MAURICIO ANTÓN

BEHAVIOUR OF *HOMOTHERIUM* IN THE LIGHT OF MODERN AFRICAN BIG CATS

How can we get a picture of the sabretooth cat *Homotherium* as a living animal? We use a methodology of paleobiological reconstruction that combines the study of fossil remains with that of their modern counterparts in order to propose hypotheses about the unpreserved anatomy and behaviour of the extinct species. In this contribution I explain how the study of the functional anatomy of the fossil species is complemented by comparative anatomy, the dissection of extant carnivores, and the direct observation of living big cats in the African savannah in order to achieve a balanced view of the hypothetical appearance, action and ecology of *Homotherium*.

ANATOMICAL RECONSTRUCTION

The first step of the process of paleobiological reconstruction is the restoration of the physical appearance of *Homotherium*. Any image that shows extinct animals in action must be the result of a careful process, based on a solid methodology. The method that we use today was originally devised by Georges Cuvier and decades later it was independently recreated by Charles Knight. More recent developments have refined the phylogenetic aspects of reconstruction (Antón / Sánchez 2004; Bryant / Russell 1992; Witmer 1995). At its core, the method consists in a step-by-step restoration of tissue from the inside out, as in a reverse dissection. First we restore the missing parts of the skeleton and articulate it in a life-like pose. Then we add succesive layers of soft tissue, starting with deep muscles and using marks in the attachment areas of the bones as a guide, and ending with speculation about fur patterns (**fig. 1**).

This procedure is only possible thanks to the existence of relatively complete fossil samples. As early as 1914, Freudenberg described parts of the skeleton of *Homotherium* on the basis of the sample from Hundsheim Cave (Bez. Bruck an der Leitha / A) in Austria, and in 1925 Schaub referred to that sample in order to remark the contrasting skeletal morphologies of *Megantereon* and *Homotherium,* the two best-known sabretooth genera from Plio-Pleistocene Europe (Freudenberg 1914; Schaub 1925). But only with the description of the nearly complete skeleton from Senèze (dép. Haute-Loire / F) did a more complete picture of *Homotherium* emerge. In 1963 Ballesio described that skeleton and showed that *Homotherium* differed greatly from the better known, classic sabretooth *Smilodon*. The latter was a short-legged, robust and heavy animal, while *Homotherium* was revealed as comparatively light and long-legged (Ballesio 1963).

Our own research efforts have brought together the information from Senéze and Hundsheim with the rich sample from the Spanish site of Incarcal (prov. Girona / E) to create an updated reconstruction of *Homotherium*. The animal's neck was long, strong and flexible, while the back was short and the tail was not much more than a stump (Antón / Galobart 1999; Antón et al. 2005). We showed that *Homotherium* had narrow forelimbs intermediate between those of lions and cheetahs, with relatively small, semi-retractable claws and a huge dewclaw (**fig. 2**).

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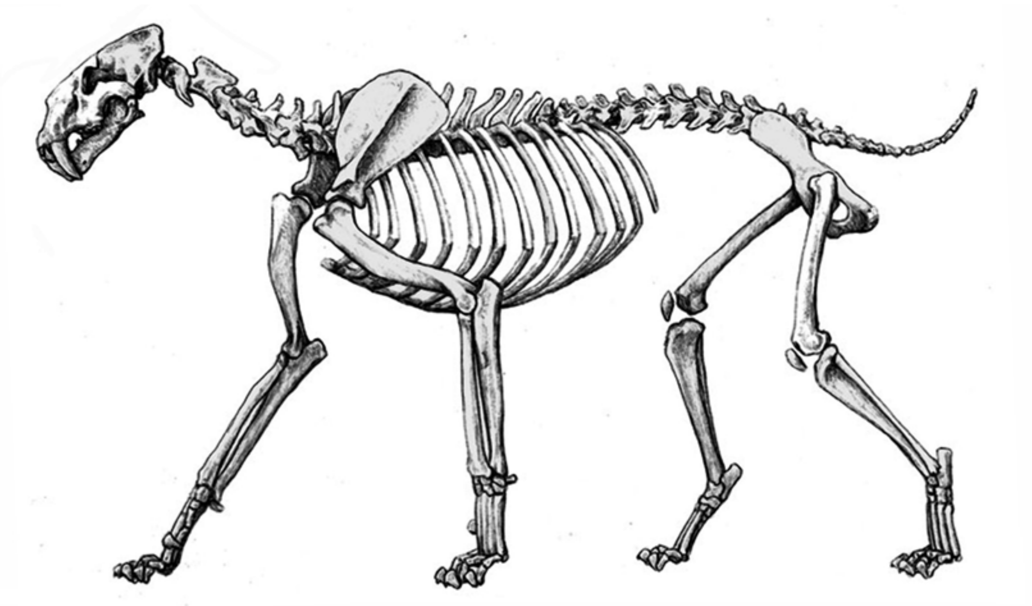

