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Changing ideas about the evolution and functional morphology of Machairodontine felids

El cambio de ideas acerca de la evolución y morfología functional de los félidos Machairodontinos

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ABSTRACT

Sabre-toothed felids, the machairodontines, have attracted much attention among palaeontologists for many decades, not only because of their spectacular morphology but also because they are a striking example of convergent evolution that is most probably linked to strong selective pressures. In this paper we provide a summary of the changing interpretations of their functional anatomy and evolution, from early hypotheses proposing a stabbing mode of attack and a pleiotropic control of the complex of machairodont morphologies, to the current views favouring the canine shear-bite model and a mosaic evolution of anatomical features.

Keywords: Felidae, Machairodontinae, Functional Anatomy, Evolutionary History

RESUMEN

Los félidos de dientes de sable, los macairodontinos, han ejercido una especial atracción entre los paleontólogos durante muchas décadas, no sólo por su espectacular morfología, sino también debido a que son un llamativo ejemplo de evolución convergente, probablemente ligada a una fuerte presión selectiva. En este trabajo suministramos una recopilación de los cambios de interpretación acerca de su anatomía functional y evolución, desde las primeras hipótesis en las que se proponía un ataque por apuñalamiento y un control pleitrópico del complejo morfológico macairodontino, hasta los actuales puntos de vista que favorecen un modelo de mordedura muy especializado y una evolución en mosaico de los carácteres anatómicos.

Palabras clave: Felidae, Machairodontinae, Anatomía functional, Historia Evolutiva

Introduction

Few mammalian fossils have attracted as much interest among both palaeontologists and the wider public as the sabre-toothed, or machairodontine, cats. With that interest has come a huge variety of interpretations of both form and function, most notably of course in relation to the extreme and seemingly bizarre development of the upper canine teeth. It would seem as though every conceivable (and in some cases inconceivable) way in which these teeth might have been used has been put forward at one time or another. Such difficulties in interpretation stem largely from the lack of any extant analogue, an absence that made it especially hard for 19th Century specialists to classify the first, fragmentary fossil finds of sabre-tooths correctly, since there was simply no concept of a cat-like animal with enlarged, flattened canine teeth. Indeed, in the early days of formal palaeontological study the leading French authority Cuvier (1824) even placed some machairodontine material from Italy and Germany within the bear genus *Ursus*, although this error was soon recognised and corrected by Bravard

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(1828) who assigned the specimens, together with others from Perrier (France), to the Felidae.

However, in this paper we have no wish to become enmeshed in the subsequent tangled arguments about precise taxonomic attributions to genera and species that have taken place over 200 years of research into the machairodontine felids, and taxonomic matters are therefore relegated to a way of identifying the material mentioned. Instead we choose to stay with the interpretations of form and function that have been applied to various members of the felid subfamily Machairodontinae as a whole, and in doing so we concentrate on two major areas of interest. The first deals with the question of the function of the dentition, especially in the more derived, crown species of the various lineages that are known from the Pliocene and Pleistocene, the members of the tribes Homotheriini and Smilodontini. The second deals with the origin of the specialised features of those dentitions and their integration with the entire morpho-functional complex of these top predators. Of course, as we hope to show, understanding of either of these two areas involves an appreciation of both. This seems to us an appropriate subject in a volume intended as a tribute to Leonard Ginsburg, whose own work has included so many aspects of that area of palaeontological interest.

Evolutionary History of the Machairodontinae

The cat family, the Felidae, appears to have originated in Eurasia, where the earliest known form is *Proailurus lemanensis*, an animal about the size of a modern ocelot, found in Late Oligocene deposits (about 30 Ma) in France. *Proailurus lemanensis* was about 40 cm high at the shoulder, and although it probably looked perfectly cat-like it had a more primitive, elongated skull than living felines and a more complete dentition, including P1, p1, double-rooted P2 and p2, a well-developed talonid on m1 and an m2. During the Miocene, primitive cats close to *Proailurus* gave rise to two different lineages, the conical-toothed cats of the subfamily Felinae and the sabre-toothed forms of the subfamily Machairodontinae. The earliest known member of this subfamily is *Pseudaelurus quadridentatus* (Beaumont, 1975; Salesa *et al.*, 2010a), best known from middle Miocene deposits in France, which was a leopard-sized cat with slightly flattened upper canines and a gently angled mandibular symphysis (fig. 1). While members of the Felinae are the only felids present in extant faunas, most of the felid fossil record from the Miocene onwards is dominated by the sabre-toothed machairodontines. Thus the African felid guild prior to the mid-Pliocene consisted almost entirely of machairodontines (Turner & Antón, 2004) with the exception of two conical-toothed species, *Diamantofelis ferox* and *D. minor,* from 17 Ma old deposits at the Namibian locality of Arrisdrift. Only from around 3.5 Ma do members of the Felinae begin to appear in Africa and it is only after the disappearance of the African machairodontines by around 1.5 Ma that they became the sole representatives of the family in the continent. In other continents this pattern of appearance and replacement has its own and often quite different pattern and timescale (Turner & Antón, 1999; Antón *et al.*, 2005). In fact, members of the Felinae are known since the early Miocene in Eurasia but in general the fossil record of this subfamily is restricted to species of relatively small body size until the pantherins became widespread in the late Pliocene, and until then, the large cat niche was exclusively occupied by sabre-toothed forms. Thus, by any standards, the machairodontines were a major and long-lived group of diverse species, and remained the dominant large mammalian hypercarnivores in the terrestrial ecosystems of four continents for most of the Neogene. They were by no means the bizarre, inefficient and rather short-term evolution-

Fig. 1.—Life reconstruction of the primitive machairodont felid *Pseudaelurus quadridentatus*, based on fossils from the French middle Miocene site of Sansan (Artwork by M. Antón).

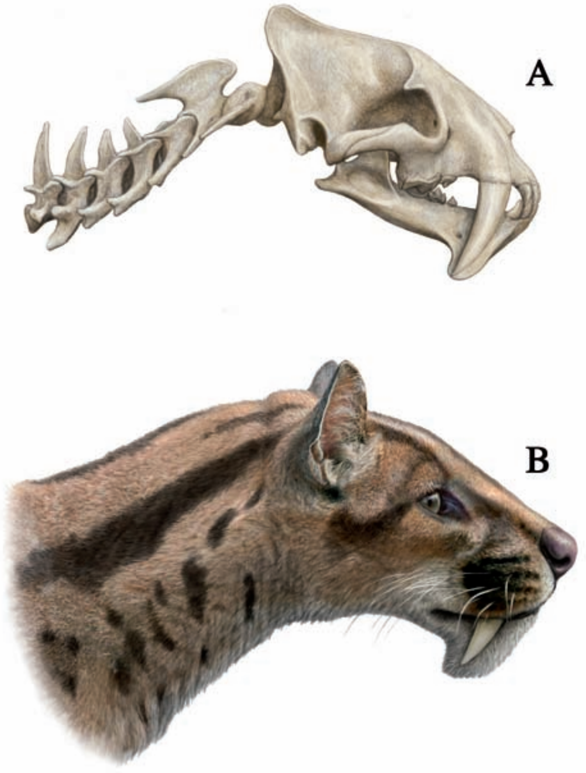

Fig. 2.—Skull, mandible and cervical vertebrae (A) and reconstructed appearance of the head and neck (B) of the American nimravid *Hoplophoneus mentalis*, based on fossils from the Chadron formation (USA). The similarities in detail with the anatomy of felid sabre-tooths like *Megantereon* are striking (Artwork by M. Antón).

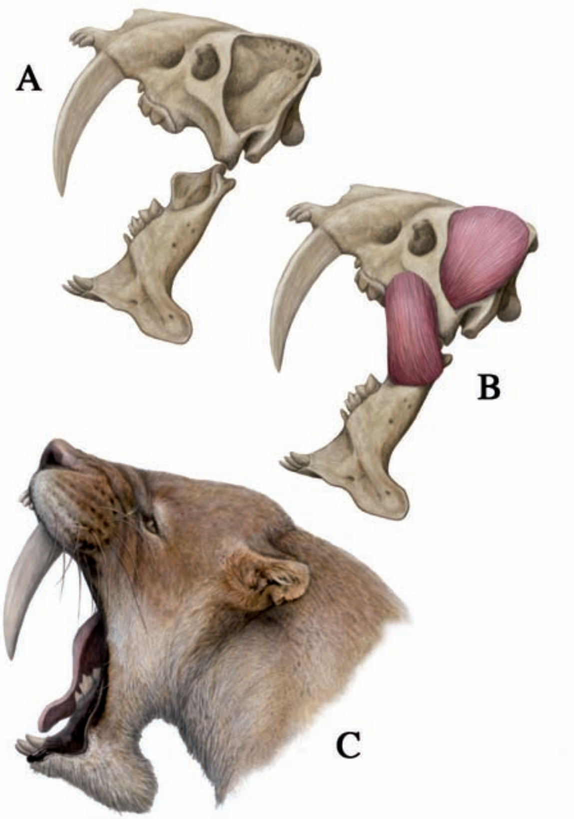

Fig. 3.—Skull (A), reconstructed masticatory muscles (B) and restored life appearance (C) of the American barbourofelid *Barbourofelis fricki*, from the late Miocene (Hemphilian) of North America. Within the order Carnivora, this is probably the species that shows the most derived machairodont specialisations in its skull (Artwork by M. Antón).

ary experiment that the popular literature would sometimes have us believe.

As is well known, other groups of mammals besides the Felidae have converged with the machairodontines in the development of sabre-toothed adaptations. Within the order Carnivora, the family Nimravidae is a striking example of convergence, with Palaeogene genera such as *Eusmilus* and *Hoplophoneus* resembling to an astonishing extent the cranial morphology of advanced felid sabre-tooths (fig. 2) such as *Megantereon*. *Barbourofelis*, *Sansanosmilus* and several related genera were also classified as members of the Nimravidae, but their anatomy is rather different from that of typical nimravids leading some specialists to include them within the Felidae (Morales *et al*., 2001). However, their ear region differs significantly from that of felids, as observed by Bryant (1991) and Hunt (1987), and it may be justified to keep those genera in a new, separate family, the Barbourofelidae, as proposed by Morlo *et al*. (2004) (fig. 3). While the nimravids were essentially a Palaeogene group, and most of them were already extinct when the felids made their first appearance, the barbourofelids evolved in the Miocene and there was overlap and possibly competition between them and the true machairodontines.

It may be worth commenting here that the word "machairodont", meaning "knife-tooth", which is often used as an adjective to denote the presence of sabre-tooth morphology in any mammalian carnivore ("machairodont cats", or "machairodont carnivores"), is sometimes used to refer to the machairodontine felids ("the machairodonts"). In fact, the genus name "*Machairodus*", which has the same Greek root, has been used more informally, (often without italics), especially by French palaeontologists, to refer to any sabre-toothed carnivore. To

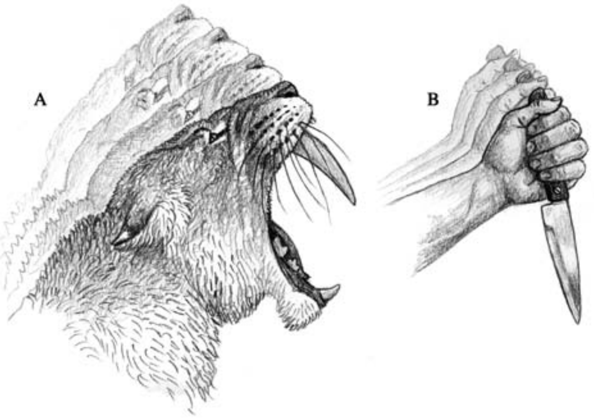

Fig. 4.—Reconstruction of the head of the American machairodontine *Smilodon* shown in a hypothetical stabbing motion (A), compared with a human hand wielding a knife (B), to illustrate the analogy proposed by the stabbing hypothesis (Artwork by M. Antón).

avoid confusion, we prefer to use here the word machairodontine when referring to felid sabre-tooths.

