooth cats | 8  | CBL  | Relw1  | 1.311 ± 1.064 | −0.564 ± 0.428 | 0.631 | 0.044 | 3.970 | 0.093 ns |
| Extant cats | 24  | C  | Relw1  | 0.533 ± 0.182 | −0.021 ± 0.007 | 0.564 | 0.039 | 10.282 | 0.004 |
| Sabretooth cats | 8  | C  | Relw1  | 0.345 ± 0.252 | −0.009 ± 0.007 | 0.650 | 0.052 | 4.396 | 0.081 ns |
| Extant cats | 24  | C  | Relw2  | 0.318 ± 0.134 | −0.013 ± 0.006 | 0.222 | 0.029 | 1.142 | 0.297 ns |
| Sabretooth cats | 8  | C  | Relw2  | 0.192 ± 0.260 | −0.005 ± 0.008 | 0.201 | 0.054 | 0.253 | 0.633 ns |
| Extant cats | 24  | CBL  | BFQ  | −37.759 ± 62.149 | 66.492 ± 29.398 | 0.012 | 11.077 | 0.003 | 0.954 ns |
| Sabretooth cats | 8  | CBL  | BFQ  | 780.366 ± 78.770 | 298.312 ± 43.124 | 0.800 | 18.087 | 10.672 | 0.017 |
| Extant cats | 24  | BFQ  | Relw1  | 111.422 ± 6.153 | −234.802 ± 103.813 | 0.010 | 11.077 | 0.002 | 0.964 ns |
| Sabretooth cats | 8  | BFQ  | Relw1  | 97.769 ± 34.234 | 504.987 ± 343.544 | 0.732 | 20.532 | 6.937 | 0.039 |
| Extant cats | 24  | BFQ  | Relw2  | 105.227 ± 4.851 | −373.795 ± 165.266 | 0.010 | 11.078 | 0.002 | 0.962 ns |
| Sabretooth cats | 8  | BFQ  | Relw2  | 87.435 ± 37.197 | 528.767 ± 470.172 | 0.456 | 26.836 | 1.573 | 0.256 ns |
| Extant cats | 24  | MAN  | Relw1  | 0.335 ± 0.129 | −0.159 ± 0.066 | 0.355 | 0.025 | 3.165 | 0.089 ns |
| Sabretooth cats | 9  | MAN  | Relw1  | 1.464 ± 1.517 | −0.699 ± 0.505 | 0.588 | 0.059 | 3.694 | 0.096 ns |
| Extant cats | 24  | MAN  | Relw2  | −0.424 ± 0.097 | 0.208 ± 0.050 | 0.843 | 0.018 | 54.196 | <0.001 |
| Sabretooth cats | 9  | MAN  | Relw2  | −0.384 ± 0.274 | 0.165 ± 0.147 | 0.063 | 0.017 | 0.028 | 0.871 ns |