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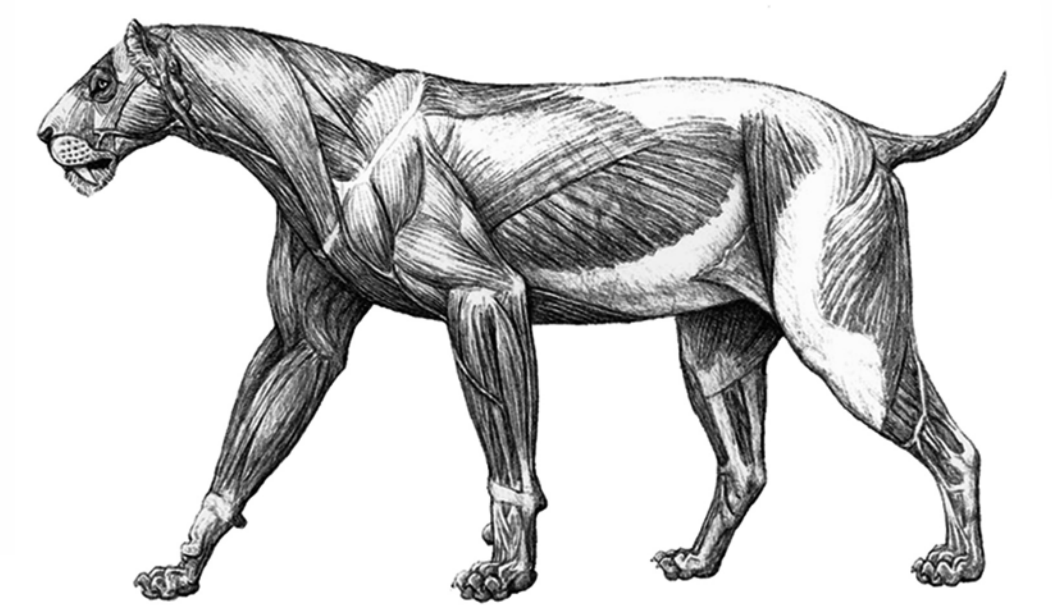

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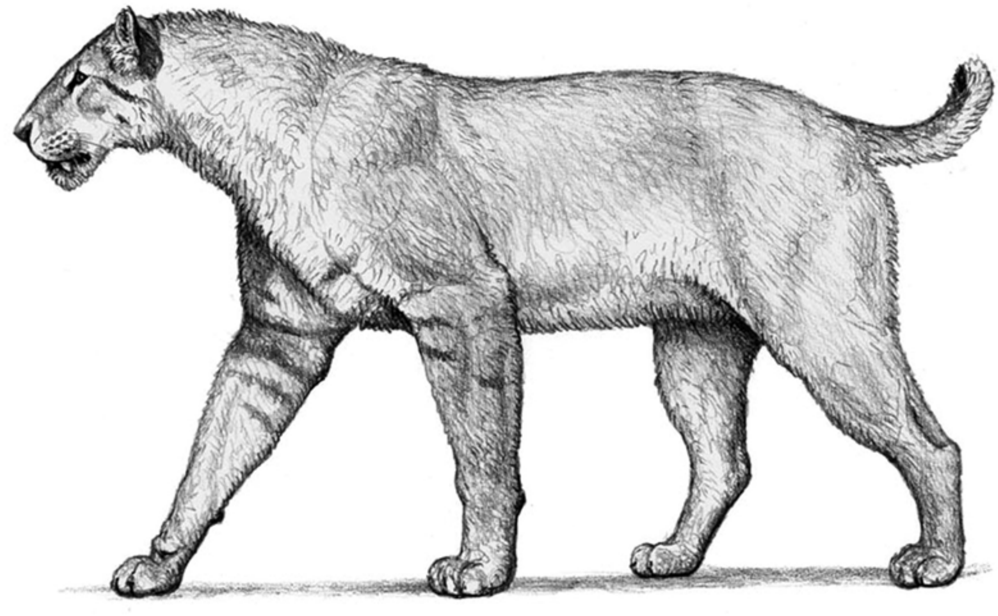

