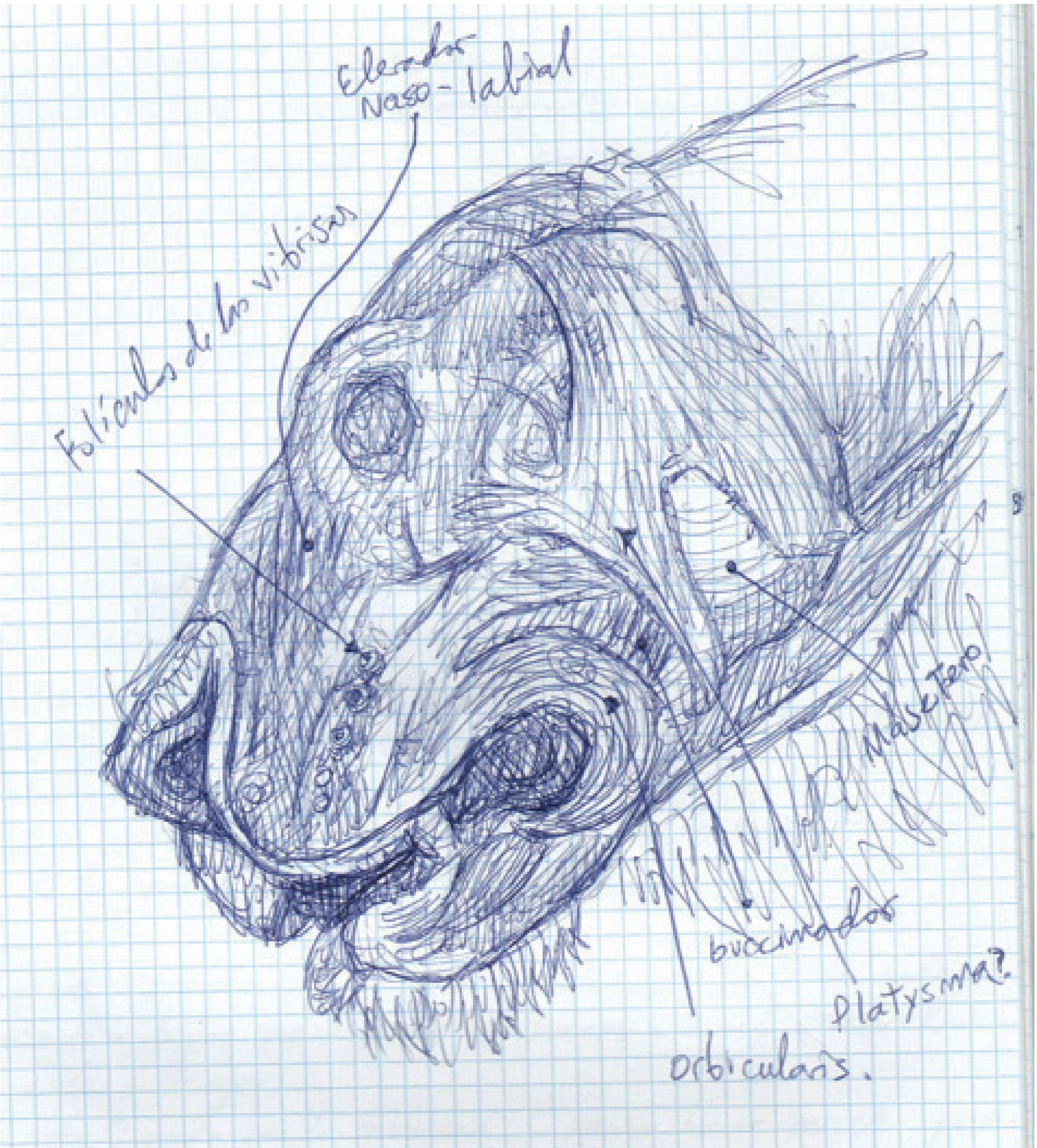
Skull and reconstructed head of Barbourofelis fricki. This animal was initially thought to be a member of the true-cat family Felidae, but is currently classified within a different family, the Barbourofelidae.
Schedel en gereconstrueerde kop van Barbourofelis fricki. Van dit dier werd aanvankelijk gedacht dat hij bij de Felidae hoorde, maar tegenwoordig wordt hij in de familie Barbourofelidae geplaatst.