Dental function in machairodontines

The elongated upper canines are one of the most striking features of the skeleton of a machairodontine felid, and in order to stress their spectacular appearance many reconstructions of the life appearance of the animals tend to feature them in an open-mouthed pose. The dagger-like nature of the canines thus exposed seems to suggest use in a stabbing manner to kill, and many of the earlier 19th and 20th Century ideas put forward in support of this notion were usefully summarised by Simpson (1941), who was himself a strong advocate of that interpretation of their function across a range of species of felids and nimravids (figure 4). Interestingly, Merriam & Stock (1932: 25), in one of the most extensive studies of any machairodontine cat ever undertaken based on the material from Rancho La Brea in Los Angeles, had concluded that the American genus *Smilodon* used both stabbing and slicing in what they termed "consumating an attack". The stabbing argument was forcibly rejected at the time by Bohlin (1940, 1947), who also summarised some of the earlier ideas and interpretations while arguing that a slicing function alone was more probable on both ecological and biomechanical grounds. Bohlin's ecological argument was also based on evidence from Rancho La Brea, which in his view indicated that *Smilodon* probably operated there as a scavenger, while his biomechanical argument was based on a lengthy discussion of the implications of attempting to stab into the body of a large ungulate and kill it, and stressed the high probability of damage to the teeth that would result. However, Kurtén (1968) in his consideration of European Pleistocene mammals suggested that while *Homotherium* may have used its canines to slice, those of *Megantereon* together with the powerful neck and massive forequarters of the latter species suggested to him a stabbing function. In his later discussion of North American Pleistocene mammals Kurtén (Kurtén & Anderson, 1980) reiterated this functional distinction between *Homotherium* and *Megantereon,* and suggested that the latter genus was ancestral, and functionally similar, to *Smilodon* (fig. 5).

In a detailed study of the functional morphology of the skull and anterior cervical vertebrae of *Smilodon,* Akersten (1985) concluded that the teeth were too blunt to permit stabbing, particularly as part of an initial attack. Like Bohlin, he also argued that excessive force would be needed to achieve a kill and that the risk of damage to the teeth was too great, and pointed out that the mandible was always likely to be an impediment to an effective stab. He then proposed a model for the machairodontine killing bite that solved many of the problems of the previous competing hypotheses. This model, known as the "Canine Shear Bite", implied that the predator would bite at a convex surface in the prey's body with jaws at full gape, and then use the mandible as an anchor to provide support while the whole skull was pulled down by the neck muscles acting on the mastoid process (fig. 6). Once this motion had caused initial penetration of the upper canines into the flesh of prey, and as the jaws closed, the gape became small enough to allow the adductor muscles of the mandible to pull efficiently during the rest of the killing bite. Akersten went on to suggest that a backwards pull of the head was used to cause further damage and to tear off a whole chunk of flesh, and thought that the belly of large ungulates was the most likely target for such a killing bite. Akersten's proposal has some parallels with that of Merriam & Stock (1932), who considered the side of the victim as the most likely target.

Akersten's view was supported by Martin (1989), although he suggested that a killing bite to the neck of prey was a more credible scenario than a belly bite since the abdomen was more easily defended

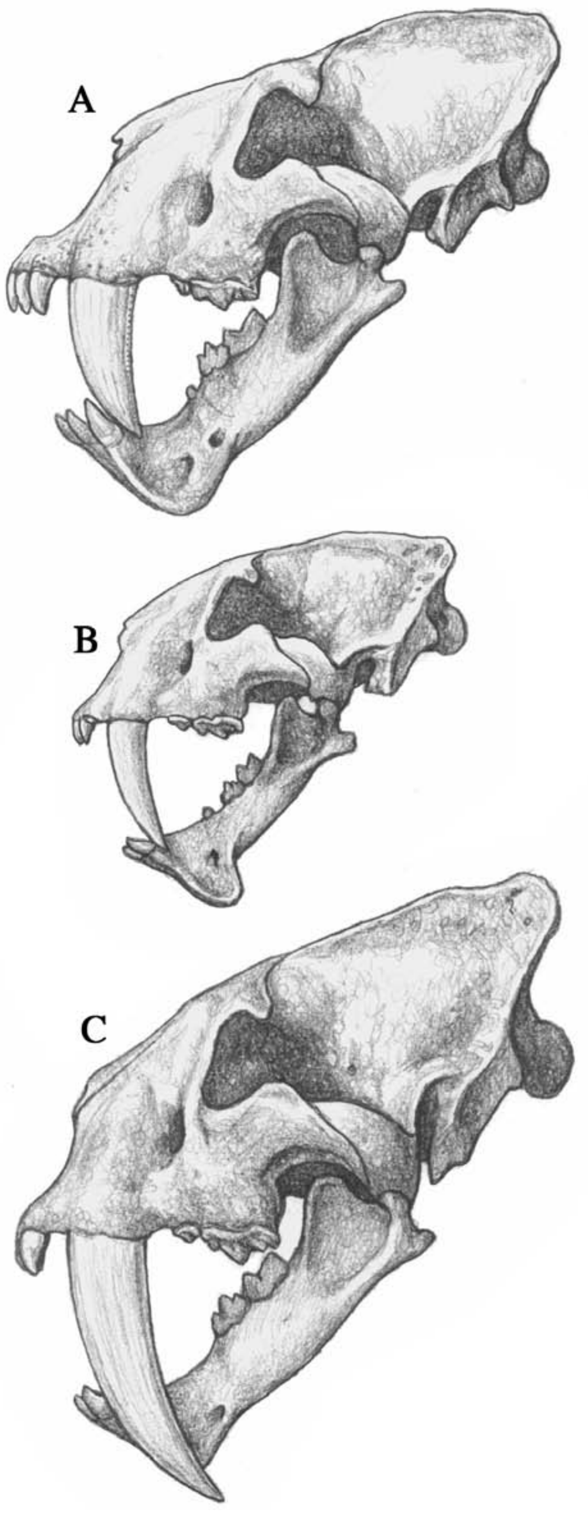

Fig. 5.—Skulls in side view of the homotheriin *Homotherium* (A), and of the smilodontins *Megantereon* (B) and *Smilodon* (C), illustrating the differences between the two machairodontine tribes that led Kurtén (1968) to suggest a more slicing function for the canines of homotheriins, and a more stabbing function for the smilodontins (Artwork by M. Antón).

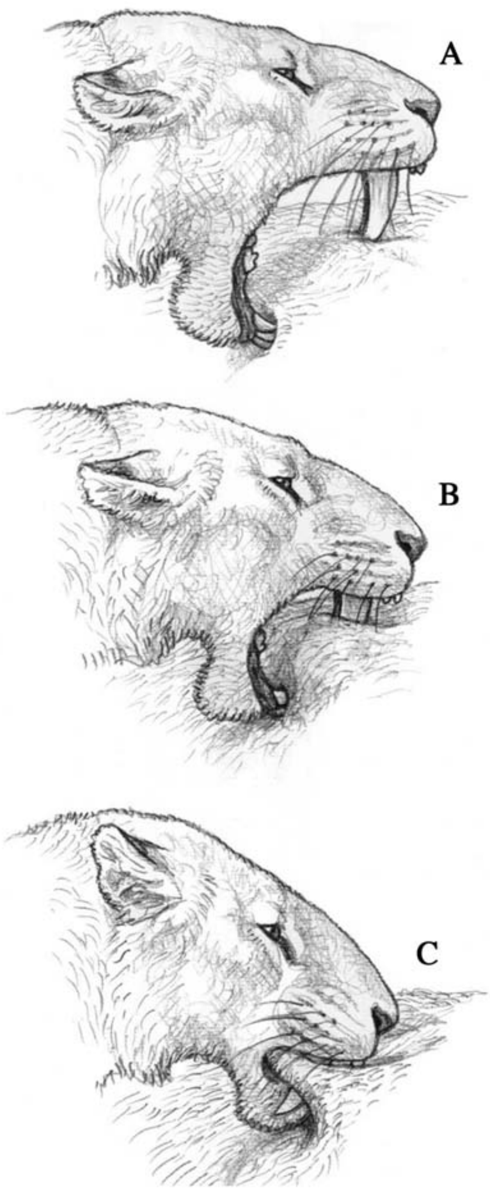

Fig. 6.—Reconstruction of the head of *Homotherium* illustrating the process of the Canine Shear-Bite as hypothesised by Akersten (1985) for the genus *Smilodon*. First (A), the predator opens its jaws at full gape to encompass a chunk of skin and flesh on a convex area of the prey's body. At such a wide gape, the adductor muscles of the mandible such as the *temporalis* and *masseter*, are too stretched to exert enough force for initiating a strong closure of the jaws. In the next stage (B), the whole head is ventrally flexed around the atlanto-cranial articulation using the force of the anterior neck musculature, while the front of the mandible, in contact with the prey's body, acts as an anchor. This motion allows the initial penetration of the canine tips into the flesh of the prey. In the next stage (C), the upper canines sink deep enough to decrease the gape of the jaws to an angle where the adductor muscles can exert their full force and produce a deeper bite. At this point it is feasible that the machairodont pulled back its whole head, tearing a large chunk of flesh from the prey. However, this pull is not a necessary condition for the effectiveness of the killing bite (Artwork by M. Antón).

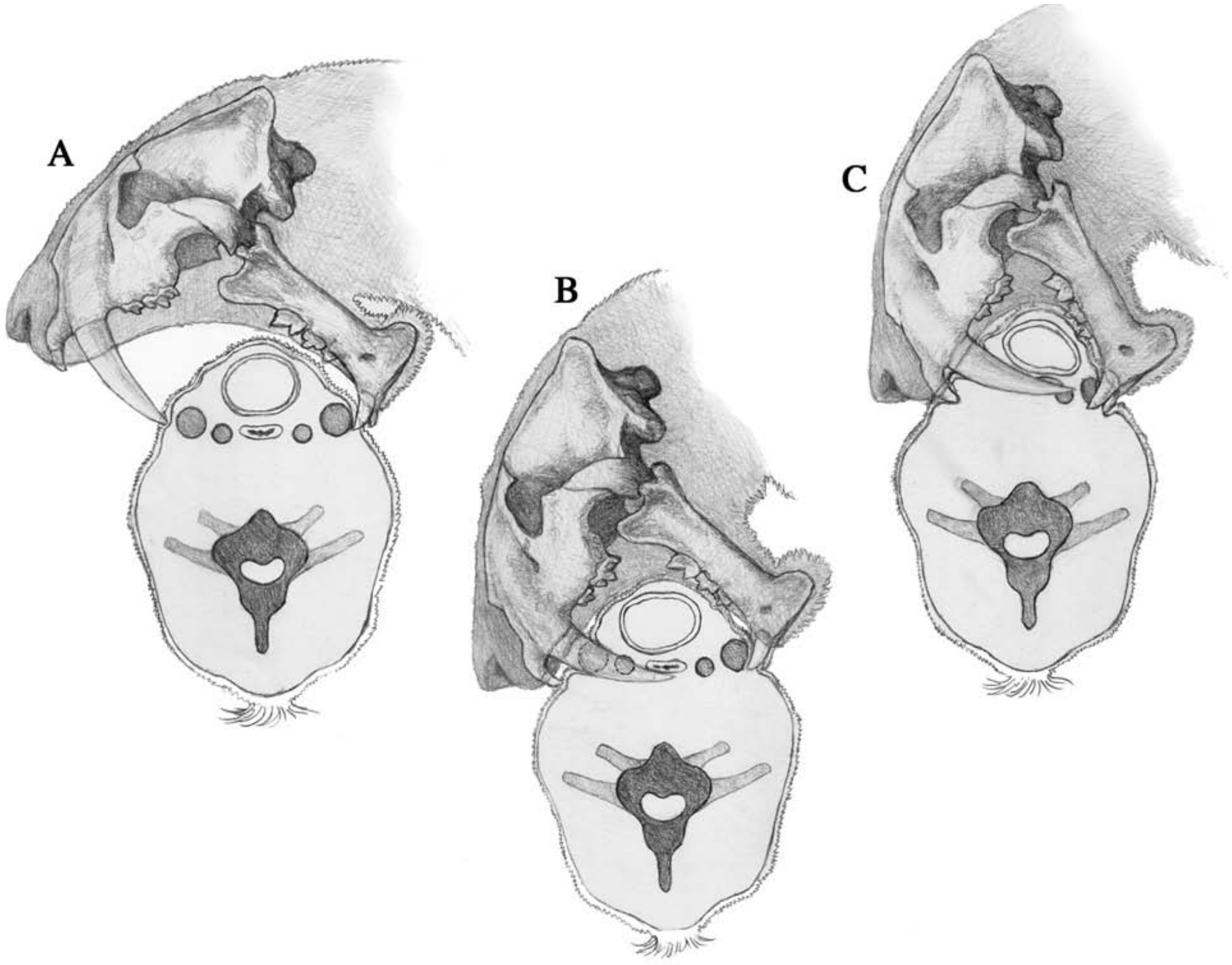

Fig. 7.—Skull and mandible of the smilodontin *Megantereon* shown in three stages of a Canine Shear-Bite applied to the neck of an equid (A, B and C), the latter shown in a transversal section at the level of the second cervical vertebra. As the illustration shows, vital structures such as larger blood vessels and the trachea of prey are in a vulnerable position in the anterior neck, making it an ideal target for the killing bite (Artwork by M. Antón).

by a struggling prey, the curvature of the belly was too low for an effective bite and even if a successful bite was made it would not lead to an especially quick death. Biknevicius & Van Valkenburgh (1996) and Turner & Antón (1997) also supported Akersten's hypothesis, but the latter authors gave further consideration to the whole problem, using Akersten's hypothesis as a starting point. Like Martin, they considered that a canine shear-bite to the throat of an immobilised prey would be more plausible than a bite to the belly, based, for instance, on consideration of the relative sizes of a skull of *Megantereon* and the neck of a horse (Turner & Antón, 1997, fig. 4.24), as shown here in fig. 7. The resultant occlusion and/or severance of the windpipe and several major blood vessels would ensure a relatively quick and efficient death and reduce risk of damage to the teeth, which would be kept well away from any larger bone masses and have any torsion produced by a struggling prey minimised, a conclusion matching that arrived at more recently by McHenry *et al*. (2007).