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**Figure 2. Skull and mandible shapes in cats as illustrated by 22 (cranium) and 17 (mandible) landmarks.** (A) Scatter plots of relative warps 1 and 2 for shape changes in the skulls of felids, along with morphological standards at the axis apices. Relative warps 1 and 2 summarize 40.1% and 20.0%, respectively, of sample variation in the analysis. (B) Scatter plots of relative warps 1 and 2 for shape changes in the mandibles of felids, along with morphological standards at the axis apices. Relative warps 1 and 2 summarize 50.7% and 18.2%, respectively, of sample variation in the analysis. Symbols: Open circles, non-pantherine ("small") felids: 1, *Acinonyx jubatus*; 2, *Caracal caracal*; 3, *Catopuma temminckii*; 4, *Felis chaus*; 5, *Felis silvestris*; 6, *Leopardus pardalis*; 7, *Leopardus tigrina*; 8, *Leopardus wiedii*; 9, *Leptailurus serval*; 10, *Lynx canadensis*; 11, *Lynx lynx*; 12, *Oncifelis geoffroyi*; 13, *Pardofelis marmorata*; 14, *Prionailurus bengalensis*; 15, *Prionailurus planiceps*; 16, *Prionailurus viverrinus*; 17, *Puma concolor*. Open squares, pantherine felids: 1, *Neofelis diardi*; 2, *Neofelis nebulosa*; 3, *Panthera leo*; 4, *Panthera onca*; 5, *Panthera pardus*; 6, *Panthera tigris*; 7, *Panthera uncia*. Closed squares, sabretoothed felids: 1, *Dinofelis barlowii*; 2, *Epimachairodus giganteus*; 3, *Homoatherium cretadates*; 4, *Homoatherium serrum*; 5, *Machairodus aphanistus* (mandible only); 6, *Megatherium cf. lucridens*; 7, *Paramachairodus oxyge*; 8, *Smilodon fatalis*; 9, *Smilodon populator*.
cats, skull shape along relative warp 1 is related to the relative size of the upper canine (Table 1), but this is most likely a side effect of large cats having proportionally longer canines, and not the relative size of the canine per se. Among sabrecats, there is a tendency towards very long-toothed forms having lower warp scores along relative warp 1, and warp scores show a weak but non-significant relationship with skull size. However, as sabrecats differ in skull shape primarily along relative warp 2, and as this warp shows no relationship with skull size, the effect of upper canine length on skull shape is not linear. Rather, skull shape is a reflection of how derived a taxon is with regards to attaining a high gape; some of the derived species (Epimachairodus, Homotherium) have shorter upper canines, whereas Megantereon has enormous upper canines, but in some respects appears less derived than Homotherium.

Mandible shape displays the reverse pattern of skull shape (Fig. 2B; Table 1). Here, the sabrecats differ primarily along relative warp 1, and again the derived species occupy an entirely different part of overall morphospace from any extant species. Extant cats differ primarily along relative warp 2. Among extant cats, Neofelis sp. groups somewhat separately from other species, and the primitive sabrecats (Dinofelis, Machairodus, Paranachairodus) group with them, indicating that their overall mandibular morphology is similar. Derived sabrecats primarily differ from extant cats and also from primitive sabrecats in having an anteroposteriorly compressed posterior part of the mandible, but a concomitant elongate anterior part of the mandible, distinctly posterior deflected mandibular condyle, greatly dorsoventrally shortened coronoid process, which is also anteroposteriorly compressed, and greatly expanded mandibular symphysis. Other changes include reduction in P3 size, and anterior deflection of the anterior-most extent of the mandibular fossa. Among modern cats, the smaller species tend to have a strongly curved horizontal mandibular ramus, whereas large species (Acinonyx, Neofelis, Panthera, Puma), have a more rectangular ramus with a straight or even concave ventral profile. There is no systematic difference in dental size, or height of the coronoid process among extant cats. Relative warp 1 is not size-dependent in modern cats, whereas relative warp 2 is strongly size-dependent (Table 1). In sabrecats, the pattern is reverse, with relative warp 2 being entirely uncoupled from mandible size, and relative 1 showing a tendency towards size-dependency, but the equation is not significant owing to lower sample size, and the fact that some large sabrecats (Dinofelis, Machairodus, Paranachairodus) have primitive mandibles, whereas others (e.g., Homotherium, Smilodon) are highly derived.