WALKING WITH SABERTOOTHS: USING SCIENCE AND ART TO SHED LIGHT ON THE ULTIMATE PREDATORS

Sabertooths are one of the groups of extinct animals with the greatest capacity to impress and fascinate. They have spurred endless debate among specialists, and almost every aspect of their biology, from their life appearance to their predatory behavior, locomotion, and final extinction has been the subject of intense disagreement. I have been interested in them for as long as I can remember, and for the last couple of decades I have devoted my best efforts to learn more about them and to materialize my findings in the shape of images and text. The most recent palpable result of this quest is the book "Sabertooth", published in late October by Indiana University Press. With the volume finally in print, I have an opportunity to look back at the years of work that have led to it, and at the way the panorama of "sabertooth-lore" has changed in the meantime. Many of the old disputes have been resolved over the last years thanks to new findings, and many old theories have been proved wrong. But some debates remain very much alive, and new ones are arising as new discoveries enrich our knowledge about sabertooths (Turner *et al.* 2011).

Inevitably, artistic reconstructions reflect those changing views. But such illustrations need not be just products created to fulfill educational or decorative needs external to the research. In my work, researching and communicating results to the wider public are part of one and the same process. This implies to live between two worlds (art and science), and to make an effort to see the sabertooths at all times as the living animals they once were; not only while drawing or painting them, but also while analyzing a set of measurements or a set of CT-Scan slices of a fossil. As the title of this article suggests, it is not a matter of just studying our subjects as abstract entities, because then we risk losing the biological perspective. To say it with a figurative expression, one should aim to "walk with sabertooths". But it is more easily said than done.

I became aware of the existence of sabertooths like so many children of my generation: through the classic paleontological illustrations of masters like Rudolph Zallinger, Charles Knight or Zdenek Burian. Those images exerted an intense fascination, and the sabertooths in particular impressed me as almost mythological creatures, combining the familiarity of the modern big cats with the added power of their oversized fangs and powerful body build, and also something more: an aura of mystery derived from the fact that they inhabited a fabulous, long lost kingdom of amazing beasts and unlimited wilderness. Such is the power of paleoart: an image can stir not only an aesthetic experience, but a sense of curiosity and a need to learn. Many of today's paleontologists were actually motivated



A sketch of the superficial muscles of the head of a lion, made during the dissection at the University of Valladolid (Spain).
Een schets van de oppervlakkige spieren in het hoofd van een leeuw, gemaakt tijdens een ontleding aan de Universiteit van Valladolid (Spanje).

to study fossils by their early exposure to paleoart.

Being fascinated by prehistoric life is one thing, but finding answers to the many questions arising from such early interest may prove to be a very long process. In the early 1970s my family moved from Spain to Venezuela and I had my first opportunity to see a real fossil of a sabertooth, and a truly overwhelming one at that. The Natural Science Museum of Caracas is a modest building with a modest paleontological exhibit, but it happens to include a complete skeleton of the sabertooth *Smilodon fatalis*, brought directly from the world-famous American site of Rancho la Brea (California). I drew and photographed that skeletal mount many times, and made my first, crude attempts to reconstruct the outline of the living animal around it. The results were far from satisfactory, not only because my knowledge of anatomy was still very elementary, but also because of problems with the mount itself which I could not possibly suspect at the time. The pose of the skeleton was rather unnatural, and the head combined a skull, a mandible, and a set of upper canines belonging to two, if not three, differently sized individuals… just too much for an aspiring paleoartist to tackle. One should never underestimate the importance of accuracy in Museum skeletal mounts!