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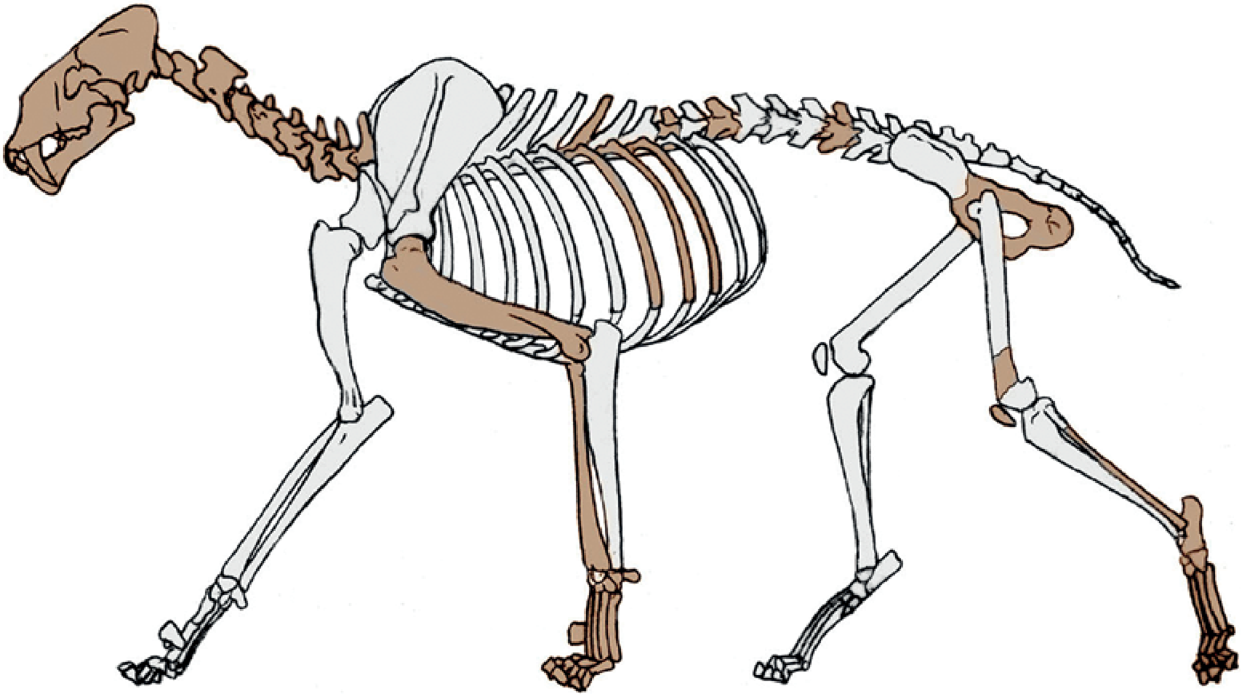


Fig. 2 Skeleton of *Homotherium* with the sections preserved at the fossil site of Incarcal shown in a darker colour. – (Artwork M. Antón).