One further way for sabre-tooths to protect their upper canines against torsion during the killing bite is to enlarge the contact surface between the canine crown and the gum or gingiva, a feature that has been inferred for *Smilodon* from the extension of the cementum beyond the root-crown contact on the cervix of the upper canines (Riviere & Wheeler, 2005). This configuration would provide several functional advantages: on the one hand, the gingival component of the periodontal ligament would pro-

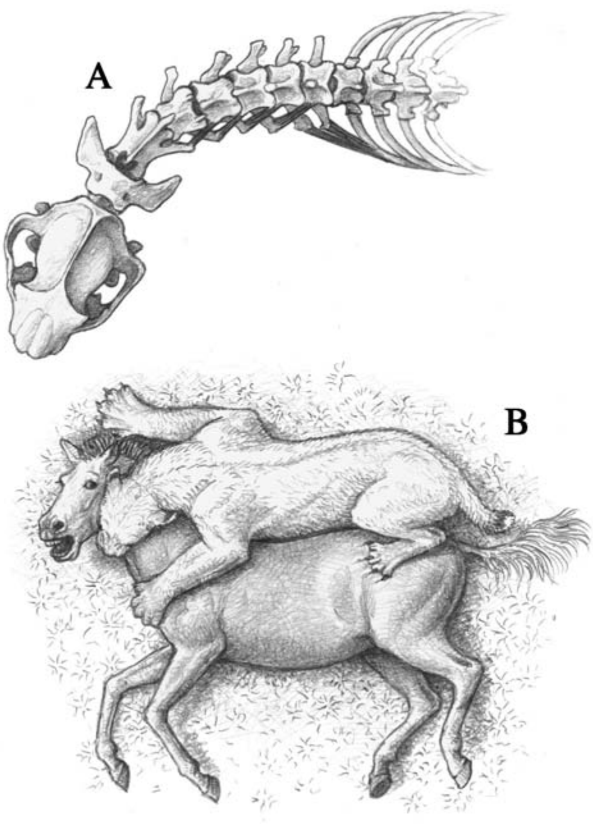

Fig. 8.—Dorsal view of the homotheriin *Homotherium* killing a horse. The detail of the skull, cervical vertebrae and anterior thoracic vertebrae (A) to which the trajectories of selected muscles have been added, shows how the great vertebral length and enlarged transverse processes provide for improved action of the muscles that rotate the neck. The drawing of the reconstructed animals (B) illustrates how the predator could position its body ideally for using its own weight to subdue and immobilise the prey, while rotating its neck in order to orientate the head with almost surgical precision for the bite (Artwork by M. Antón).

vide additional stability to the tooth; on the other hand, since the gingiva also acts as a tactile organ, it would help the animal know when the tooth had reached maximum functional penetration.

Biknevicius & Van Valkenburgh (1996) suggested that the strength of the upper canines, at least in *Smilodon,* would have meant that it could have resisted breakage during struggles with a wounded prey, provided that the jaws were fully closed during a canine shear-bite. However, they proposed that this fully closed bite was most likely to have been an effective method of control for “a weakened prey that had already received several quick but debilitating canine sheer-bites” (Biknevicius & Van Valkenburgh, 1996, p. 422), which seems a self-contradictory argument. In fact they went on to suggest that death may have been induced by means of a throat hold, which seems to us more likely but which in our view could only have been achieved with the prey held firmly using claws and the body weight of the predator and without preliminary attempts to bite elsewhere. Such a quick death, minimising danger to the predator, strikes us as the most plausible interpretation of canine shear-bite function, since it is hard to see how even a well-placed bite in the abdomen of a prey animal is likely to be achieved either with any degree of control or in a manner that would produce a rapid fatality. The interpretation of a single throat bite to an immobilised prey would apply broadly across the range of derived machairodontine cats, as exemplified in the case of *Homotherium* (Antón & Galobart, 1999), and would imply that the original functional advantage of large canines lay in the speed and efficiency of the kill of medium-sized prey using the canine shear-bite (fig. 8). We shall see in the subsequent section how this interpretation in turn sheds light on the evolution of the machairodontine cat functional complex.

Feeding, gape and implications for the reconstruction of soft tissues

The killing bite is only one of the aspects of the cranio-dental function of sabre-toothed felids that has led to conflicting interpretations. An equally important problem is how machairodontines dealt with the carcass and got food from it. Large canine teeth may appear something of an impediment to eating in a cat-like manner, and this led Miller (1969) to propose that sabre-toothed cats would need an especially elongated lip line, reaching further back than is the case in extant cats, in order to get food into the side of the mouth. But the relatively and absolutely large incisor battery of many species, often set well forward of the upper canines and in the derived crown species in particular incorporating the lower ones, must have helped to overcome that problem, as summarised by Bohlin (1940) and discussed in detail by Turner & Antón (1997, fig. 4.25). That the incisors would be used by some machairodontines to pull flesh from the bones of a carcass is further suggested by the evidence of tooth marks attributed to *Homotherium* on the bones of prey from a possible den in Friesenhahn Cave (Texas, USA) (Marean, 1989). Just as important is the fact that modern cats use their car-

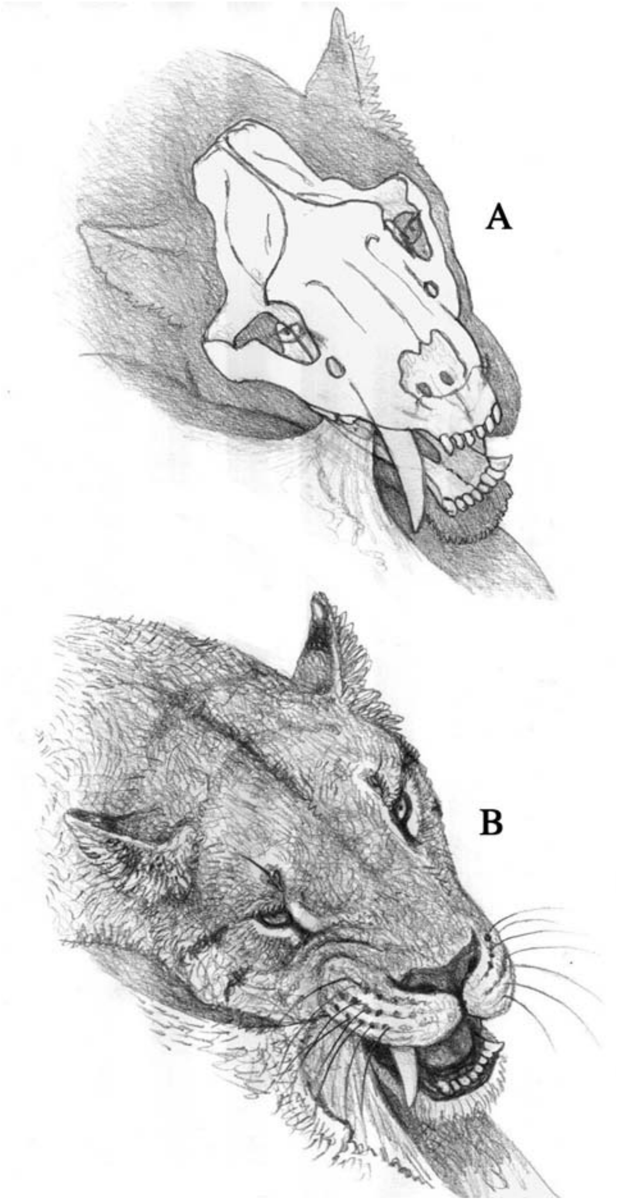

Fig. 9.—Reconstructed head (A) and skull (B) of *Smilodon* applying a carnassial bite to a carcass. As this illustration shows, the large upper canines of machairodontines were not an obstacle for this kind of bite, in which the food is taken directly through the side of the mouth, and where a normal cat-like mouth opening allows the carnassial teeth to separate and puts them in direct contact with the body of the prey (Artwork by M. Antón).

nassials to cut the skin and flesh of prey, and a comparison of the skull morphology and inferred position of soft tissues in pantherins and machairodontines shows that they were perfectly able to use their carnassials in a similar fashion without any interference from their elongated upper canines (Turner & Anton, 1997) (fig. 9).

Fig. 10.—An illustration of the proposed life appearance of *Smilodon* based on the arguments of Miller (1969). This drawing is consistent with the proportions of the actual skull, but shows such hypothetical features as the caudally elongated lip line and the shortened nasal cartilage (Artwork by M. Antón).

These considerations lead us to the next major source of debate about function and reconstructed appearance: the gape needed for the mandible to clear the upper canine tips and the length of the lip line. Life appearance of machairodontines has been as much a matter of debate as function, especially because of their highly specialised dentition and jaw apparatus (Bryant, 1996). In earlier reconstructions, such as those of *Smilodon* undertaken by C. R. Knight (Merriam & Stock, 1932, figs. 4-5), the head was usually distinctly cat-like, but Miller (1969) raised objections to that view, based not only on the argument mentioned above that a cat-like lip line would not allow food to enter the side of the mouth but also that it would not permit the gape needed to accommodate the canines (fig. 10). Besides suggesting that the lip line should be set much farther back, he also proposed that the external nose should be considerably shorter and the nostrils retracted, the dorsal profile of the skull straightened and the ears set relatively lower on the skull, thereby giving the animal a distinctly non-catlike appearance.

Turner & Antón (1997, p. 138-142) rejected Miller's argument at some length, but returned to the point in more detail in a subsequent publication (Antón *et al*., 1998) with a fuller consideration of the reconstructed facial appearance of *Smilodon* in view of the wider support that Miller's interpretations appeared to have enjoyed. After a thorough