At about that time I set out to learn as much as I could about the sabertooths, and the memory of the difficulties I found back then to access any relevant information is one of the motivations that have led me to publish not only academic works, but also semi popular books that can make information available to non-academic readers. From the standpoint of the Internet era, it can be difficult to imagine how frustratingly hard it was for a schoolboy in the 1970s to search for anything beyond the same few, oft-repeated clichés about sabertooths. The problem today is different for the curious layperson: on one hand, access to truly specialized knowledge is still largely restricted to academic libraries or paid online publications; on the other hand, an overabundance of "popularized" information makes it difficult to sort out the good sources from the less than reliable ones. So, the role of well-founded popular science, crafted by those who

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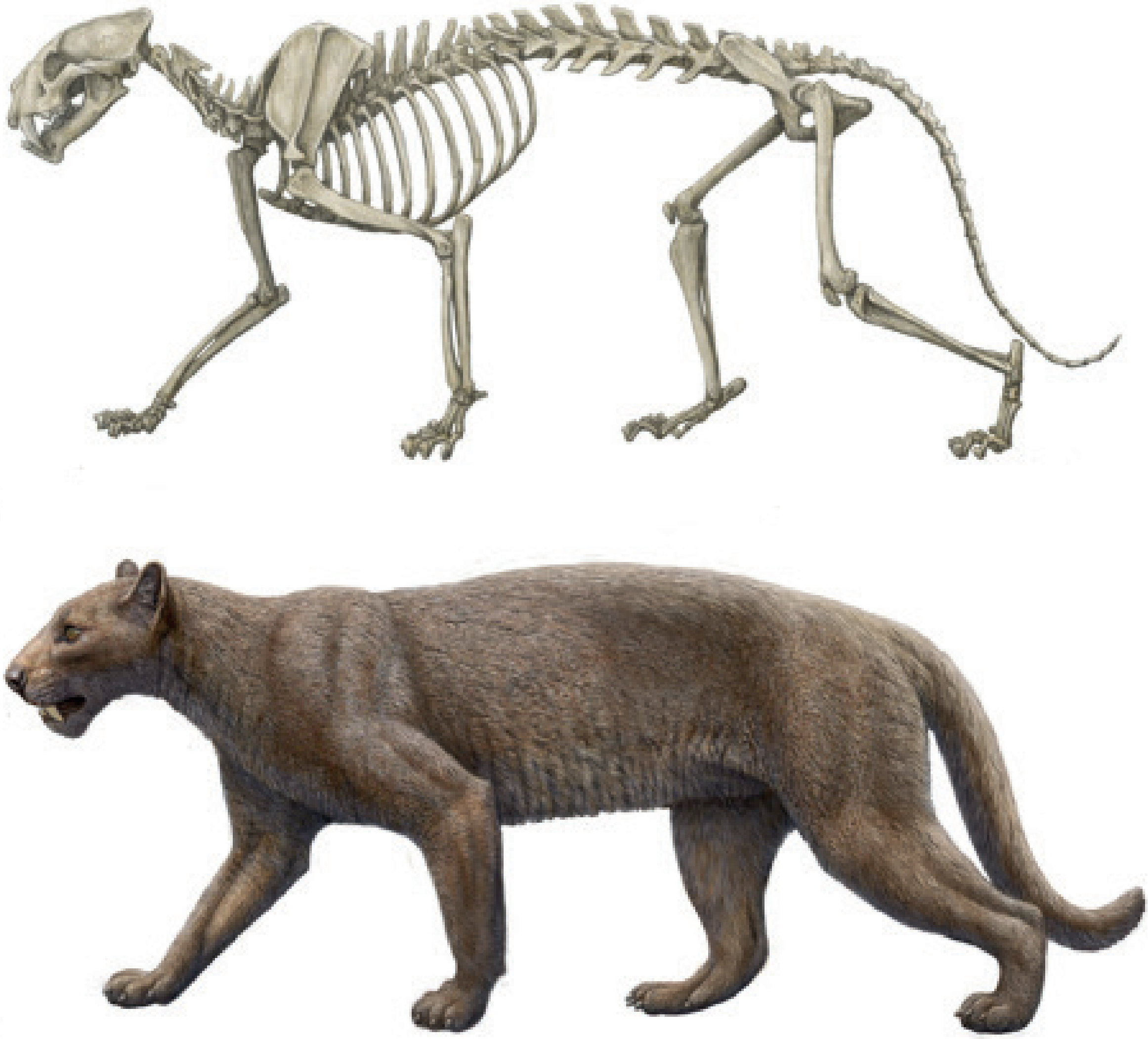


