Reconstructed facial appearance of the sabretoothed felid *Smilodon*

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Received April 1997; accepted for publication October 1997

Life reconstructions are a useful means of providing a package of information about morphology, functionality, behaviour, biology and ecological characteristics of an extinct organism. These reconstructions are of interest not only to researchers but also to a wider public. Reconstructions of sabretoothed cats in particular are widely published and exhibited, despite the absence of a general consensus on either how their canines were used or the prey sought. Cat-like restorations of the American Pleistocene sabretooth genus *Smilodon* prepared by Charles Knight under the direction of J.C. Merriam were accepted as valid for over three decades until G.J. Miller criticized them, claiming that *Smilodon* should have looked very different from modern felids. In particular, he argued for a longer mouth opening and lip line to provide a wider gape, a retracted nose and ears set relatively lower on a head with a straighter dorsal profile. These arguments were accepted by many authors employing reconstructions, and have lead to depictions of bizarre appearance and interpretations of rather specialized feeding behaviour. We believe that phylogenetic, anatomical and functional considerations point to substantial flaws in the basis for such depictions, and argue for a return to more felid-like morphology and to interpretations of broadly cat-like eating patterns.

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ADDITIONAL KEY WORDS—*Smilodon*—sabretoothed cats—reconstruction.

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INTRODUCTION

Living cats, including the subfamilies Felinae, Acinonychinae and Pantherinae (Wilson & Reeder, 1993), are animals with conical upper canines (Turner & Antón, 1997). Much of the fossil record of the family is however dominated by the sabretoothed felids of the subfamily Machairodontinae. The life appearance and behaviour of sabretoothed machairodontine felids, especially that of members of the American genus Smilodon, has been a matter of debate for several decades, not least because of the highly specialized dentition and jaw apparatus (Bryant, 1996). In early reconstructions, such as those by C.R. Knight (Merriam & Stock, 1932), the head of Smilodon was depicted as roughly similar to that of modern cats (Fig. 1A). Miller (1969) questioned that view, proposing several major differences so that the lip line would be set much farther back, the external nose would be considerably shorter and the nostrils retracted, the dorsal profile of the skull would be straightened and the ears would thus be set relatively lower on the skull. Taken together, these would give the head of Smilodon a decidedly non-cat-like and somewhat bizarre appearance; with a long mouth rather like that of a dog (Fig. 1B).

Miller supported his proposals by arguing firstly that a long lip line would allow a wider gape for the use of the sabres and would also enable the animal to take food into the side of the mouth in a manner otherwise impossible, in his view, for an animal with such elongated upper canines. The shortened nose and retracted nostrils were then argued to be a simple, direct interpretation of the markedly shortened nasal bones set well back relative to the premaxilla. Finally, the straightened dorsal profile of the skull, produced by the high sagittal cresting towards the rear of the cranium, was argued to produce the relatively lower positioning of the external ears.

Miller’s arguments have had considerable influence upon later authors and artists. As a result, reconstructions of Smilodon and other sabretoothed carnivores that either follow those principles to various degrees or accept them as broadly valid have appeared in numerous publications (Martin, 1980; Martin & Schultz, 1975; Akersten, 1985; Diamond, 1986; Kitchener, 1991; Seidensticker & Lumpkin, 1991; Shaw, 1992; Janis, 1994).

We have reconsidered this subject in the course of various studies on felid skull morphology and reconstruction (García-Perea, 1994, 1996; Turner & Antón, 1997), and find no support for Miller’s ideas on phylogenetic, comparative or functional grounds. In this paper we address the subject, basing our analysis on phylogenetic and anatomical arguments to provide a set of criteria for reconstructing the heads of sabretoothed felids. We discuss our findings here, and broaden the discussion somewhat to argue for sabretoothed species that, while undeniably different from living felids, were still of broadly cat-like appearance.

MATERIAL AND METHODS

Our researches have between us involved first-hand study of skulls and dissected heads of a number of living felids and a wide-ranging examination of the skulls of
fossil feline and machairodontine taxa as well as those of other larger Carnivora. This work has also involved a considerable amount of reconstruction of the facial musculature of fossil felids by Antón, both in illustrations and in three-dimensional models and life-size depictions.