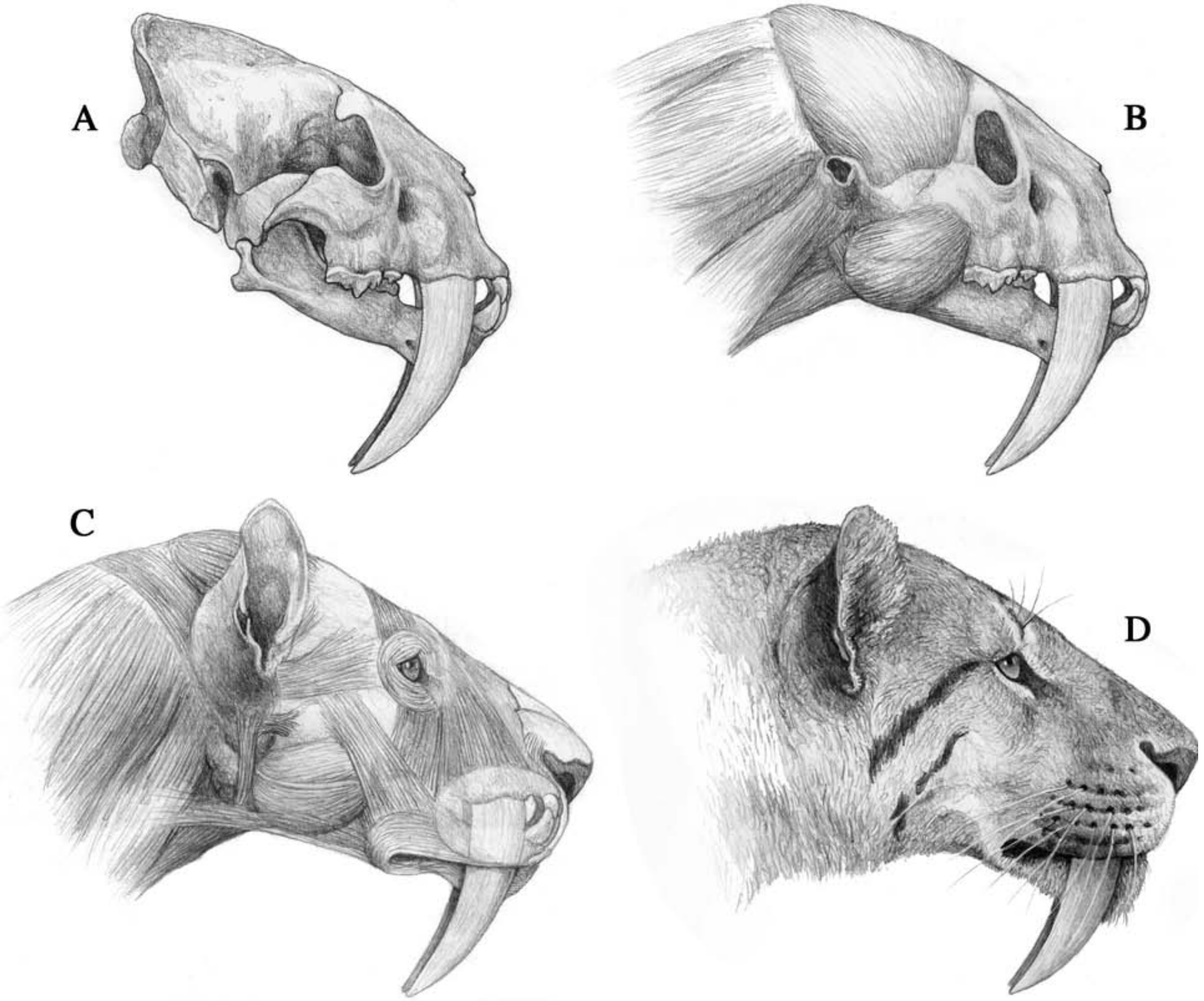

Fig. 11.—Step by step reconstruction of the head of *Smilodon*. A, skull and mandible; B, with reconstructed masticatory muscles and neck musculature; C, with superficial musculature; D, life appearance (Artwork by M. Antón).

review, employing first-hand study of skulls, dissections of a number of living felids and an extensive examination of the skulls of fossil felines, machairodontines and other larger Carnivora together with detailed reconstructions of the facial musculature of fossil felids, they were able to conclude that a broadly cat-like appearance was entirely appropriate (fig. 11). Although based on a detailed consideration of *Smilodon*, their conclusions have clear applicability across the range of machairodontine taxa, and imply not only a cat-like appearance but also a cat-like pattern of eating, with the incisors pulling off soft tissues and the cheek teeth employed in slicing. A later facial reconstruction of *Homotherium* (Antón *et al*., 2009) showed a combination of broadly cat-like appearance with a unique head shape resulting from unmistakable homotheriin cranial proportions such as a straight dorsal profile, a projecting incisor battery and a deep mandibular symphysis implying an elongated, tall and square muzzle (fig. 12). This detailed reconstruction not only revealed the likely life appearance of the Pleistocene scimitar-tooth cats, but also led to questions about early interpretations of an Upper Palaeolithic statuette from the French Pyrenees site of Isturitz as a stone-age depiction of *Homotherium*. In fact, comparison of our reconstruction with images of the statuette indicated that the latter was most likely a representation of a cave lion.

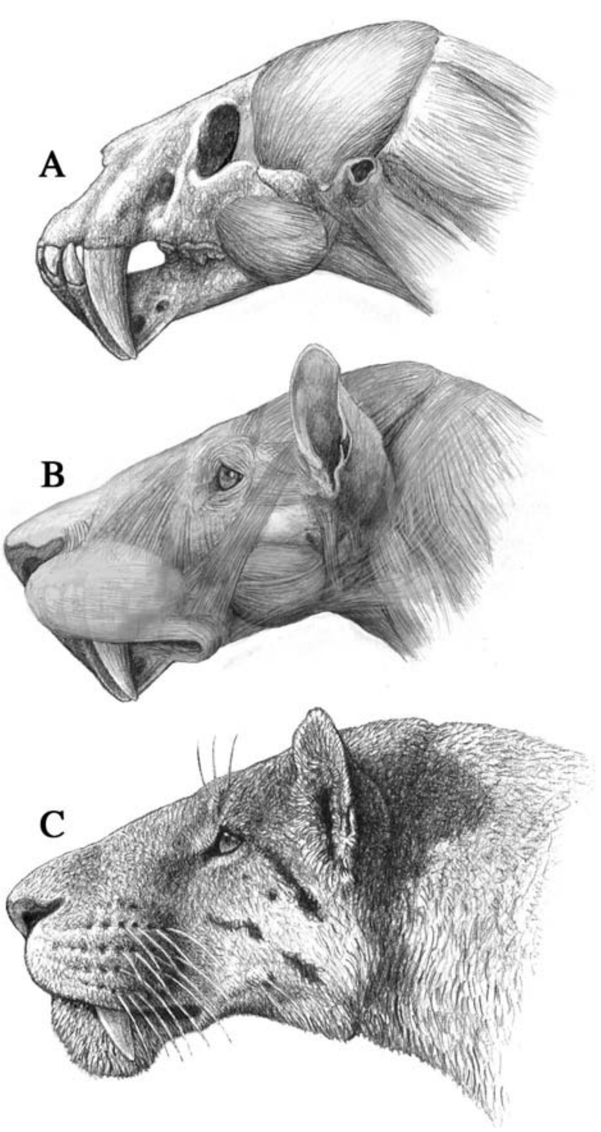

Fig. 12.— Skull (A), reconstructed musculature (B) and restored life appearance of the head (C) of *Homotherium*. Notice the prominent, square outline of the muzzle due to the straight nasals, high mandibular symphysis and protruding incisors (Artwork by M. Antón).

The origin of the specialised machairodont features

Since machairodontines, despite an undoubtedly cat-like appearance, are so obviously different from living species, an assumption underlying many attempts to interpret the functional morphology of the machairodonts has been that they preyed on unusually large and usually thick-skinned ungulates, or "pachyderms" to use an obsolete term, as exemplified in the paper by Simpson (1941) and more recent authors (Anyonge, 1996; Bakker, 1998). A second, but less explicitly expressed assumption has been that the extreme suite of machairodontine morphologies exemplified in the crown taxa *Smilodon*, *Megantereon* and *Homotherium* are typical of all machairodontines, and have evolved in parallel "under strong pleiotropic control" (Dawson *et al.*, 1986) as an adaptation to tackling such large prey. But of course these three taxa are known from Pliocene and Pleistocene deposits; they are the latest and probably most derived of the machairodontines, and we have until recently known very much less about the morphology of earlier taxa. The extent and nature of mosaic evolution in morphology has therefore been unknown, with only the recognition that a functioning complex of characters must have been the pattern at any one time as a guide to interpretation.

This situation changed with the recovery of machairodontine remains from ~ 9 Ma deposits at the Spanish fossil locality of Batallones-1, near Madrid. The material provides numerous complete or semi-complete individuals of two species, the large, lion-sized *Machairodus aphanistus* (Antón *et al.*, 2004) and the smaller, leopard-sized *Promegantereon ogygia,* previously referred to the genus *Paramachairodus* (Salesa *et al.*, 2005, 2006) but now referred to a genus first erected by Kretzoi (Salesa *et al.*, 2010a). In both cases we are able to discern something of the origins of the large upper canine of the machairodont functional complex within a more primitive cranio-mandibular morphology and a biomechanical structure much more like that of a modern feline cat (fig. 13).

In the case of *M. aphanistus*, the highly derived, elongated and flattened upper canines are similar to those seen in later taxa such as *Homotherium*, where they were evidently used within a complex of equally derived cranio-mandibular adaptations (fig. 14). But in *M. aphanistus* they are present in a cranium where the incisor arc is not well-developed, the lower canines are large, the post-canine teeth are not particularly derived in the machairodontine direction and the gape size was only moderately greater than that in modern felid species (Antón *et al.*, 2004). The force of head depression to assist bite, as indicated by size and direction of neck muscle insertions, is greater than that of modern pantherin cats but clearly much less than that seen in derived machairodontines (fig. 15). These morphological features suggest predatory behaviour that differed both from

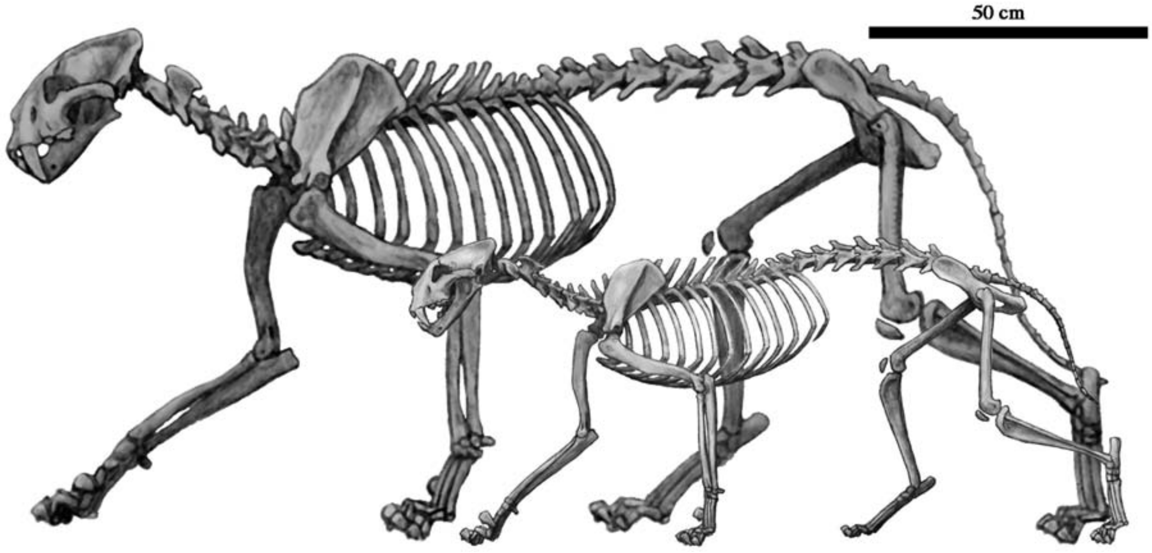

Fig. 13.—Reconstructed skeletons of the machairodontines *Machairodus aphanistus* (left, background) and *Promegantereon ogygia* (foreground), based on material from the Vallesian (late Miocene) site of Batallones-1 (Artwork by M. Antón).

that of extant pantherins and from that hypothesized for derived machairodontines. While it may have killed by penetrating the flesh of the throat with its canines to induce blood loss, just as has been inferred for the derived taxa, the upper canines of *M. aphanistus* would have been inadequate for either a crushing nape bite or a suffocating throat bite. On the other hand, features such as the insertions and orientations of the *masseter* and *temporalis* muscles and the size of the lower canines indicate that the force applied to both upper and lower canines through contraction of the jaw-closing musculature at moderate gapes provided the main power for the bite, just as in pantherins and other modern cats.