Reconstructed skeleton (top) and life appearance (bottom) of the nimravid Dinictis felina showing a hypothetical coat pattern inspired in a non-felid carnivore, concretely in the fossa (Cryptocprocta ferox).
Gereconstrueerd skelet (boven) en hoe het dier er bij leven uitzag (beneden) van de nimravide Dinictis felina, waarbij het patroon op de vacht geinspireerd is op een niet-katachtig roofdier, de fossa Cryptocprocta ferox.

can offer an inside view of their fields, is today as vital as ever.

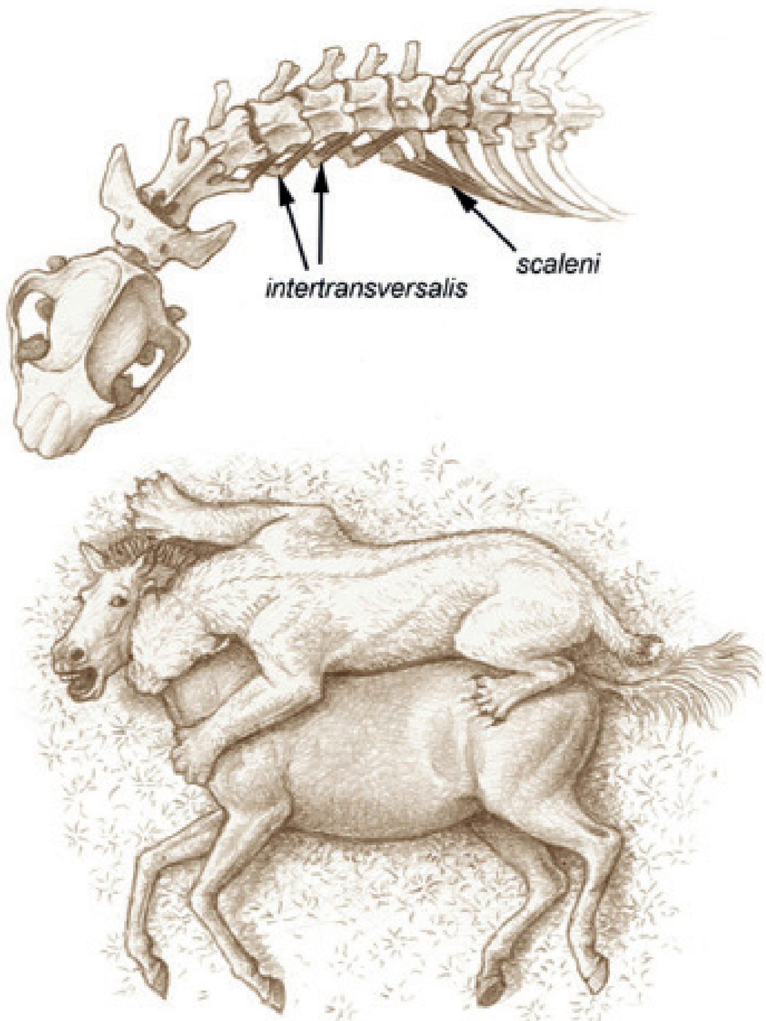
I chose an artistic training, but with the years, and especially after my return to Spain, I came into closer contact with the world of paleontology, and I started to combine the input from my scientist collaborators with my own artistic background in order to develop a consistent reconstruction methodology. But as I finally started to formulate the right questions about the appearance and action of the sabertooths, I found that in many cases the answers were simply not available, even from the specialized literature, and new ground had to be broken. So I got ever more involved in research and I had the luck to work with some of the most insightful specialists in the field. My single most important collaboration has been with the late British paleontologist Alan Turner, whom I met in 1991 and with whom I not only collaborated in the making of several books and academic papers, but also shared two decades of great friendship.