Cranial measurements used for quantifying nasal retraction (Fig. 2) were taken on 45 specimens belonging to seven living felid species and two specimens of smilodonte sabretooths (see Table 1). Based on our experience with the study of the anatomy of fossil and living carnivores, and following the methodology proposed by Bryant and Russell (1992) and Witmer (1995) for reconstructions employing phylogenetic criteria, we have tested Miller's arguments for the arrangement of cranial soft-tissue structures. The morphological traits examined consisted of the length and position of the lip line relative to the dentition and muscle insertion.
areas, the position of the nostrils relative to the premaxilla and nasal bones, and
the position of the ears relative to the sagittal crest and external auditory meatus.

The proposals put forward in the programmes of Bryant and Russell and
Witmer include phylogenetic and extrapolatory inference about the morphology of
unpreserved features of extinct taxa based on the characteristics of the closest living
relatives (sister group), and on those of the outgroup, as well as on form—function
correlation. Phylogenetic relationships between Machairodontinae (including Smi-
lodontini) and other Feliformia are shown in Figure 3, following the hypotheses of
Neff (1982), Martin (1989) and Werdelin (1996). In this scheme, the sister group of
the Machairodontinae is the living Felidae. The Hyaenidae are placed as the sister
group to the Herpestidae, and the sister group to that combination is then the
Viverridae. This trio is then seen in its entirety as the sister group of the Felidae,
and therefore the outgroup of the Machairodontinae.

As explained below in the results section, we have found that the morphological
traits analysed show a similar configuration among the extant taxa reviewed. The
presence of these traits in not only the Feliformia but also among the whole of the
Carnivora strongly suggests that these are plesiomorphic features for the Feliformia
and thus renders a phylogenetic analysis superfluous. However, the Felidae (including
the Machairodontinae and living subfamilies) and the remaining families of the
Feliformia provides the framework of a small monophyletic group, which according
to Bryant and Russell (1992) increases the likelihood that anatomical-functional
extrapolations apply among all the taxa compared. In other words, phylogenetic
relatedness often involves constraints on complex structures related to complex
functions, resulting in similar solutions for close relatives. An example of this is
illustrated by Werdelin (1996), based on a study of hypercarnivory in canids by Van

Figure 2. Cranial measurements used in this work for quantifying nasal retraction (see Table 1). Points
2 and 3 demarcate the nasal bone. Nasal length, NL, 2–3; Rostral length, RL, 1–3; Total length of
skull, TL, 1–4.
Table 1. Average adult values, ranges and standard deviations (as appropriate) of three metric variables (in mm; see Fig. 2) measured on skulls of two fossil Smilodontini sabretooths and seven felid living species. Two ratios have been calculated for quantifying the shortness of the nasal bones (NL/TL) and nasal retraction relative to the premaxilla. (NR). NR, Nasal Ratio, calculated as (RL-NL)/TL.

<table>
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<tr>
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<th>TL</th>
<th>NR</th>
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Figure 3. Phylogenetic relationships among feliform Carnivora. Based on Neff (1982), Martin (1989) and Werdelin (1996).

Valkenburgh (1991), Several canid species show a similar pattern of hypercarnivory in their dental morphology, but it is very different from the pattern seen in other families of Carnivora, such as the Felidae.
Figure 4. Different examples of the relative positions of nostrils and lip line in living Feliformia. A, Lion (Panthera leo), relaxed face. B, Lion demonstrating 'flehmen'. C, Genet (Genetta genetta), relaxed face. D, Spotted hyaena (Crocuta crocuta), relaxed face. Drawn from photographs of live animals and museum skulls. Striped area shows the masseter muscle, carnassials are shown in black.

With these phylogenetic considerations as a backdrop, our analysis has focused on anatomical and functional arguments.