Rather than suggesting concentration on animals much larger than themselves, the limited adaptation for gape and the primitive biting mechanism in *M. aphanistus* suggest that its upper canines originally evolved as an adaptation for killing prey within the size range of those killed by modern felids of comparable size, and that a horse or antelope was the largest prey that *M. aphanistus* could kill efficiently and regularly. The key advantage of the initial development of sabre-like teeth would then lie in the efficiency of a killing bite that caused massive blood loss instead of suffocation. Such a mosaic of features also contradicts the idea of "strong pleiotropic control" for the derived machairodontine features as some kind of "all or nothing package", and suggests instead that they have evolved

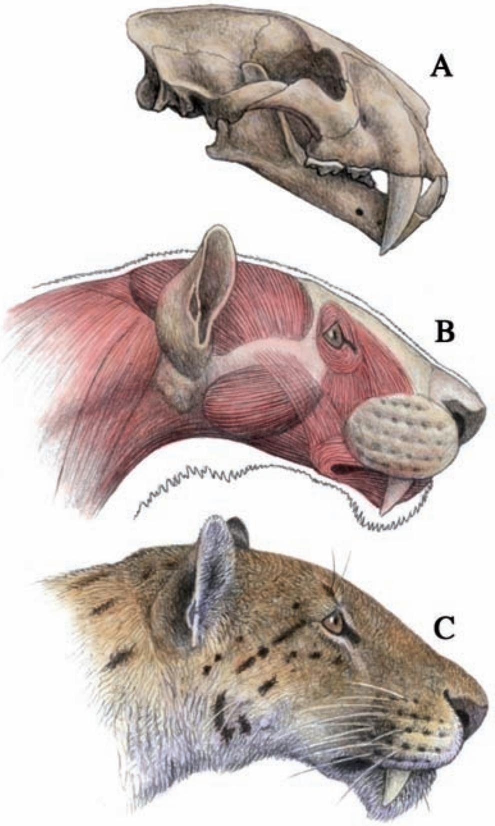

Fig. 14.—Skull (A), reconstructed musculature (B) and restored life appearance of the head (C) of *Machairodus aphanistus*. Notice the gently convex dorsal outline of the skull and scarcely protruding incisor battery compared with *Homotherium* in figure 12 (Artwork by M. Antón).

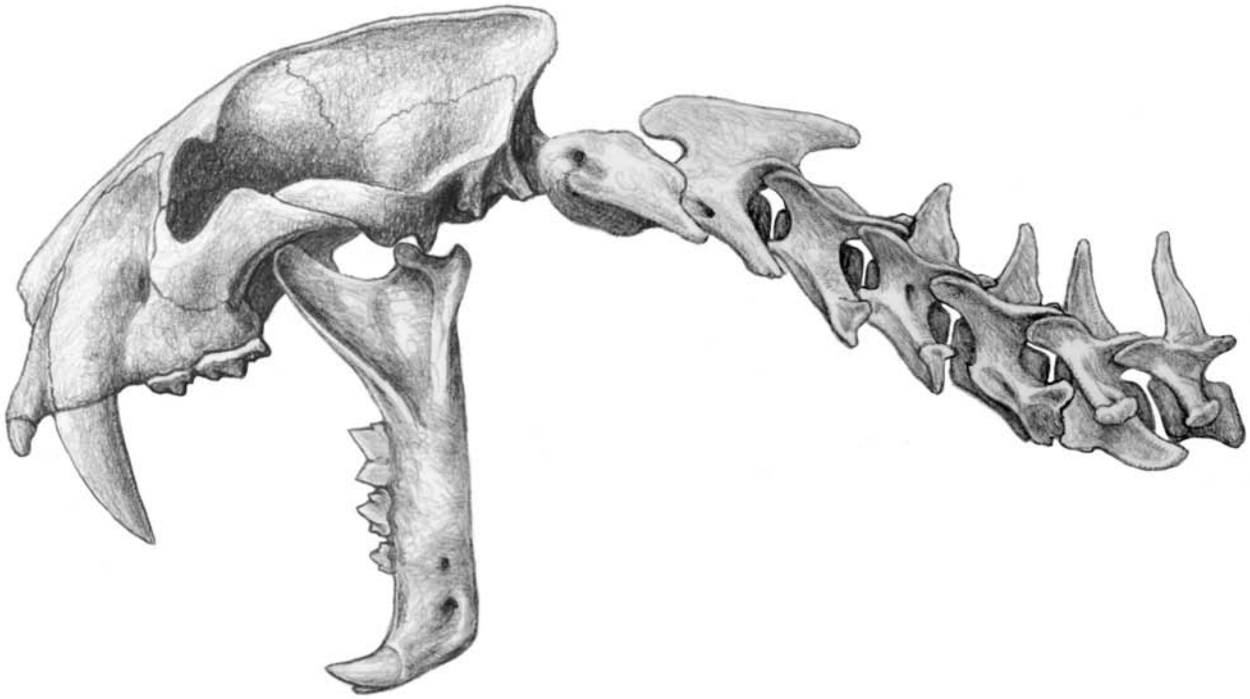

Fig. 15.—Skull and cervical vertebrae of *Machairodus aphanistus*, based on fossil material from Batallones-1 (Artwork by M. Antón).

independently in each lineage of sabre-toothed mammalian predators.

This interpretation is strengthened when we consider the pattern seen in the second machairodontine from Batallones-1, *Promegantereon ogygia*. In overall appearance the skull and many features of the dentition of this smaller species are broadly similar to those of a pantherin felid, but the upper canines are moderately elongated and flattened and the mandibular symphysis is strongly verticalised (Salesa *et al*., 2005) (fig. 16). These features are allied to a neck morphology that shows only modestly-developed machairodontine traits, but the total package points to the importance of a canine shear-bite where head flexion operated in conjunction with the mandible acting as an anchor (Salesa *et al*., 2005). Thus while the overall morphology is still very far from the functional complex seen in the Plio-Pleistocene sabre-toothed crown taxa, it is again most plausibly interpreted as an adaptation to quick and efficient killing of prey close in size to the predator. Moreover, the risk of canine damage from bone contact probably meant that the animal would have avoided smaller prey species (Salesa *et al*., 2006). Further support for these interpretations comes from consideration of the forelimb anatomy in *P. ogygia* (Salesa *et al*., 2010b), where the morphology is clearly adapted for powerful extension and supination of the forearm while providing reinforced stability to the elbow and shoulder. The first phalanx, or dewclaw, is particularly robust, and the overall impression is of great strength able to provide rapid capture and immobilisation of prey so that a throat bite could be made with minimal risk to the predator and its teeth. With such increased efficiency in killing, there would also be a significant reduction in energy expenditure (Salesa *et al*., 2006). At the time of writing, investigations of the functional anatomy of the forelimb of *Machairodus aphanistus* have yet to be completed, but it will be interesting to see the extent to which these parallel features are seen in *P. ogygia*.

Hunting, ecology and social behaviour

Hunting is the most obvious aspect of machairodontine behaviour about which the fossils are likely to provide useful clues, but any attempt to reconstruct such activities must take into account other aspects, such as sociality and ecology, which are also closely linked with their predatory strategies. Of course

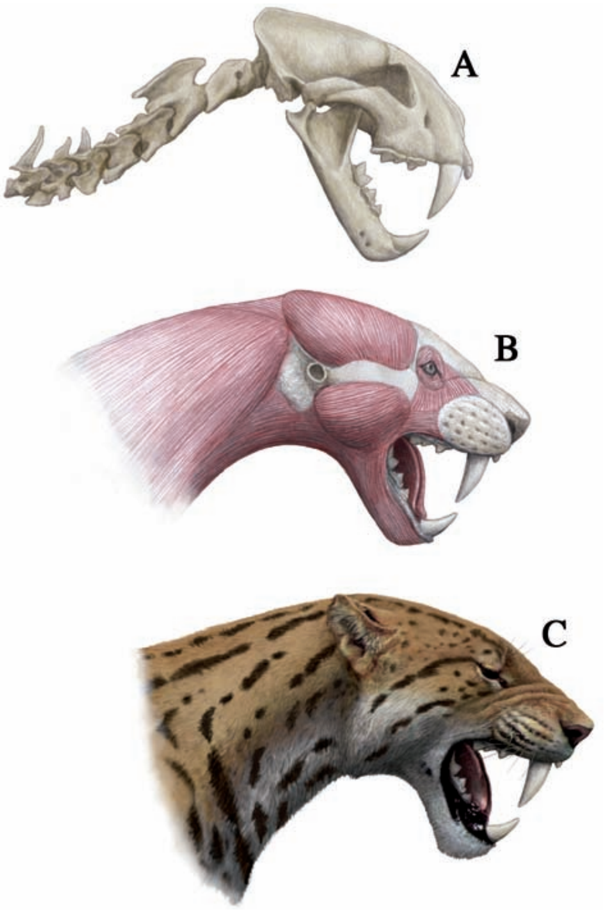

Fig. 16.—Skull (A), reconstructed musculature (B) and restored life appearance of the head (C) of *Promegantereon ogygia* (Artwork by M. Antón).

with extant felids, direct observation is all we need to determine if they are social or solitary or if they live in open or closed environments, but with fossil cats we are left to make inferences from their anatomy and from the context of the fossil sites. Strong sexual dimorphism in extant Carnivora has been suggested to correlate with breeding behaviour, particularly amongst the Felidae where it is evident in the highly social lion, a species in which males compete aggressively for females (Gittleman & Van Valkenburgh, 1997). On this basis, sexual dimorphism in extinct Felidae may therefore be of some palaeoecological significance (Turner, 1984), and is an obvious avenue to explore.

Van Valkenburgh & Sacco (2002) applied the idea of a relationship between sexual dimorphism and breeding system to the study of social behaviour in *Smilodon fatalis* from the Rancho La Brea. They found a low level of sexual dimorphism, which they took to be consistent with a typical felid social structure in which both sexes are usually solitary, and males defend a territory that includes those of the females. But the precise significance to be attached to any given level of dimorphism across a range of species is open to debate. As Van Valkenburgh & Sacco (2002) pointed out, both lions and leopards appear quite dimorphic, despite the fact that one is solitary and the other social. They also argued that both tigers, *Panthera tigris*, and jaguars, *Panthera onca*, are significantly less dimorphic, and concluded from this that while high dimorphism does not necessarily imply a lion-like social structure, reduced dimorphism does imply its absence. Turner & Antón (1997) had argued that the high numbers of *Smilodon* remains found at Rancho La Brea in relation to remains of prey species could themselves be an indication of higher levels of social interaction, and a more recent study by Carbone *et al.* (2009) has suggested that parallels between events at modern simulated kill sites and the relative abundance of predators at Rancho La Brea may now support ideas of sociality in that species at that site. In fact, and as suggested by Van Valkenburgh & Sacco (2002), it is possible that *Smilodon*, or any machairodontine for that matter, could have been social while not sharing the particular social system of lions with its consequent intense competition between males for access to females. An alternative system could be one with a monogamous alpha pair acting as the centre of the social group, as happens among extant carnivores in the moderately dimorphic modern wolves.

One feature of the *Smilodon* sample from Rancho La Brea that has been seen as evidence of group behaviour is the presence of healed injuries in fossil bones of the sabre-tooth, since it has been suggested that injured individuals would have died before their fractures healed unless allowed to eat at the kills of other group members (Heald, 1989). This idea has been rebutted extensively by MacCall *et al.* (2003) who provide veterinary data about the timing of bone healing in injured felines and about their resistance to starvation, suggesting that the examples of healed injuries found at La Brea are compatible with solitary behaviour. According to these authors, injuries like the ones seen at the site can heal naturally fast enough to allow the animal to survive until it is capable of hunting or at least of opportunistic scavenging. Furthermore, since felids can only get a fraction of their water requirements from their kills, dehydration comes about earlier than starvation, and consequently any injured cat must be mobile enough to walk to water during the healing period, a mobility that would also allow it to scavenge opportunistically. Additionally, they argue that the frequency of injuries is comparatively low at the site, suggesting that animals with really severe fractures usually died before healing and would not have been able to get to the asphalt seeps for scavenging. Thus the question of sociability of *Smilodon* from Rancho La Brea remains an open one and more data are obviously required.

The data from Batallones-1 have been argued to suggest that *Promegantereon ogygia*, a smaller animal with a low degree of sexual dimorphism, may have exhibited a low degree of competition among males for the access to females (Salesa *et al*., 2006) while the larger *Machairodus aphanistus* shows evidence of greater dimorphism (Antón *et al*., 2004), implying that the males of the latter species would had been much more intolerant of the presence of other adult males in their territories. The vast majority of the Batallones-1 machairodontine sample is made up of young adults, suggesting that it was precisely the dispersing individuals that came across the natural trap when they entered a territory left vacant by an adult previously entrapped, a process that repeated over time could lead to the accumulation of felid fossils found at the site (Antón & Morales, 2000).