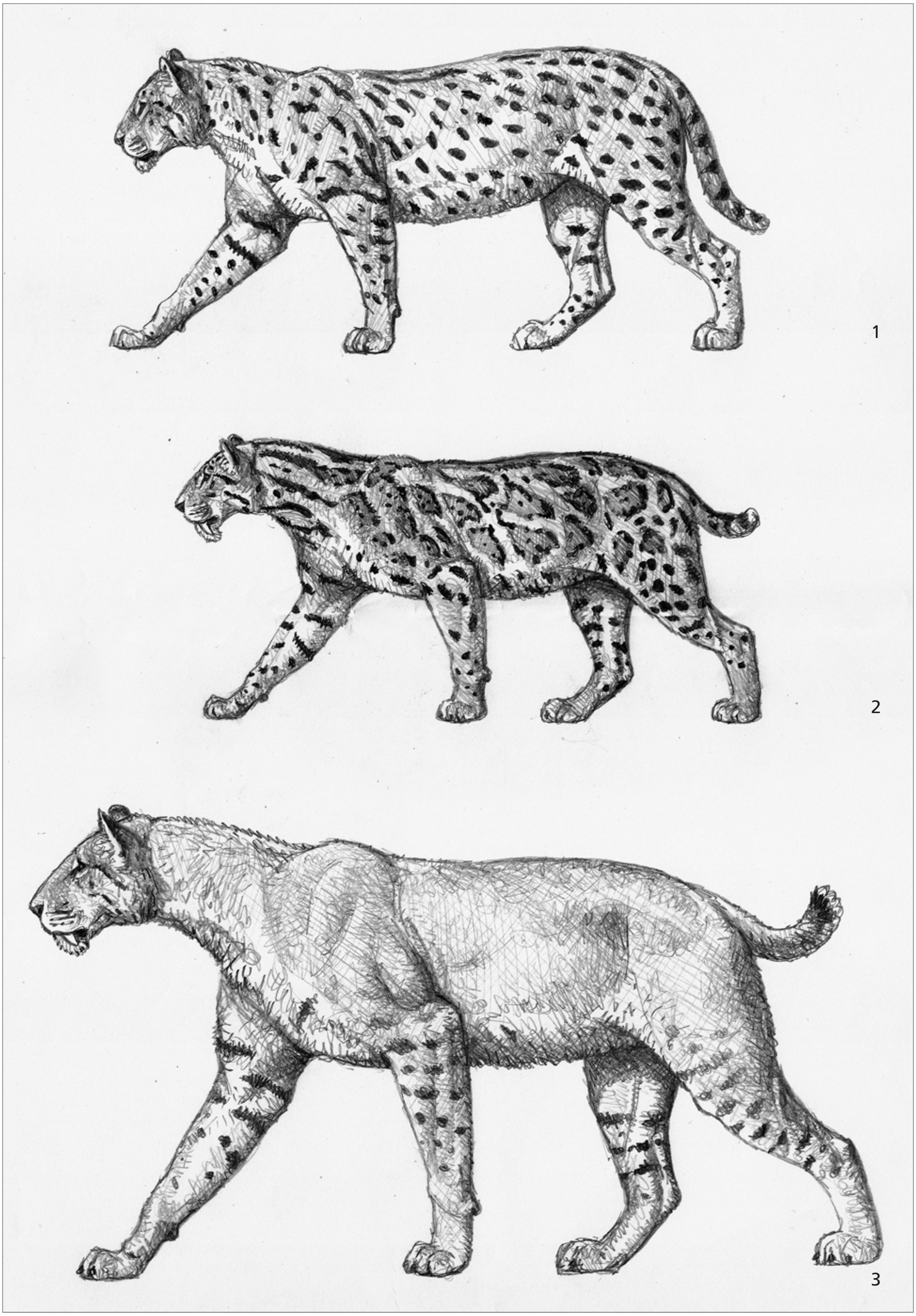
Combining these data with those about the other sabretooth cats from the Pliocene and Pleistocene of the Old World we could make an overall comparison of sizes and proportions (**fig. 3**). The differences in body size and proportions between species in turn imply a partitioning of available resources. But in order to know how this partition would take place, it is essential to interpret the morphology of sabretooths in functional terms, and to look again at the morphology and ecology of modern big cats for reference (Turner/Antón 1999).