RESULTS

Length of the lip line

A review of the masticatory apparatus in living felids shows that the lip line reaches back to a point near the anterior border of the carnassial teeth (Fig. 4), and that it does so independently of the length of the rostrum (Barone, 1967, 1989; Kingdon, 1977). On the other hand, the anterior border of the masseter muscle lies right behind the carnassial teeth, as illustrated here in Figure 4A. Consequently, the lip line is always anterior to the masseter muscle. In members of the Carnivora with a longer post-carnassial tooth row, such as dogs, the lip line may reach further back, but it still remains anterior to the masseter (Turnbull, 1970).

The shape and extent of muscle attachment areas in the skull and mandible of Smilodon, in particular the position and orientation of the masseteric fossa, clearly
indicates that the masseter muscle was positioned just behind the carnassials (Fig. 5B), as it is in modern felids.

Position of the nostrils

In the case of his arguments for a retracted nose, Miller refers to the “short nasal bones of Smilodon”, a perfectly correct observation since the nasal bones are decidedly shorter in smilodontines than in some living felids, as shown by the ratio nasal length/overall skull length (NL/TL, see Fig. 2 and Table 1). This phenomenon is in part due to the different morphology of the naso-frontal suture (Fig. 6).

Miller concluded from the fact that the nasal bones were set back in relation to the premaxilla that this implied a similarly posterior position of the nostrils. However, an overview of living felid species shows that the nostrils always extend to a similar position, above and slightly ahead of the premaxilla (Fig. 4), and we assume this to be independent of the nasal length and the more or less posterior position of the nasal bones. In order to test this assumption, we have calculated a ‘nasal ratio’ (NR, see Table 1) for seven living felids (Panthera tigris, P. leo, P. onca, P. pardus, Puma...

*concolor*, *Lynx rufus*, *Leopardus wiedii*) and two smilodonteine sabretooths (*Smilodon fatalis* and *Megantereon cultridens*). Our results shown in Table 1 confirm that modern cat species show variability in nasal bone length and in nasal bone position relative to

the pre maxilla, but also show that the values for smilodontine cats are within the ranges observed for modern species. The retracted nasals of the felid sabretooths seem to be at the end of the continuum from smaller to larger cats, rather than something unique. Furthermore, the difference in nasal ratio values between lion and tiger is far greater than that separating smilodontines from the lion.

Positioning of the ears

So far as the sagittal crest and the positioning of the ears are concerned, it is true that the sagittal crest is prominent in sabretooths (Fig. 7D, E). However, we find a great deal of variation among modern cat species (Fig. 7A, B, C), depending on age, absolute size and sex (Garcia-Perea, 1996). Some male leopards show enormous crests reminiscent of sabretooth cats (Fig. 7C), and yet the external appearance of the individual remains catlike to the observer. The appearance of the living animal is also related to the shape and position of the pinna (external ear). Our dissections and the published descriptions (Barone, 1967, 1989; Evans & Lahunta, 1991) show that the position of the lower point of the ear notch (incisura intertragica) is always similar relative to the external auditory meatus of the skull. Data from our dissections
of Iberian lynx, *Lynx pardinus*, (Fig. 8) and cheetah, *Acinonyx jubatus*, indicate that the distance between these points is less than 10% of the total length of skull (TL), although a slightly different ratio can be expected in felids with a relatively longer muzzle.

The more-or-less dorsal appearance of the ears depends not only on the position of the meatus relative to the dorsal profile of the head but also on the relative size of the pinna, since larger ears will tend to come closer to each other across the top of the head, thus looking more dorsally placed (Turner & Antón, 1997: fig 4.5). Ear size can only be estimated for *Smilodon*, but it is unlikely that they were larger than in modern lions, because *Smilodon* lived in a temperate climate and large ears would tend to lose too much heat in winter. As for the morphology of the cartilage itself,
it is fairly constant among felids (Pocock, 1917), so we have inferred a similar morphology for sabretooths (Fig. 5).