Whatever interpretation we place on the evidence for dimorphism, *Promegantereon ogygia* and *Machairodus aphanistus* differed considerably in their body size (fig. 13), which in turn implies a set of ecological differences. When different species of extant felids live in sympatry a marked segregation exists between them, with the small-sized species constantly avoiding the often violent encounters with the large ones. It is known that lions and leopards kill adults and cubs of other felids, and leopards are killed by lions and tigers (Turnbull-Kemp, 1967; Schaller, 1972; Bailey, 1993; Daniel, 1996; Alderton, 1998; Bothma & Walker, 1999). Thus in modern ecosystems, the coexistence of two species of large felids usually occurs in habitats with some tree cover, which allows the smaller species to take refuge from the attack of the larger one and so avoid being killed or having its prey stolen (Morse, 1974). This is the case for lions and leopards in Africa (Bailey, 1993) and tigers and leopards in Asia (Seidensticker, 1976). In the case of cheetahs and lions, both of which can be found in more open environments, sympatry is possible because cheetahs constantly avoid encounters with lions, hunting during the hours of maximum heat when lions and hyaenas tend to be inactive and resting in the shade (Hanby & Bygott, 1979; Durant, 2000). There is also sympatry among felids of similar size, such as pumas and jaguars in most of the American continent (Nuñez *et al*., 2000), but this is only possible when resources are rich enough to allow both species to exist while developing a marked ecological segregation based on the avoidance of adult encounters (Rabinowitz & Nottingham, 1986; Nuñez *et al*., 2000). In summary, the sympatry of two large felid species seems to be determined not only by the presence of enough tree cover, but also by high prey biomass (Seidensticker, 1976). In the case of lions and leopards, this sympatry is facilitated by the fact that leopards preferably occupy wooded sections of the habitat, which are less favourable for lions (Bailey, 1993). The body proportions of *P. ogygia* and *M. aphanistus* are very similar to those of the extant pantherin felids (Salesa *et al*., 2005; Antón *et al*., 2004), probably reflecting similar habitat preferences for wooded environments (fig. 17). The predominance of *P. ogygia* in Batallones-1 could imply that the trap was in a wooded area with at least enough cover to allow this species to coexist with the larger *M. aphanistus* (Antón & Morales, 2000).

It is clear that what is taken as the primary characteristic of these animals, the enlarged upper canine, evolved in a very different biomechanical context from that generally considered to be the norm for machairodontines based solely on consideration of the derived crown taxa. Both *M. aphanistus* and *P. ogygia* show cranio-dental morphologies that differ from those of both the extant, conical-toothed felines and the crown machairodontine taxa, but which can plausibly be seen to lie at or close to the root of development of those features along the subsequent lineages leading to the Homotheriini and Smilodontini. Indeed, as Wroe *et al*. (2008) have emphasised, the crown machairodontines show an interesting pattern of postcranial morphological divergence, with the dirk-toothed Smilodontini displaying an emphasis on more power and less speed while the scimitar-toothed Homotheriini, although distinct, depart less from the generalised felid morphology seen in *Panthera pardus* in terms of the robustness of the limb bones (fig. 18).

Fig. 17.—Reconstruction of the Vallesian environments and fauna around the fossil site complex of Cerro de los Batallones. From left to right: *Micromeryx* sp.*; Promegantereon ogygia* (on the tree); *Magericyon anceps* (on the ground); *Aceratherium incisivum; Microstonyx major* (far background); *Tetralophodon longirostris; Hipparion* sp.*; Machairodus aphanistus*; undetermined sivatherine giraffid; undetermined boselaphine bovid (background); *Protictitherium crassum* (foreground). As in many other Tertiary fossil sites, the presence of two sabre-tooth species of different sizes, combined with the presence of several species of browsing herbivores, points to the presence of some tree cover around the site (Artwork by M. Antón).

The study of the specific function of the dentition and of the evolution of the craniodental complex in the Batallones-1 felids shows that an emphasis on rapid and efficient killing by means of blood loss was quickly developed. Flattened and elongated canine teeth, together with an angular mandibular symphysis, were therefore incorporated into a morphological suite that initially showed few developments in the direction of the derived machairodontine condition, and a greater emphasis on strong head depression only appears later in the sequence. At least in *P. ogygia* these craniodental features were matched by great strength in the forelimbs, massive dewclaws and an evident ability to hold prey securely. This combination allowed the animal to minimise the energy expenditure and the risk of canine breakage (and other injuries) and these would have been the main advantages associated with the origin of the machairodontine adaptations (Salesa *et al*., 2006). The classic explanation that has linked machairodontine dentitions with such strong forelimbs in the derived crown taxa as evidence of concentration on very large prey from the earliest stages of evolution within each lineage is now seen to be based on a questionable set of interpretations, as emphasised by Salesa *et al*. (2010b).

Promegantereon ogygia is recorded in Spain in both MN 10 (Batallones-1) and MN 11 (Crevillente-2), and the type material is from MN 9 deposits at Epplesheim in Germany (Salesa *et al*., 2010a). The two more derived species *Paramachaerodus maximilliani* and *P. orientalis* became extinct in the Turolian (Late Miocene), and were replaced by the more derived and jaguar-sized crown genus *Megantereon*, although the exact nature of the relationship between the older and

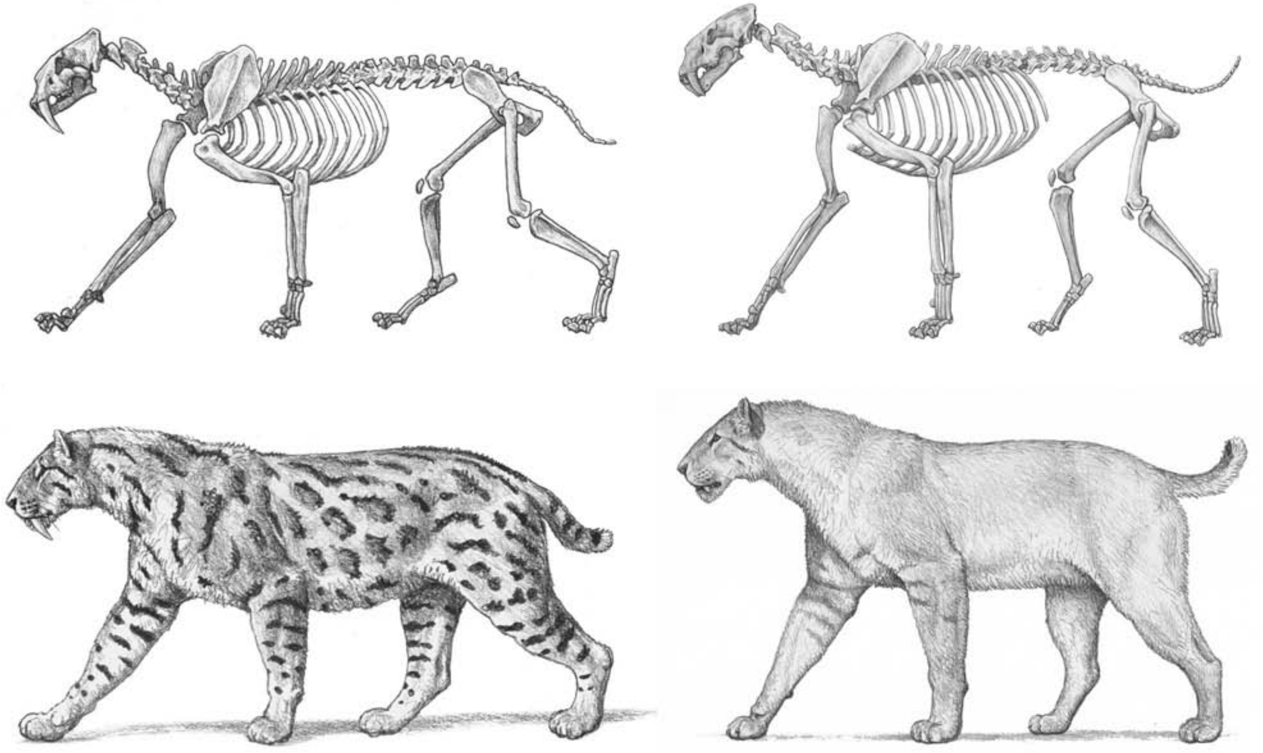

Fig. 18.—Skeleton and reconstructed life appearance of *Smilodon* (left) compared with *Homotherium*. Note the more robust proportions of the smilodontin felid (Artwork by M. Antón).

younger genera remains to be established. The disappearance of both *Promegantereon* and *Paramachaerodus* may be associated with the progressive aridification that occurred during the Vallesian and Turolian (Fortelius *et al*. 2002), which led to the predominance of savannas over wooded habitats. However, the body proportions of the Plio-Pleistocene genus *Megantereon* were broadly comparable with those of *P. ogygia*, with a similarly low brachial index, suggesting similar preference for wooded environments, and it thus seems obvious that it also required some degree of tree cover to survive. But whilst the cranial and skeletal features related to the machairodontine type of killing were still moderate in *P. ogygia* (Salesa *et al*., 2005, 2006) they were much more developed in *Megantereon,* suggesting a more specialised killing behaviour in the latter genus, possibly associated with larger prey size.

Machairodus aphanistus, as the first member of the machairodontine lineage to attain lion size, was previously considered ancestral to the more dentally derived Turolian species *Amphimachairodus giganteus*. However, this relationship was questioned by Ginsburg *et al*. (1981), who argued that several features of *M. aphanistus*, such as the large lower canines, are too specialized to permit direct ancestry and went on to propose the smaller, more primitive species *M. alberdiae* as the likely ancestor of *A. giganteus*. Our own detailed study of the Batallones-1 material (Antón *et al*., 2004) revealed differences in cranial and mandibular anatomy between *M. aphanistus* and *A. giganteus* that were not evident from the less complete material previously available (fig. 19). This led to the formal proposal that *A. giganteus*, which most authors still included in *Machairodus*, should indeed be referred to a separate genus, *Amphimachairodus* Kretzoi, 1929, although the question of the relationship between *A. giganteus* and any particular species of *Machairodus* was not addressed. Other early species of *Machairodus* are known from Asia (Schmidt-Kittler, 1976; Sotnikova, 1992) but in all these primitive taxa the skull morphology remains virtually unknown. In contrast, complete skulls of *A. giganteus* are known from sites in China (Chang, 1957) and Moldavia (Riabinin, 1929), clearly showing that, unlike the overall primitive cranial mor-

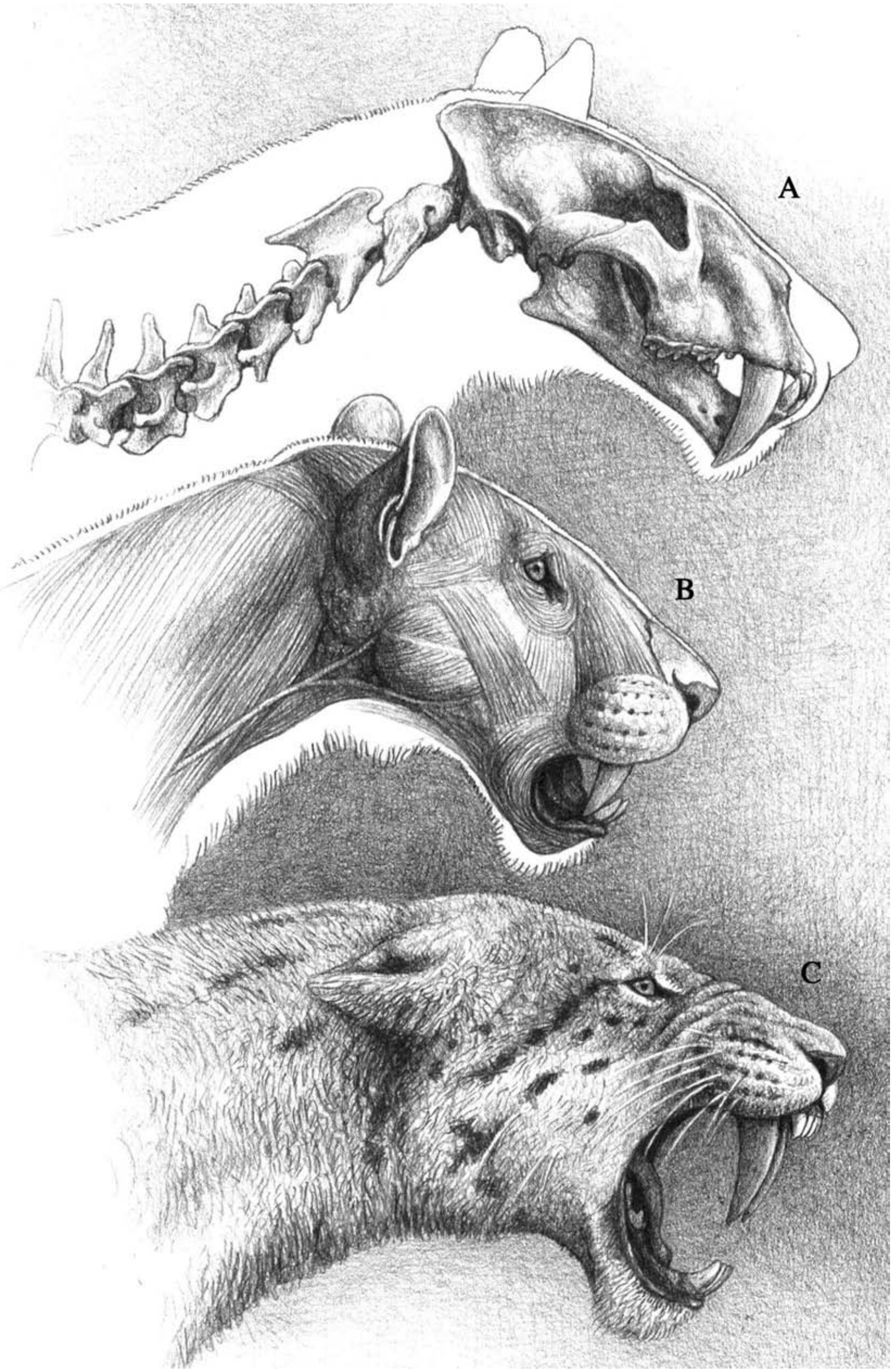

Fig. 19.—Skull (A), reconstructed musculature (B) and restored life appearance of the head (C) of *Amphimachairodus giganteus* (Artwork by M. Antón).

phology seen in the Batallones-1 *M. aphanistus* material, it had all the cranial features typical of advanced machairodonts. Thus, whatever the precise nature of their relationship, *M. aphanistus* clearly exemplifies a less derived stage in machairodintine evolution than the Turolian taxon, and it remains likely that *A. giganteus* had its origins among animals of *Machairodus* grade. The features seen in *A. giganteus* are further developed in the Plio-Pleistocene *Homotherium*, known from complete skulls from many sites in four continents (Turner & Antón, 1997).