One important aspect of my research has been the possibility of making dissections of extant animals, so necessary whenever the specific aspects of anatomy relevant for your reconstruction have never been described in detail. Fortunately I have collaborated with anatomist Juan Francisco Pastor who over the years has organized many dissections which have resulted in vital insights for the task of reconstruction.

But when and to what degree can you apply to extinct animals your findings about the soft anatomy of modern ones? The answer must take into account the phylogenetic relationships between the animals we want to reconstruct and the modern species in which we can still observe the attributes that are lost in the fossils. This is something that "paleoartists" have been doing in a more or less intuitive way since the times of Charles Knight (Milner, 2012), but in this regard the work of paleontologists like Larry Witmer or Harold Bryant has provided a welcome theoretical framework, giving us a solid, phylogenetically-grounded program to follow (Bryant & Russell, 1992; Witmer, 1995). Witmer's protocol, called the Extant Phylogenetic Brackett, is now extensively used whenever specialists need to make decisions about unpreserved attributes, be it for the creation of reconstructions or for any other aspect of paleontological research.

So, in order to reconstruct the sabertooths we need a phylogenetic framework, and a good phylogeny should closely reflect the evolution of the group. But sabertooth evolution is at times a tricky subject. If sabertooths are remarkable for one thing, it is for their many instances of convergent evolution, or "repeat performances" as defined by American paleontologist Christine Janis (Janis, 1994). In "Sabertooth" I set out to deal with all the major groups of sabertooths, not only the familiar sabertoothed felids which Alan Turner and me had treated in our book "The Big Cats" (Turner & Antón, 1997). And that has made for a

An illustration showing the "stabbing" hypothesis, which saw the attack of sabertooth cats as similar to the action of a human hand stabbing with a knife.
Een afbeelding die de "steek" hypothese illustreerd, waarbij de aanval van een sabeltandkat wordt vergeleken met het steken met een mes door een menselijke hand.



A reconstruction of Homotherium biting the neck of a horse as seen from above. The skull, cervical vertebrae and selected neck muscles of the felid are drawn to show the role of neck lateral flexion in positioning the head for the killing bite (Modified from Antón & Galobart 1999).
Een reconstructie van Homotherium die de nek van een paard bijt, van bovenaf gezien. De schedel, nekwervels en nekspieren van de kat laten de rol van het buigen van de nek zien, zodat de kop in de juiste positie gebracht kan worden om de dodelijke bijt toe te brengen (veranderd naar Antón & Galobart 1999).

lengthy book, in part because the trend in the study of sabertooth classification over the last years has been to reveal ever more diversity. This is not only due to the discovery of new species, but also to the fact that groups formerly thought to be closely related are now found to be more distant and to have evolved their adaptations independently. For example, in the early classic paleontology textbooks that I read back in the 1970s, the family Felidae was said to be divided in 2 subfamilies, Felinae (the "normal" or conical toothed cats) and Machairodontinae, the sabertooths. The current classification of the Felidae still reflects such a dichotomy, but many of the species that back then were classified within the Machairodontinae are now known to belong in totally different families, such as the Nimravidae and the Barbourofelidae (Turner *et al.* 2011). Those animals were no cats, but the degree of convergence with sabertooth felids deceived the best paleontological minds of the early 20th century into thinking all of them were members of the cat family. Such splitting of the sabertooth classification has all sorts of implications, some of them rather unexpected. For instance, and following the phylogenetic criteria of reconstruction, if a sabertooth is thought to belong in the family Felidae, then we can reconstruct its coat colour pattern in accordance with those found among extant felids. But if a species is reclassified and found to be much more distantly related to cats, then we need to open the "bracket" to consider also patterns typical of other carnivores.