DISCUSSION

One point should be made immediately clear in any discussion of the lip line in the Carnivora; it varies according to the activities undertaken. The rather posterior position of the line evident in some dissected specimens (Fig. 9) is due to a post-mortem contraction of the platysma and zygomaticus muscles, which pull back the comparatively weaker orbicularis oris. In life, members of the Carnivora can actively contract the orbicularis, bringing the lip line considerably further forward as lions do when they roar (Schaller, 1972).

Observations of the feeding behaviour of modern carnivores do not support previous assertions that the sabres of Smilodon would have been a hindrance for the feeding action. The bulk of food consumed by felids is muscle, and recent research shows that in both felids and other large African carnivores the muscle is pulled from the carcass by the incisors (Van Valkenburgh, 1996). The anteriorly projected, well-developed incisors of Smilodon (Figs 5 and 7) were perfectly suited for that function, as Miller himself correctly observed, and the sabres would pose no obstacle to such action. The size, orientation and use of the incisors of the machairodont species is discussed and illustrated in some detail by Turner and Antón (1997: fig. 4.25) and Biknevicius et al. (1996).

The same study by Van Valkenburgh shows that the carnassials are used most
often to cut skin. In assessing the carnassial bite, Miller and several earlier authors seem to have assumed that a gape between the tips of the upper and lower canines in living cats is necessary to allow the entrance of chunks of meat into the mouth so that they can be chewed by the carnassials, something that would be impossible in Smilodon (Bohlin, 1947; Scott, 1937; Miller, 1969). It was thus further assumed in such schemes that the food item would enter the mouth both frontally and laterally. But observation of living animals does not confirm such assumptions. Modern cats apply the carnassials directly to the carcass (Leyhausen, 1979), but the gape of the jaws is usually so small that there is often no clearance between the tips of the canines (Fig. 10). Such animals are therefore in much the same situation as the sabretooths, clearly implying that a canine gape is simply not necessary in order to bite with the carnassials. Indeed, the size of skin pieces cut from the carcass with the carnassials appears to be rather small, and earlier authors apparently overestimated the size of such ‘chunks’.

Miller (1969) further argued that “the area available for getting food into the side of the mouth to be cut by the carnassials . . . may, of course, be limited somewhat by the double lips”. This point formed the basis for his interpretation of an unusually
long lip line in *Smilodon*. However, we consider that the most important, limiting factor is actually the position of the masseter muscle, which occupied a similar position in *Smilodon* to that of modern cats (Figs 4 and 5). Based on the reasonable assumption that *Smilodon* fed in a way broadly similar to that of modern cats, we suggest an equally similar lip line position. There are clear structural reasons for such a position. A slight contraction of the muscles that pull back the lips is enough to expose the carnassials, allowing the animal to shear the food with them in the manner typical of all living cats (Leyhausen, 1979). It is thus apparent that any further lengthening of the lip line to enable chewing would be pointless, because the masseter muscle itself would then simply get in the way of the food item.

In support of a longer lip line, Miller (1969) also argued that the gape necessary for using the sabres, the opening that would permit the tips of the upper canines to clear that of the lower canines, would “seriously tax” the elastic properties of the soft tissues of a normal felid mouth with a normal length of lip. We believe this conclusion is directly contradicted by simple observation. When modern cats yawn, and once the maximum gape of about 70° in the living animal (as estimated directly from numerous photographs and video stills) has been reached, the animals often grimace, further exposing their cheek teeth and gums and showing very clearly that the elastic limit of the tissues has not been reached. Furthermore, the ability to pull back the lips is not strictly linked to jaw gape, as indicated by the facial expression known as ‘flehmen’ (Fig. 4B). This gesture, which enables the animal to taste scents with the Jacobson’s organ (Schaller, 1972; Leyhausen, 1979), exposes the cheek teeth fully at no more than a medium gape, underlining the fact that the teeth can also be bared at will during a carnassial bite.