The spreading of grasslands at the expense of forest at the end of the Vallesian (Agustí *et al.*, 1999; Fortelius *et al.*, 2002) may have restricted the species diversity of the forest-dwelling sabre-toothed felids. The postcranial elements of the largest species of *Paramachaerodus*, *P. maximilliani*, are virtually unknown, making it impossible to assess the body proportions of this species; its size was intermediate between that of the earlier species of the genus and that of *Megantereon*, and if we assume that it was proportioned like a forest-dwelling felid then this could have meant that the niche occupied by *P. maximilliani* became progressively narrower, leading to the disappearance of the species. Subsequent phases of moist climate during the Pliocene and Pleistocene would have favoured the wide expansion of *Megantereon*, which would also have preferred wooded habitats. In fact, the earlier part of the Pliocene with its more warm, humid climate and extensive forests, saw the expansion of another type of forest-adapted big felid, the so called "false sabre-tooths" of the genus *Dinofelis*.

Did the larger *Machairodus aphanistus* and subsequent members of the lineage operate as social predators? Apart from the considerations about sexual dimorphism and breeding system discussed above, the most important factors affecting social behaviour in modern carnivores are predator body size, prey size and vegetation cover. Thus it has been shown that all the extant larger carnivore species that are social tend to take prey larger than themselves and live in mixed or open habitats (Packer, 1986; Packer *et al.*, 1990; Sunquist & Sunquist, 1989), and competition for prey and territory in such high-visibility environments is exacerbated as kills and dens are easily detected by competitors. It thus becomes even more beneficial for large carnivores to join forces with conspecifics in order to defend territory, kills and offspring. Observations about the conditions of life in extant social predators cannot establish if such conditions necessarily led to the evolution of group behaviour in the past, but they do suggest that, if large carnivores adapted to take large prey lived in an open environment, then the likelihood of group behaviour is greater than if they lived in more closed habitats.

Machairodus, Amphimachairodus and *Homotherium* were obviously adapted to take prey larger than themselves and what is known about their postcranial skeleton indicates they were well adapted to efficient terrestrial locomotion, with later forms further departing from the scansorial model typical of primitive felids and becoming more adept at sustained locomotion at medium speeds over long distances (Antón *et al.*, 2004). Such features are compatible with group behaviour as discussed above, and it is conceivable that an opening of the vegetation could have been to the advantage of these animals, particularly if they were able to kill quickly and efficiently by employing their upper canines to inflict a fatal bite to the throat.

Hypotheses about sabre-tooth ecomorphs

The morphological differences between crown members of the Homotheriini and Smilodontini, which led Kurtén (1968) to coin the terms "scimitar-toothed cats" for the former and "dirk-toothed cats" for the latter, were further interpreted by Martin (1989) as features indicating the existence of two discrete, well differentiated ecomorphs among sabre-toothed carnivorans. According to this view, the possession of moderately high-crowned, strongly flattened and coarsely serrated upper canines like those of *Homotherium* or *Machairodus* would be predictably associated with relatively slender, long-limbed skeletons implying fast pursuit of prey and even possible group behaviour, while the high-crowned, less flattened canines of *Smilodon* or *Megantereon*, with fine or absent crenulations on their edges, would correspond with robust, short-limbed skeletons implying ambush predation and obligate solitary behaviour. Such ecomorphs are seen as essentially taxon free, so that although they coincide with the taxonomical differentiation between Smilodontini and Homotheriini within the Felidae, other, non-felid sabre-tooths would also fit predictably within one or other ecomorph. Thus, the barbourofelid *Barbourofelis* or the thylacosmilid marsupial *Thylacosmilus* would be typical dirktooths, while the nimravid *Dinictis* was seen as an example of a non-felid scimitar-tooth.

However, it is now clear that such a rigid demarcation does not exist. The discovery of the short-limbed homotheriin genus *Xenosmilus* in Pleistocene deposits in Florida (Martin *et al.*, 2000) has provided a clear example of a machairodontine combining scimitar-like canines with an extremely robust skeleton, showing that these felids had considerable evolutionary plasticity and were not constrained by a rigid ecomorph model. The Oligocene nimravid *Dinictis* is also poorly characterised as a scimitar-tooth (Scott & Jepsen, 1936) because its upper canines, while not as high-crowned as those of other nimravids such as *Hoplophoneus* or *Eusmilus*, were neither exceptionally flattened nor coarsely crenulated and its limbs, while relatively gracile, had remarkably short, probably semi-plantigrade feet very different from the long, digitigrade feet of Neogene felids such as *Homotherium*. Furthermore, a recent geometric morphometric analysis of a wide range of sabre-tooth taxa, felid and non-felid, has found no support for a differentiation between "dirk-tooh cats" and "scimitar-tooth cats" in terms of the morphology of the skull and mandible, so that it increasingly appears that this distinction has little relevance beyond the description of canine morphology and the coincidence with a tribal separation within the Machairodontinae (Prevosti *et al.*, 2010).

Conclusions

After decades of research on the evolution of sabre-tooth felids, several trends can be recognised in this field of investigation. In terms of dental function, the stabbing hypothesis has gradually lost ground in favour of the canine shear-bite model, refined by subsequent studies of the functional anatomy of fossil and extant felids. Suggestions about the need for radically non-felid facial musculature and external appearance in order to explain machairodontine feeding behaviour and gape are largely falsified by detailed anatomical studies of felines and other extant carnivores. Thus the main differences in life appearance between felid sabre-tooths and their extant relatives are a direct consequence of different skull proportions and muscle insertion areas, implying generally cat-like appearance but unmistakable proportions for the heads of crown-taxa within the Smilodontini and Homotheriini.

The origin of the sabre-tooth complex of adaptations has been difficult to interpret because the crown taxa of each sabre-tooth lineage have been traditionally more conspicuous and apparently better represented in the fossil record, a bias that has made the detailed similarities between unrelated species all the more striking. Such a degree of convergence led to the idea of a strong pleiotropic control over the entire "machairodont complex" of anatomical features. The finding of complete and abundant fossils of the basal machairodontine felids *Machairodus* and *Promegantereon* at the fossil site of Batallones-1 has provided for the first time an opportunity to study in detail the early stages in the evolution of this group, revealing a clear case of mosaic evolution, with some features such as the derived upper canine morphology evolving first within the context of a relatively generalised, feline-like cranio-mandibular complex.

In terms of their ecology and inferred behaviour, proposals concerning possible social behaviour and group hunting in sabre-tooths remain purely hypothetical at present. The presence of *Smilodon* bones with healed injuries is considered by some as evidence of some type of social structure in that species, but other specialists see it as compatible with solitary behaviour. Probably the best way to infer the presence of social behaviour in fossil carnivores is to learn more about the biological and ecological constraints of predation, something that requires more data from alarmingly shrinking wild populations of modern large carnivores. Current knowledge suggests that group living and hunting may become advantageous for all large predators that hunt large prey in relatively open environments, while it may be the only way to catch large prey for carnivores (like canids and hyaenids) that lack powerful, muscular forepaws for subduing prey. Such reasoning points towards homotherins, rather than smilodontins, as the more likely candidates for group living among machairodontine cats.

The mosaic nature of the evolution of sabre-tooth adaptations points towards evolutionary plasticity, which is against the concept of rigid "ecomorphs" that would comprise whole complexes of anatomical features of the cranial and postcranial skeleton. In fact, the discovery of *Xenosmilus*, a homotheriin with an extremely robust skeleton, confirms that the idea of two contrasting and clear-cut ecomorphs among sabre-tooths is too rigid to fit the diversity of this group.

We may hope that the machairodontine cats will continue to excite the interest of palaeontologists and the wider public, as befits a group that exemplifies better than most several core concepts of evolutionary biology, such as mosaic evolution, convergence and the opposition between adaptation and phylogenetic constraints. In this process of rethinking the evolution of sabre-toothed felids, the contribution of the Batallones fossil sites has been crucial, and will continue to provide valuable insights. We can do no better than finish with a quotation from Leonard Ginsburg (1961, p. 1):

"*Les carnivores . . . ne dépendent en principe que de l'abondance et de la facilité de capture des proies et se sont peu à peu adaptés, au cours des temps géologiques, à des régimes alimentaires variés, réalisés dans les circonstances très différentes*."

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References

Agustí, J.; Cabrera, L.; Garcés, M. & Llenas, M. (1999). Mammal turnover and Global climate change in the late Miocene terrestrial record of the Vallès-Penedès Basin (NE Spain). 390-397. In*: Hominoid evolution and climatic change in Europe, Vol. 1.* (Agustí, J., Rook, L. & Andrews, P., eds.). Cambridge University Press, Cambridge, 528 pp.

Akersten, W.A. (1985). Canine function in *Smilodon* (Mammalia, Felidae, Machairodontinae). *Los Angeles County Museum Contributions in Science,* 356: 1-22.

Alderton, D. (1998). *Wild Cats of the World*. London, Blandford.

Antón, M. & Galobart, A. (1999). Neck function and predatory behaviour in the scimitar toothed cat *Homotherium latidens* (Owen). *Journal of Vertebrate Paleontology,* 19: 771-784.doi:10.1080/02724634.1999.10011190

Antón, M. & Morales, J. (2000). Inferencias paleoecológicas de la asociación de carnívoros del yacimiento de Cerro Batallones. In: *Patrimonio Paleontológico de la Comunidad de Madrid* (Morales, J., Nieto, M., Amezua, L., Fraile, S., Gómez, E., Herráez, E., Peláez-Campomanes, P., Salesa, M.J., Sánchez, I.M. & Soria, D., eds). Servicio de Publicaciones de la Comunidad de Madrid, Madrid, 190-201.

Antón, M.; Galobart, A. & Turner, A. (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 Reviews,* 24: 1287-1301.doi:10.1016/j.quascirev.2004.09.008

Antón, M.; Garcia-Perea, R. & Turner, A. (1998). Reconstructed facial appearance of the sabretoothed felid *Smilodon. Zoological Journal of the Linnean Society,* 124: 369-386. doi:10.1111/j.1096-3642.1998.tb00582.x.

Antón, M.; Salesa, M.J.; Galobart, Á.; Pastor, J.F. & Turner, A. (2009). Soft tissue reconstruction of *Homotherium latidens* (Mammalia, Carnivora, Felidae). Implications for the possibility of representation in Palaeolithic art. *Geobios,* 42: 541-551. doi:10.1016/j.geobios.2009.02.003

Antón, M.; Salesa, M.J.; Morales, J. & Turner, A. (2004). First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus* (Felidae, Carnivora) from the Spanish Late Miocene site of Cerro Batallones-1. *Journal of Vertebrate Paleontology,* 24: 957-969. doi:10.1671/02724634(2004)024[0957:FKCSOT]2.0.CO;2

Anyonge, W. (1996). Locomotor behaviour in Plio-Pleistocene sabre-tooth cats: a biomechanical analysis. *Journal of Zoology,* 238: 395-413. doi:10.1111/j.1469-7998.1996.tb05402.x

Bailey, T.N. (1993). *The African Leopard: Ecology and Behaviour of a Solitary Felid*. Columbia University Press, New York.