The diversity of unrelated groups that have tried the "sabertooth model" points to the great adaptive value of such morphology: after all, if something evolved successfully so many times it must be because it worked! But, how did it work? Dissecting the big cats, comparing muscle insertion areas in the bones of extant felids and sabertooths and interpreting our findings in terms of the Extant Phylogenetic Brackett is a line of research that we originally launched with the idea of giving a more solid ground for life reconstructions. But inevitably it led us into the field of functional interpretation. The transition from reconstructing appearance to reconstructing action is just natural in paleoart, but it took us into an ever more complex area of research.

One aspect of sabertooth action where our dissections provided essential insights is the role of the neck musculature in the killing bite. Back when I started to read about this topic, the leading hypothesis was the stabbing model, according to which the sabertooths attacked with jaws wide open in order to sink the canines into the flesh of prey. This violent action was compared to the action of a human arm wielding a knife, and in this

Life reconstruction of Promegantereon ogygia, climbing.
Reconstructie van een klimmende Promegantereon ogygia.

scenario the mandible was given no role; it simply needed to be kept out of the way. This idea was controversial, as several specialists thought that the thin, laterally compressed sabers were just too fragile to withstand such violent use. Many of the problems of this model where elegantly solved with a new hypothesis, the "Canine Shear Bite", put forward by William Akersten (Akersten, 1985). According to this theory, the killing bite of sabertooths was a variation of the killing bite of "normal" cats, but one where the disadvantage that large gapes created for jaw closing muscles was compensated by the recruitment of anterior neck muscles, which generated a downward motion of the whole head and thus helped initial penetration of the canines, with the mandible acting as an anchor during that part of the process. As the sinking of the canines allowed reduction of the initial gape, the jaw-closing musculature had a more advantageous situation for effective contraction.

Brilliant though it was, the Canine Shear Bite model left some ambiguity regarding the homology of the muscles involved in the depression of the skull, because the only detailed descriptions of the relevant muscles available to Akersten were those of a giant panda, not of a big cat. But perhaps more

Lokotunjailurus emageritus in a riverine woodland in the late Miocene of Lothagam (Kenya). In the background is the early elephantid Stegotetrabelodon.
Lokotunjailurus emageritus in een door rivieren doorkruist boslandschap in het Laat Mioceen van Lothagam (Kenia). Op de achtergrond is de slurfdrager Stegotetrabelodon te zien.

importantly, the role of the posterior neck musculature was left out of the explanation, and the morphology of muscle insertions in the posterior cervicals was precisely one of the arguments used by earlier specialists to defend the stabbing hypothesis. Our dissections of big cats allowed us to shed some light on this matter, by making clear the homology of the atlanto-cranial muscles involved in skull depression (Antón *et al.* 2004a). But it was the study of an exceptional sample of *Homotherium* fossils from a Spanish Plesitocene fossil site that helped us understand the role of posterior neck muscles in the sabertooth killing bite. I was invited by paleontologist Angel Galobart to study the sabertooth fossils from Incarcal, and we found that the extraordinary preservation of neck vertebrae in that sample revealed something new about the arrangement of the cervical muscles. The muscle insertion processes in the posterior cervical vertebrae of *Homotherium* from Incarcal showed that these animals had both great strength and precise control of rotation of the neck in all directions, not predominantly downwards as the stabbing theory would require. Such action fits excellently with the Canine Shear Bite model, where the neck must provide a strong and stable base for the motions of the head during the killing bite (Antón & Galobart, 1999).

Such investigations reveal the sabertooths, and in particular the Pleistocene genera such as *Smilodon* and *Homotherium*, as quite sophisticated specialists, predators that had reached the apex of their adaptations and which dominated terrestrial ecosystems in Africa, Eurasia and the Americas. But this is only the final chapter in the sabertooth story: in order to know the key to their success it is essential to look at the development of their adaptations through time. All those spectacular, derived sabertoothed species have evolved from more "generalist" ancestors, and finding out exactly how the various changes proceeded through time can give us the key to why those changes were selected -what advantages they gave to the early sabertooths over their non-sabertoothed relatives. One problem here is that we have a better fossil record of the more specialized, "terminal" taxa in each lineage than of the earlier forms. So, when we look at extreme sabertooth felids like *Smilodon* and *Homotherium* we can only speculate about what were the key aspects of their morphology that led to their evolution from an ancestor that was much more similar to a modern feline, an ancestor whose morphology has been retained with little change, and to great success, by extant cats.