The maximal estimated bite forces at the canines normalised for differences in body size (the Bite Force Quotient or BFQ) is highly significantly higher among feline cats (F = 50.152; p < 0.00001) than among sabrecats. The BFQ scores among modern cats are entirely uncoupled from skull size, whereas there is a significant correlation among sabrecats (Table 1). However, as noted above, this is a function of the highly modified skulls of derived sabrecats, not their size per se [see ref. 23]. Primitive sabrecats such as Paranachairodus ogyga and tiger-sized Machairodus apphanistus have much stronger bite forces that more derived forms (Epimachairodus), which again have stronger bite forces than the most derived forms, such as Homotherium, Megantereon, and Smilodon, which are of equal size to Machairodus [see supplementary information and ref. 28 for bite forces in Machairodus apphanistus]. This is also evident in that bite forces covary with skull shape among sabrecats (Table 1; Fig. 3C,D), although relative warp 2 is non-significant. This is probably a function of low sample size and the fact that Machairodus apphanistus could not be included in the skull shape analysis. Among extant cats, bite forces normalised for body size show absolutely no relationship with skull shape (Fig 3A,B); modern cats have uniformly high bite forces irrespective of body size and apparent, but merely size-related differences in skull shape.

Discussion

The ability to attain a high gape and administer powerful forces during the killing bite are key factors in predation for all carnivores, but both cannot be optimized simultaneously; in fact, they show a reciprocal relationship, in that, as gape increases, muscle force levers decrease, and so do bite forces [4,6,29,30]. The cat family graphically demonstrates this principle, and also demonstrates how divergent evolutionary selective driving forces may be within a relatively narrow taxonomic unit (traditionally called a Family) of animals with an even more restricted feeding ecology and morphological diversity (exclusively meat-eaters; long bodies, powerful limbs, retractile claws; reduced and trenchant post-canine dentition). The results of this study indicate that the cranium and mandible in sabretoothed and feline cats were subjected to fundamentally different selective forces during the course of evolution.

In the modern cat lineage, the primary evolutionary driving force appears to have been uniformly high bite forces, irrespective of body size, enabling these cats to dispatch prey with a powerful killing-bite [3,31]. Since large predators need large prey for energetic reasons alone [32,33], this also implied enlargement of the upper canines to facilitate a more deeply penetrating killing bite. Historically, it has been noted that skull morphology appears to differ in large vs. small felid species [24,26,34,55], but evolution of skull shape is tightly coupled with absolute skull size, implying that large pantherines are, in fact, not anatomically different from small species; they are simply larger, and selection for uniformly high bite forces implies elongation and elevation of the posterior part of the skull, and a stronger zygomatic arch to encompass increases in adductor musculature. Brain size in cats scale with slopes far below isometry [36], implying that in small cats, the braincase makes up more of the total skull volume. This relationship, and the accommodation of great adductor musculature to maintain high bite forces to body mass necessitates elongation, elevation, and dorsal straightening of the posterior part of the skull in large species, the latter two due to a large sagittal crest, resulting in a skull shape as observed in large pantherine species and in the puma.

In contrast, sabretooth evolution was strongly directed towards precision killing with very large upper canines, which implies efficient biting at greatly increased gape angles [2,6,10,13,14]. This led to far greater evolutionary changes in skull and mandible shape than occurred during evolution in the feline cat lineage, probably for functional reasons. Primitive sabrecats had high bite forces, and a skull and mandible morphology which differed from those of most extant felids, but not Neofelis sp. [14,23,28,37]. As sabrecats became more specialised, the entire shape of the skull and mandible changed dramatically to facilitate and properly adapt to biting at very high gape angles. This happened at the expense of high bite forces, but in sabrecats, parts of the force driving the canines into the throat of the prey probably came from the upper cervical muscles [2,11,12]. The abbreviated, dorsoventrally tall skull, upwards-curving zygomatic arch, and reduced coronoid process were probably adaptations facilitating longer muscle fibres, and, thus higher gape angles [6,14].

The reasons for such a derived and unusual killing ecology are less clear, but may have had to do with predator competition. During much of the Miocene-Pliocene, sabretooth fossils appear to
be more numerous than fossils of feline cats [2,38]. In modern ecosystems with numerous large, sympatric predators, interspecific harassment, mutual antagonistic behaviours, often resulting in even fatal encounters [39], and kleptoparasitism of kills are very common, and under such circumstances, reduced exposure time is an effective way of reducing the risk of carcass theft [40–44]. In many prehistoric ecosystems, predator competition appears to have been more intense than today [42,45,46], so rapid killing of prey would have been important, and this could have acted as a selective driving force favouring rapid killing of prey [47,48]. This could have been the underlying reason for the extreme specializations of derived sabrecats, but eventually proved an ecological cul de sac.