Among other mammals, the hippopotamus is able to open its jaws to 150° (Fig. 11B), although the ‘corner’ of its mouth is located well ahead of the orbits in resting position and is actually just posterior to the canines (Herring, 1975; Kingdon, 1977). Such a gape is achieved by a moderate amount of folding of the orbicularis muscle, as illustrated here in Figure 11A, and by the ‘probable’ inclusion of ‘elastic tissue’ (Herring, 1975: 92). Folding of the orbicularis can be observed to varying extents in living large cats (Fig. 11C) and other large carnivores, although it differs from that of the hippo in that it involves the upper lip hanging somewhat over the lower. Our observations suggest that folding may be more pronounced in larger cats, but it is also evident that leopards, *Panthera pardus*, have rather more folding of the lip tissues than the similar-sized puma, *Felis concolor*. Such differences may relate in part to roaring ability, since the pantherine cats pull the lip forward considerably during this activity (Schaller, 1972: 93), probably in order to produce a resonance chamber.

These observations indicate the great elasticity of the lips and surrounding tissue in extremely diverse taxa, and suggest that the lips of *Smilodon*, if reconstructed in a normal cat-like way, are unlikely to have restricted gape even faced with the need to accommodate separation of the greatly elongated upper canines from the lower teeth.

Any comparisons with the length of the lip line in dogs are actually misleading, because if dogs appear to have a longer mouth opening it is because they generally have a longer muzzle. The lips of dogs and cats reach back just as far as each other, to the masseters, but those of the dog extend forwards from the masseters along a much longer pre-carnassial toothrow, and that is what produces the longer lip line.

When we examine the question of nasal bone retraction, our results show that lions (*Panthera leo*) have the most retracted nasal bones among living cats, much
more so than do tigers (*Panthera tigris*), as can be seen in the illustrations given by Boule (1906) in his discussion of cave lions and illustrated by Turner & Antón (1997: Fig. 3.33) as well as here in Figures 6 and 7. But the position of the external nose is not retracted in the lion and therefore the essentially cat-like appearance of the living head is maintained (Fig. 4A). In all cases the nasal cartilage spans the distance, and it seems likely to us that the length of the cartilaginous nose in felids is always enough for the nostrils to be in a similar position above the incisor battery. There are thus no reasons to infer that felid sabretooths had a different nostril position from that found in modern felids based on the size and positioning of the nasal bones.

In any event, it is clear from studies of modern felids that most cats have the ability to retract the nose and upper lip area in a way that would obviate the need
RECONSTRUCTED FACIAL APPEARANCE OF SMILODON

Figure 12. A male baboon exhibiting gape, with a superimposed outline of the skull. Notice how the external nose folds up in front of the anterior end of the nasal bone. Drawn from a photograph with a museum skull superimposed.

to evolve a retracted nose. The levator nasolabalis muscle, which originates in the region of the frontal and maxillary bone just in front of the orbit, acts to retract and ‘fold up’ the anterior nasal region. The insertion for this muscle appears to have been just as well developed in the sabretoothed species, implying a similar retraction ability. Moreover, an interesting and very relevant parallel may be seen in the anatomy and behaviour of male baboons, which use a yawning gape in intergroup displays. We illustrate one such gaping display here in Figure 12. The upward folding and retraction of the nostrils is readily apparent, but particular attention should also be given to the highly retracted nasal bones in an extremely long-snouted animal and the fact that in their normal position the nostrils show no evidence of retraction.

The short-nosed appearance of Miller’s reconstruction of Smilodon (Fig. 1B) resembles a bulldog, a point underlined in his discussion by his emphasis on the prognathous condition of that sabretooth. In fact, what Miller calls ‘prognathism’ in Smilodon is just a forward projection of upper and lower incisors, instead of the maladaptive condition seen in bulldogs, caused by a retraction of the whole midface, with the lower incisors projecting and no longer occluding properly (Barone, 1989). While on the topic of comparisons with bulldogs, it is also worth pointing out that Kurtén (1976) had considered this point in relation to reconstructions of the European cave bear, Ursus spelaeus, a species that also exhibits shortened nasal bones. As Kurtén (1976: 15) pointed out, “many life restorations show the cave bear with a puglike face. I feel rather doubtful about this sort of restoration, for a retracted nasal bridge might also mean that the nose was well developed and movable. The nasal bones are actually very much shortened in animals provided with a trunk, like
tapirs and elephants. Also, the cave bear does not have the underslung jaw of the
gnu. So I think the nose probably was not flat but quite long and protruding, and
this is also the image seen in the art of Ice Age man."