What paleontologists need in order to properly "read" the process of sabertooth evolution is a detailed snapshot of early, transitional forms where the sabertooth adaptations were still in a more incipient form. And that snapshot appeared, almost miraculously with the discovery in 1991 of the Batallones fossil site complex near Madrid (Antón & Morales 2000). That such a discovery took place so near from my home at the time when I was beginning my serious approach to sabertooth reconstruction is what I call a remarkable coincidence.

Cerro Batallones is a hill where 9 fossil sites have been found this far, each site corresponding to what was a cavity during the late Miocene. For some time prior to being filled with sediments, the cavities acted as carnivore traps, and as a result two of the sites (Batallones-1 and Batallones-3) have yielded an incredibly high proportion of carnivore fossils –well over 90 percent. This is on a par with Rancho la Brea (another carnivore trap), but unlike the American site, Batallones yields fossils of some of the earliest species of felid sabertooths. In fact, the sabertooth genera from Batallones, *Machairodus* and *Promegantereon*, are reasonably close to the ancestry of the Pleistocene genera *Smilodon* and *Homotherium*. Here is the missing snapshot of the early evolution of the felid sabertooth lineage.

Thanks to the Batallones sample, *Machairodus* and *Promegantereon*, previously recorded from a collection of fragmentary fossils, became two of the best known felid sabertooths in the fossil record (Antón *et al.* 2004b). Each bone in their skeletons is known from several specimens, allowing us to characterize their anatomy and adaptations in great detail. Working with paleontologists Manuel Salesa (who did his PhD thesis on the anatomy of *Promegantereon*) and Jorge Morales, from the Museo Nacional de Ciencias Naturales in Madrid, I was able to reconstruct the life appearance of these Miocene machairodontines, whose body proportions are now known to resemble those of modern cats more closely than in the case of Pleistocene sabertooths (Salesa *et al*. 2005, 2006, 2010). Like the similarly-sized modern leopard, *Promegantereon* would have been quite at home in the trees, while among *Machairodus* only the smaller females would occasionally take a catnap in the more accessible branches, something more difficult for the enormous males. But our study of the Batallones sabertooths also provides insights into the early evolution of the group. One important discovery was that the skull of *Machairodus* had a striking mosaic of characters with a few advanced sabertooth features (especially the upper canines which were already quite enlarged, laterally flattened and with strongly serrated margins) together with many rather primitive ones (especially the mastoid area of the skull, which in many ways resembled that of felines more than that of advanced sabertooth cats). At least in this lineage, the development of saber-like teeth took place ahead of the other adaptations we associate with sabertooths, and it seems that it was enough to provide the animal with an advantage over other predators (Antón *et al.* 2004b). And that advantage most likely was the ability to kill large prey extremely fast through rapid blood loss. Only through subsequent evolution would the lineage of *Machairodus* develop a set of anatomical features which can be seen as "refinements" that made the use of its deadly weapons (the sabers) ever more efficient.

Many other sabertooth discoveries have taken place in recent years. A superb complete skeleton from the late Miocene of Lothagam in Kenya turned out to be a new genus and species, named *Lokotunjailurus emageritus* by paleontologist Lars Werdelin who described the animal. I had the privilege to study the skeleton first-hand in order to produce the first reconstruction of this animal, published with the original description (Werdelin, 2003). Closely related to the Batallones *Machairodus*, this animal was more recent and specialized, with a remarkably light build and long legs. The complete articulated forepaw of *Lokotunjailurus* revealed that it shared with *Machairodus* the possession of a spectacular, disproportionately large dewclaw, which in fact now seems to be a feature shared by most sabertooth felids.