Such extreme specialisations indicate predation on large prey exclusively, and make a wider dietary regime, as found in modern large cats [3,31] unlikely. This is in accord with all available evidence of prey preference among sabretooths, which unanimously indicates predation on large prey [49–52]. Additionally, by following this evolutionary route, the sabretooths were apparently unable to exploit the wide size regime of the feline cats, which specialised in powerful precision biting instead, and this technique appears effective against large and small prey alike. To date, no derived sabretoothed cat the size of a lynx, let alone a margay or a sand cat, have been discovered. The sabrecats appear to have been a prime example of strong selective forces for an unusual feeding ecology, resulting in highly derived species, which probably monopolized the large-predator niches so long as the ecosystems and climate zones remained relatively stable. The tradeoffs were powerful bite forces, a narrow dietary and body size regime, collectively probably implying greater risk of extinction if the environmental conditions to which these cats had become specialised changed too much or too rapidly [6,46,53].

Materials and Methods

Data sample and shape analysis

A sample of extant feline felids of 424 specimens representing 24 different species was studied, and encompassed male and female adult specimens of every species; the sample of extinct, sabretoothed felids consisted of nine species, and 20 crania and...
25 mandibles (see Composition of data sample S1). All specimens were digitally photographed in high resolution in the direct lateral perspective with a millimetre scale ruler positioned directly in line with the long axis of the image perspective and the specimen. Specimens had to be near complete and undistorted in lateral view to be of use in digital surface morphometry, and, accordingly, no skull of Machairodus aphanistus was included in such analyses, because all known specimens are either highly incomplete or have suffered at least some post-mortem distortion. All included specimens were scaled to a uniform condylobasal skull length or mandibular length, as appropriate, of 100 mm, at an image resolution of 700 dpi. Twenty-two landmarks were digitally scored on each skull and seventeen on each mandible to encompass overall shape (Fig. 1), and Thin Plate Spline (TPS) Relative Warp analyses [54] were conducted on the digitized specimens (see Procedure for digital shape analysis S2); TPS models shape differences as deformations among a set of homologous landmarks, and the TPS function interpolates a surface that is fixed at the landmarks, and is computed so as to minimize overall bending energy, implying minimizing spatially localized information [25,54]. A non-arbitrary and non-local consensus configuration, defining the point of tangency between shape space and approximating tangent space in the computation of the thin plate splines is computed by the generalized orthogonal least squares Procrustes superimposition procedure [54,55]. It constitutes an initial consensus shape, and from this, differences in coordinate distances are computed for every specimen. Displacements occur in a two-dimensional (X, Y) plane, but may be visualised as being vertical displacement in the Z-plane. Relative warps summarize the variation in shape among specimens with respect to their partial warp scores, and at total shape space (I = 0), constitute a Principal Components Analysis (PCA) of shape changes based on the covariance matrix of partial warp scores [54,56]. The relative warps are orthogonal and uncorrelated, and account for virtually all of the variation in the sample [54,57]. A relative warp analysis is thus similar to a traditional PCA in that relative warp I describes most of the variation in the sample, followed by relative warp 2, and so on. The principal difference is that relative warps are coordinate distances of shape variation derived through Procrustes superimposition of specimens [54,55] and not measured variables, and that the variance captured by the relative warps is therefore related to differences in shape and not linear measurements.