We believe that the results of our studies clearly point to a broadly feline
appearance for the head of Smilodon when reconstructions of soft-tissue anatomy are
based on phylogenetic and anatomical arguments. The positions of the nose, ears
and ‘corner’ of the mouth are all most logically placed as shown in Figure 5, and
argue for a return to more felid-like morphology and to interpretations of broadly
cat-like eating patterns. However, the true appearance, the final character of the
head, would also have been conditioned by two other major factors.

The first concerns coat patterns. Their presence in Smilodon is conjectural; but it
would be a reasonable inference (Fig. 5) since all living cats and other members of
the Feliformia, including those with plain-coloured bodies, show some degree of
patterning in their faces. Functionally, the patterns serve to reinforce expression,
helping animals to avoid violent confrontations (Schaller 1967, 1972). This is
important for dangerously armed carnivores as such as modern cats and sabretooths.

The second factor concerns the presence of vibrissae, or whiskers. Cats, like many
carnivores, have well-developed vibrissae, and the size of the mystacial in particular
suggests that these are of some importance. Vibrissae were omitted, however, in
Miller’s reconstruction of Smilodon. The whiskers, which are extremely sensitive to
touch, consist of very enlarged and stiff hairs, and their bases in the vibrissal pad
are richly supplied with sensory nerves. Leyhausen (1979), in his classic study of cat
behaviour, describes how blindfolded domestic cats were still able to seize and kill
mice with a precisely directed bite once their whiskers made contact with the prey.
The same cats were unable to direct their biting when the whiskers were removed,
although their sighted ability to do so was unimpaired. Leyhausen provides pictures
of cats attacking a bird and carrying a mouse, and in each case the whiskers are
clearly employed to sense the precise positioning of the prey, almost enveloping the
prey in the case of the carried rodent. It seems clear that, for the domestic cat at
least, the whiskers are an important addition to its sensory equipment. Among the
larger cats, the size of the mystacial vibrissae, and the extent of innervation to them,
suggests that they too can convey considerable sensory information. This is really
not surprising, since precision in biting during the final stages of the kill can be an
important factor even for large cats (Schaller, 1972).

The incidence of whiskers is high among the Carnivora and among living Felidae,
and as such is therefore probably a primitive condition that would be shared with
extinct machairodontines. If living cats need to make precise bites then it would be
at least as logical for the extinct machairodont species to have had a well-developed
sense of where the prey was in relation to their teeth, in order to avoid damage
when biting. One possible clue to their presence may be seen in the size of the
infra-orbital canal, since the sensory nerves for the vibrissal pad pass through it and
make up most of the nerves that do so. Larger infra orbital canals are seen in living
cats in comparison with dogs and hyaenas, which have much less developed mystacial
vibrissae, and this morphological feature is certainly true of machairodontine taxa
such as Smilodon and Megantereon. Direct observations by ourselves in the course of
dissections of Iberian lynx and cheetah show the canal to be fully occupied by the
nerves and blood vessels, although whether this is equally true for larger cats is at
present the subject of some debate (Martin & Naples, 1996). Further study of this
matter is currently in hand, but in the meantime we have therefore depicted Smilodon with well developed mystacial vibrissae.

ACKNOWLEDGEMENTS

We thank H. Bryant, R. Tedford, L. Werdelin, J. Morales, Julio Gisbert, L. Martin and V. Naples for useful discussions, and two anonymous referees for constructive comments and helpful suggestions to improve the manuscript. The figures were drawn by MA. Julio Gisbert helped with the figures and made the dissections of Lynx pardinus. J. Latova and J. Sandoval supplied several pictures of relevant material. RGP received a postdoctoral fellowship from the Spanish Ministry of Education and support under project DGICYT PB92-0121. MA received a Collection Study Grant from the American Museum of Natural History. All three authors collectively thank those in charge of modern and fossil collections at numerous institutions.

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