Yet another surprising discovery was a complete skeleton of a sabertooth from the fossil site of Haile 21A in Florida, which upon study by Larry Martin and colleagues not only revealed to be a new genus and species, but also to have an unexpected combination of characters (Martin *et al.* 2000). Named *Xenosmilus hodsonae*, the new animal was a close relative of *Homotherium* or *Lokotunjailurus*, with relatively short and very flattened sabers that had coarsely serrated margins. But unlike all its close relatives, *Xenosmilus* did not have long and gracile legs, but it rather had the stocky, muscular build typical of the other "branch" of the machairodontines, the one including *Smilodon* and *Megantereon*. This was a surprising proof of the ability of sabertooth cats to adapt over time to changing conditions through remarkable changes in body proportions. But the unusual skeleton of *Xenosmilus* posed an additional challenge for the reconstructor, because its feet were so short and broad that the authors of the description proposed that the animal would be plantigrade like a bear, rather than digitigrade like a cat. Many fossil carnivores have foot bones that leave little doubt about their usual posture (plantigrade or digitigrade), but in the case of *Xenosmilus* there is conflicting evidence, so in the reconstruction I made for the book "Sabertooth" I simply could not reach a clear conclusion about the posture of its hind feet, and I decided to show the animal just sitting!

I have no doubt that future studies will determine clearly the posture of *Xenosmilus*, but for the time being, my inability to make a decision about

Life appearance of Xenosmilus hodsonae.
Reconstructie van Xenosmilus hodsonae.

that particular aspect of its locomotion served as a lesson in humility, and also to remind me of the basic characteristic of any reconstruction of a sabertooth, or of any extinct animal for that matter: they are provisional. But provisional doesn´t mean ungrounded. In fact, as the methodology for the creation of life reconstructions advances, it can help solve enigmas from other disciplines such as archeology. That was the case of a Paleolithic figurine from the Isturitz cave in the French Pyrenees, which for decades had been considered by some specialists to be a representation of the sabertooth *Homotherium*. A careful application of anatomical analysis and the Extant Phylogenetic Brackett allowed us to produce a rigorous reconstruction of *Homotherium* and to compare key aspects of its appearance with the Isturitz sculpture, allowing us to conclude with reasonable certainty that the Paleolithic sculptor was not representing a sabertooth, but more likely a cave lion, possibly a young one (Antón *et al.* 2009).

This article has only glimpsed at some aspects of the world of sabertooths, but the fact is even the book format quickly becomes too limited. When I started work in the volume I was convinced I would be able to force between two covers all the more interesting aspects of the subject and all the artistic concepts that those aspects called for. But by the time the book began to take some serious shape I realized I would have to leave much of the interesting stuff out, including many discussions and many sketches that will just have to wait for the next book. And of course there will be new discoveries to incorporate, in fact some have already happened since I submitted the final manuscript, and it has been difficult to restrain myself from trying to incorporate more last-minute additions. It seems we have a long road ahead to keep walking with sabertooths.

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SABERTOOTH

Sabeltandkatten behoren tot de meest populaire prehistorische dieren. Toch is het verrassend hoe weinig informatie er over hen te vinden is voor het grote publiek. En dan waren er ook nog sabeltanden die geen katten waren, met exotische namen als Nimraviden, Barbourofeliden en Thylacosmiliden. Sommige hadden de grootte van een huiskat, andere waren groter dan een leeuw en sommige waren net zo raar als hun naam doet vermoeden. Sabeltanden leveren allerlei vragen op, zelfs voor de specialisten. Hoe zagen ze eruit? Hoe gebruikten ze hun spectaculaire tanden? Waarom stierven ze uit? In dit zowel visueel als tekstueel prachtige boek vertelt Mauricio Antón hun verhaal in woord en beeld, compleet gebaseerd op het laatste wetenschappelijke onderzoek. Het boek is een fantastisch samenspel van wetenschap en kunst en laat een opzienbarende diversiteit zien van het leven in het toch niet zo verre verleden.

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