Bite force estimations and Bite Force Quotients

For this purpose, the included specimens were digitally photographed in high resolution in direct lateral, ventral, and postero-dorsal perspective with a millimetre scale ruler positioned directly in line with the long axis of the image perspective and the specimen. Bite forces were computed from the digital images using Thomason’s dry-skull procedure of muscle cross-sectional area estimation and computation of inlever and outlever moments arms [50]. Bite forces are, however, greatly size dependent, and to facilitate comparison among differently-sized specimens, the Bite Force Quotient [3,59] was computed for every specimen, and average values were used for regression analyses. This requires a body size as well, and this was computed directly from specimens which had been weighed prior to death by allometry comparisons (see Procedure for computation of Bite Force Quotients BFQ S3).

Regression analysis and data transformation

Bivariate Reduced Major Axis (Model II) regression analyses were carried out on the various variables. This procedure was chosen as opposed to traditional Least Squares (Model I) regression, because it does not depend to a given variable (Y), and is further appropriate since uncertainty has to be assumed on both variables, and the included specimens are derived from a larger population [60]. Relative Warp scores and Bite force Quotients were analysed without transformation, condylobasal skull length and mandibular length were logarithmically (log 10) transformed prior to analysis, and ratios of upper canine height to condylobasal skull length were angular (or arcsine) transformed prior to analysis to restore normality [60].

Supporting Information

Composition of Data Sample S1

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Author Contributions

Conceived and designed the experiments: PC. Performed the experiments: PC. Analyzed the data: PC. Contributed reagents/materials/analysis tools: PC. Wrote the paper: PC.

References

1. Martin LD (1980) Functional morphology and the evolution of cats. Trans Nebraska Acad Sci 8: 141–154.
2. Turner A, Antón M (1997) The big cats and their fossil relatives. An illustrated guide to their evolution and natural history. New York: Columbia University Press. 234 p.
3. Leyhausen P (1979) Cat behavior. New York: Garland STPM Press. 340 p.
4. Biknevicius AR, Van Valkenburgh B (1996) Design for killing: Craniodental adaptations of predators. In: Gittleman JL, ed. Carnivore behavior, ecology, and evolution. vol II. New York: Cornell University Press. pp 393-429.
5. Christiansen P, Wroe SM (2007) Bite forces and evolutionary adaptations to feeding ecology in carnivores. Ecology 88: 347–358.
6. Emerson SB, Radinsky LB (1980) Functional analysis of sabertooth cranial morphology. Paleobiol 6: 295–312.
7. Simpson GG (1941) The function of saber-like canines in carnivorous mammals. Am Mus Novit 1130: 1–12.
8. Kurten B (1954) The Chinese Hippopotamus fauna. Comment Biol Soc Sci Fenn 13: 1–42.
9. Miller GJ (1984) One the jaw mechanism of Smilodon californicus Bovard and some other carnivores. Imperial Valley College Mus Soc Occ Pap 7: 1–107.
10. Akrensen WA (1985) Canine function in Smilodon (Mammalia; Felidae; Machairodontinae). Contri Sci Nat Hist Mus Los Angeles County 356: 1–22.
11. Antón M, Galobart A (1999) Neck function and predatory behavior in the scimitar toothed cat Homotherium latidens (Owen). J Vert Paleontol 19: 771–784.
12. Antón M, Salesa MJ, Pastor JF, Santiago EM, Fraile S, et al. (2004) Implications of the mastoid anatomy of larger extant felines for the evolution and predatory behavior of sabertoothed cats (Mammalia, Carnivora, Felinea). Zoo J Linn Soc 140: 207–221.
13. McHenry GR, Wroe SM, Clausen PD, Moreno K, Cunningham E (2007) Supermodeled sabercat, predatory behaviour in Smilodon fatalis revealed by high-resolution 3D computer simulation. Proc Natl Acad Sci 104: 16010–16015.