Bakker, R.T. (1998). Brontosaur killers: late Jurassic allosaurids as sabre-tooth cat analogues. *Gaia*, 15: 145-158.

Beaumont, G. de (1975). Recherches sur les Félidés (Mammifères, Carnivores) du Pliocène inférieur des sables à *Dinotherium* des environs d'Eppelsheim (Rheinhessen). *Archives des Sciences Physiques et Naturelles, Genève*, 28: 369-405.

Biknevicius, A.R. & Van Valkenburgh, B. (1996). Design for killing: craniodental adaptations of predators. In: *Carnivore Behaviour, Ecology and Evolution, Vol. 2* (Gittleman, J.L., ed.). Cornell University Press, London, 393-428.

Bohlin, B. (1940). Food habit of the machairodonts, with special regard to *Smilodon*. *Bulletin of the Geological Institute of Upsala,* 28: 157-174.

Bohlin, B. (1947). The sabre-toothed tigers once more. *Bulletin of the Geological Institute of Upsala,* 32: 11-20.

Bothma, J & Walker, C. (1999). *Large Carnivores of the African Savannas*. Springer-Verlag, Berlin.

Bravard, A. (1828). *Monographie de la Montagne de Perrier, près d'Issoire (Puy-de-Dôme) et de deux espèces fossiles du genre* Felis *découvertes dans l'une de ses couches d'alluvions*. Clermont-Ferrand, 145 pp.

Bryant, H.N. (1991). Phylogenetic relationships and systematics of the Nimravidae (Carnivora). *Journal of Mammalogy*, 72: 56-78. doi:10.2307/1381980

Bryant, H.N. (1996). Force generation by the jaw adductor musculature at different gapes in the Pleistocene sabretoothed felid *Smilodon*. In: *Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals* (Stewart, K.M. & Seymour, K.L., eds.). Toronto: University of Toronto Press, Toronto, 283-299.

Carbone, C.; Maddox, T.; Funston, P.J.; Mills, M.G.L.; Grether, G.F. & Van Valkenburg, B. (2009). Parallels between playbacks and Pleistocene tar seeps suggest sociality in an extinct sabretooth cat, *Smilodon. Royal Society Biology Letters,* 5: 81-85.

Chang, H. (1957). On new material of some machairodonts of Pontian age from Shansi. *Vertebrata Palasiatica,* 1:193-200.

Cuvier, G. (1824). *Recherches sur les ossements fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces*, Vol 5. Edmund d'Ocagne, Paris, 547 pp.

Daniel, J.C. (1996). *The Leopard in India. A Natural History*. Natraj Publishers, Allahabad.

Dawson, M.R.; Stucky, R.K.; Krishtalka, L. & Black, C.C. (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.

Durant, S.M. (2000). Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*. *Animal Behaviour*, 60: 121-130. doi:10.1006/anbe.2000.1433

Fortelius, M.; Eronen, J.; Jernvall, J.; Liu, L.; Pushinka, D.; Rinne, J.; Tesakov, A.; Vislobokova, I.; Zhang, Z. & Zhou, L. (2002). Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research*, 4: 1005-1016.

Ginsburg. L. (1961). Plantigradie et digitigradie chez les carnivores fissipedes. *Mammalia,* 25 (1): 1-21. doi:10.1515/mamm.1961.25.1.1

Ginsburg, L.; Morales, J. & Soria, D. (1981). Nuevos datos sobres los carnivoros de Los Valles de Fuentidueña, Segovia. *Estudios Geologicos,* 37: 383-415.

Gittleman, J.J. & Van Valkenburgh, B. (1997). Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology*, 242: 97-117. doi:10.1111/j.1469-7998.1997.tb02932.x

Hanby, J.P. & Bygott, J.D. (1979). Population changes in lions and other predators. In: *Serengeti, Dynamics of an Ecosystem* (Sinclair, A.R.E. & Norton-Griffiths, M., eds.). University of Chicago Press, Chicago, 248-262.

Heald, F. (1989). Injuries and diseases in *Smilodon californicus*. *Journal of Vertebrate Paleontology,* 9: 24A.

Hunt, R.M. (1987). Evolution of the aeluroid Carnivora: significance of the auditory structure in the nimravid cat, *Dinictis*. *American Museum Novitates,* 2886: 1-74.

Guggisberg, C.A.W. (1975). *Wild Cats of the World*. David and Charles, London.

Kurtén, B. (1968). *Pleistocene Mammals of Europe*. Weidenfeld and Nicolson, London.

Kurtén, B. & Anderson, E. (1980). *Pleistocene Mammals of North America*. Columbia University Press, New York.

Larson, S.E. (1997). Taxonomic re-evaluation of the jaguar. *Zoo Biology,* 16: 107-120. doi:10.1002/(SICI)1098-2361(1997)16:2<107::AID-ZOO2>3.0.CO;2-E

MacCall, S.; Naples, V. & Martin L. (2003). Assessing Behavior in Extinct Animals: Was *Smilodon* Social? *Brain Behavior and Evolution,* 61: 159-164. doi:10.1159/000069752

Macdonald, D.W. (Ed.) (1984). *The Encyclopedia of Mammals*. New York: Facts on File Publications. 895 pp.

Marean, C.W. (1989). Sabertooth cats and their relevance for early hominid diet and evolution. *Journal of Human Evolution*, 18: 559-582. doi:10.1016/0047-2484(89)90018-3

Martin. L.D. (1989). Fossil history of the terrestrial Carnivora. In: *Carnivore Behaviour, Ecology and Evolution* (Gittleman, J.L., ed.). Chapman and Hall, London, 535-568. doi:10.1007/978-1-4613-0855-3_20

Martin. L.D.; Babiarz, J.P.; Naples, V.L. & Hearst, J. (2000). Three Ways to be a Sabertoothed Cat. *Naturwissenschaften,* 87: 41-44. doi:10.1007/s001140050007

McHenry, C.R.; Wroe, S.; Clausen, P.D.; Moreno, K. & Cunningham, E. (2007). Supermodeled sabercat, predatory behaviour in *Smilodon fatalis* revealed by high-resolution 3D computer simulation. *Proceedings of the National Academy of Sciences*, 104 (41): 16010-16015. doi:10.1073/pnas.0706086104

Merriam, J.C. & Stock, C. (1932). *The Felidae of Rancho La Brea*. Carnegie Institute of Washington Publications, 442: 1-231.

Miller, G.J. (1969). A new hypothesis to explain the method of food ingestion used by *Smilodon californicus* Bovard. *Tebiwa,* 12: 9-19.

Morales, J.; Salesa, M.J.; Pickford, M. & Soria, D. (2001). A new tribe, new genus and two new species of Barbourofelinae (Felidae, Carnivora, Mammalia) from the Early Miocene of East Africa and Spain. *Transactions of the Royal Society of Edinburgh: Earth Sciences,* 92: 97-102. doi:10.1017/S0263593300000067

Morlo, M.; Peigné, S. & Nagel, D. (2004). A new species of *Prosansanosmilus*: implications for the systematic relationships of the family Barbourofelidae new rank (Carnivora, Mammalia). *Zoological Journal of the Linnean Society,* 140: 43-61. doi:10.1111/j.1096-3642.2004.00087.x

Morse, D.H. (1974). Niche breadth as a function of social dominance. *American Naturalist*, 108: 808-813. doi:10.1086/282957

Nuñez, R.; Miller, B. & Lindzey, F. (2000). Food habits of jaguars and pumas in Jalisco, Mexico. *Journal of Zoology*, 282: 373-379.

Packer, C. (1986). The ecology of sociability in felids. In: *Ecological Aspects of social Evolution: Birds and Mammals* (Rubenstein D.I. & Wrangham R.V., eds.). Princeton university Press, Princeton, 429-451.

Packer, C.; Scheel, D. & Pusey, A. (1990). Why lions form groups: food is not enough. *American Naturalist,* 136: 1-19. doi:10.1086/285079

Rabinowitz, A.R. & Nottingham, B.G. (1986). Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology,* 210: 149-159. doi:10.1111/j.1469-7998.1986.tb03627.x

Riabinin, A. (1929). Faune de mammifères de Taraklia. Carnivore vera, Rodentia, Subungulata. *Travaux du Musée de Géologie de l'Académie des Sciences d'URSS*, 5: 75-134.

Riviere, H.L. & Wheeler, H.T. (2005). Cementum on *Smilodon* sabers. *The Anatomical Record*, 285A: 634-642. doi:10.1002/ar.a.20199

Salesa, M.J.; Antón, M.; Turner, A. & Morales, J. (2005). Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed 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. doi:10.1111/j.1096-3642.2005.00174.x

Salesa, M.J.; Antón, M.; Turner, A. & Morales, J. (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. doi:10.1111/j.1469-7998.2005.00032.x

Salesa, M.J.; Antón, M.; Turner, A.; Alcalá, L.; Montoya, P.; Morales, J. (2010a) Systematic revision of the Late Miocene sabre-toothed felid *Paramachaerodus* in Spain. *Palaeontology*, 53 (6): 1369-1391. doi:10.1111/j.1475-4983.2010.01013.x

Salesa, M. J.; Antón, M.; Turner, A. & Morales, J. (2010b). Functional anatomy of the forelimb in the primitive felid *Promegantereon ogygia* (Machairodontinae, Smilodontini) from the Late Miocene of Spain and the origins of the saber-toothed felid model. *Journal of Anatomy,* 216: 381-396. doi:10.1111/j.14697580.2009.01178.x

Sankhala, K. (1978). *Tiger!*. Collins, London.

Schaller, G.B. (1972). *The Serengeti Lion. A Study of Predator-Prey Relations*. University of Chicago Press, Chicago.

Schmidt-Kittler, N. (1976). Raubteiere aus dem Juntertiär Kleinasiens. *Palaeontographica,* 155: 1-131.

Scott, W.B, & Jepsen, G.L. (1936). The mammalian fauna of the White river Oligocene. Part I-Insectivora and Carnivora. *Transactions of the American Philosophical Society, new series*, 28: 1-153.

Seidensticker, J. (1976). On the ecological separation between tigers and leopards. *Biotropica*, 8: 225-234. doi:10.2307/2989714

Simpson, G.G. (1941). The function of sabre-like canines in carnivorous mammals. *American Museum Novitates,* 1130: 1-12.

Sotnikova, M. (1992). A new species of *Machairodus* from the late Miocene Kalmakpai locality in eastern Kazakhstan (USSR). *Annales Zoologici Fennici,* 28: 361-369.

Sunquist M.E. & Sunquist F.C. (1989). Ecological constrains on predation by large felids. In: *Carnivore Behavior, Ecology and Evolution* (Gittleman J. L., ed.). Chapman & Hall, London, 220-245. doi:10.1007/978-1-4613-0855-3_11

Turnbull-Kemp, P. (1967). *The Leopard.* Howard Timmins, Cape Town

Turner, A. (1984). Dental sex dimorphism in European lions (*Panthera leo* L) of the Upper Pleistocene: palaeoecological and palaeoethological implications. *Annales Zoologici Fennici,* 21: 1-8.

Turner, A. (1993). New fossil carnivore remains. In*: Swartkrans: a Cave's Chronicle of Early Man* (Brain, C.K., ed.). Transvaal Museum Monograph No. 8, Pretoria, 151-165.

Turner, A. & Antón, M. (1999). Climate and evolution: implications of some extinction patterns in African and European machairodontine cats of the Plio-Pleistocene. *Estudios Geologicos,* 54: 209-230.

Turner, A. & Antón, M. (2004). *Evolving Eden: An Illustrated Guide to the Evolution of the African Large Mammal Fauna.* Columbia University Press, New York.

Van Valkenburgh, B. & Sacco, T. (2002). Sexual dimorphism, social behavior, and intrasexual competition in large Pleistocene carnivorans. *Journal of Vertebrate Paleontology,* 22: 164-169. doi: 10.1671/02724634(2002)022[0164:SDSBAI]2.0.CO;2

Wroe, S., Lowry, M.B. & Antón, M. (2008). How to build a mammalian super-predator. *Zoology*, 111: 196-203. doi:10.1016/j.zool.2007.07.008

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