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14. Christiansen P (2006) Sabertooth characters in the clouded leopard (Neofelis nebulosa Griffith, 1821). J Morphol 267: 1186–1198.
15. Goswami A (2006) Morphological integration in the carnivorian skull. Evolution 60: 169–183.
16. Christiansen P (2000) Evolutionary changes in craniomandibular shape in the great cats (Neofelis Griffith and Panthera Oken). Biol J Linn Soc 92.
17. Tucker R (1954) Studies in functional and analytical craniology. I–III. Austr. J Zool 2: 381–411.
18. Buckland-Wright JC (1978) Bone structure and the patterns of force transmission in the cat skull (Felis catus). J Morphol 155: 35–62.
19. Roberts D (1979) Mechanical structure and function of the craniofacial skeleton of the domestic dog. Acta Anat 103: 422–433.
20. Russell AP, Thomason JJ (1993) Mechanical analysis of the mammalian head skeleton. In: Hanken J, Hall BK, eds. The Skull, vol. 3. Chicago: Chicago University Press. pp 343–383.
21. Wroe SM, Mäde N (2007) Convergence and remarkably consistent constraint in the evolution of carnivore skull shape. Evolution 61: 1251–1260.
22. Gray JE (1867) Notes on the skulls of the cats (Felidæ). Proc Zool Soc Lond 1867: 258–277.
23. Christiansen P (2008) Evolutionary convergence of primitive sabertooth craniomandibular morphology: the clouded leopard (Neofelis nebulosa) and Parasaurolophus sp. compared. J Mammal Evol.
24. Werdelin L (1981) Morphological patterns in the skulls of cats. Biol J Linn Soc 19: 375–391.
25. Zelditch ML, Fink WL, Swiderski DL (1995) Morphometrics, homology, and phylogenetics: Quantified characters as synapomorphies. Syst Biol 44: 179–189.
26. Salles LO (1992) Felid phylogenetics: Extant taxa and skull morphology (Felidae, Aeluroidea). Am Mus Novit 3047: 1–67.
27. Van Valkenburgh B, Slater G (2007) Long in tooth: Evolution of sabertooth cat cranial shape. J Morphol 268: 1144.
28. Christiansen P (2007) Comparative biteforces and canine bending strengths in feline and sabertooth felids: implications for predatory ecology. Zool J Linn Soc 151: 425–437.
29. Herring SW, Herring SE (1970) The superficial musenter and gape in mammals. Am Nat 104: 561–576.
30. Bryant HN (1996) Force generation by the jaw adductor musculature at different gaps in the Pleistocene sabretoothed felid Smilodon. In: Stewart KM, Seymour KL, eds. Palaeoecology and paleoenvironments of Late Cenozoic mammals. Toronto: University of Toronto Press. pp 283–299.
31. Sunquist ME, Sunquist F (2002) Wild cats of the World. Chicago: University of Chicago Press. 452 p.
32. Carbone C, Mac G, Roberts SC, MacDonald DW (1999) Energetic constraints on the diet of terrestrial carnivores. Nature 402: 296–298.
33. Carbone C, Teacher A, Rowcliffe JM (2007) The costs of carnivory. PLoS Biol 5: e22.
34. Haltenorth T (1936) Die verwandtschaftliche Stellung der Großkatzen zueinander. I. Beschreibung der Schädelknochen. Z Sa¨ugetierk 11: 32–105.
35. Haltenorth T (1937) Die verwandtschaftliche Stellung der Großkatzen zueinander. VII. Z Sa¨ugetierk 12: 97–240.
36. Gittleman JL (1986) Carnivore brain size, behavioral ecology and phylogeny. J Mammal 67: 25–30.
37. Therriens F (2005) Mandibular force profiles of extant carnivores and implications for the feeding behaviour of extinct predators. J Zool Lond 267: 249–270.
38. Hunt RM Jr (1996) Biogeography of the order Carnivora. In: Gittleman JL, ed. Carnivore behavior, ecology, and evolution, vol. II. New York: Cornell University Press. pp 485–541.
39. Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153: 492–500.