BIOMECHANICAL IMPLICATIONS

The image that emerges from our physical reconstruction of *Homotherium* shows a mosaic of similarities and differences with other sabretooths but also with modern big cats. What are the implications of that mosaic in terms of the locomotor and predatory behaviour of *Homotherium*? In order to know that, we needed to interpret the anatomy of *Homotherium* in the light of the relationships between morphology and locomotion in modern cats. To explore those relationships we conducted dissections and we also analysed video footage to study the gaits of living cats.

The detailed comparison of individual bones between *Homotherium* and lions shows differences that influence locomotion (Antón et al. 2005). The short, less asymmetrical second phalanges and the small claws point to more »dog-like« feet. Less retractable claws provide better traction, but they get worn and thus

Fig. 1 Three steps of the reconstruction of *Homotherium latidens*: **1** reconstruction of the skeleton in a life-like pose. – **2** reconstruction of the musculature. – **3** reconstructed life appearance, with inferred fur pattern. – (Artwork M. Antón).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are less efficient for grasping prey. The narrow distal humerus with a more vertical olecranon fossa implies a more parasaggital trajectory of the forearm and wrist during the walk, again resembling the efficient walk of dogs more than that of cats with its marked supination of the forepaw as the limb moves forward. Analysis and comparison of my footage of free-ranging lions and hyaenas in Africa provides clear evidence of the walking styles associated with different forelimb morphologies (**fig. 4**: frames from videos of carnivores walking in front view). It is likely that the walk of *Homotherium* would be intermediate between those extremes. One interesting observation is the fact that the locomotion pattern of primitive sabretooths, such as *Machairodus* from the late Miocene, would be similar to that of extant cats, while the pattern of *Homotherium* is more derived and subtly different (Antón 2013).

Concerning gait, some old artistic reconstructions showed *Homotherium* as a plantigrade animal, on the basis of some features of the hind limb that could fit with a plantigrade stance (**fig. 5**). But Ballesio's study clearly proved the contrary, and our own observations add further evidence to confirm a fully digitigrade hind limb. In fact, apparent »plantigrade« adaptations in *Homotherium* would not be related to its walking gait, but to its posture while bringing down and immobilising struggling prey (Antón et al. 2005). Body proportions and morphology indicate that the animal could run at moderate speeds more efficiently than smilodontines, and even lions, and for greater distances (**fig. 6**).

Our dissections of modern cats further clarified aspects of the sabretooth's killing bite. We identified the muscles attaching to precise areas of the skull and cervical vertebrae in modern cats, allowing a more accurate inference of the musculo-skeletal system in sabretooth felids (Antón et al. 2004). The upper canines of sabretooths, and especially those of *Homotherium*, were longer and more flattened, and thus more fragile than those of modern cats. This requires a greater gape, if only to achieve a similar clearance between canine tips (and thus for biting at prey of similar size), and also a greater contribution of neck muscles to the bite, since they can bring the whole head down providing extra strength for the penetration of the canines into the flesh of prey (**fig. 7**). But it also becomes necessary to avoid hitting bone during the bite in order to prevent canine breakage, a requisite that would lead the sabretooths to avoid killing smaller prey, as hitting bone is more likely with smaller animals. Also, sabretooths need to control the struggles of the prey in order to avoid sudden motions that could break the canines. In some sabretooth species this is achieved by developing very robust and powerful bodies with enormously strong grasping forepaws. But that was not the case with *Homotherium*, where a somewhat different solution was apparently achieved.

PREY SIZE

It seems clear that *Homotherium*'s locomotion shared some aspects of cats and hyaenas, and that its craniodental adaptations point to the quick killing of large prey. But the resulting picture is somewhat contradictory because precisely the adaptations for sustained running that it shares with hyaenas pose limitations for bringing down the large prey that its craniodental anatomy was adapted to kill. Observations of modern carnivores give further indications about *Homotherium*'s habits and help to clarify those apparent contradictions.

Fig. 3 Comparison of body proportions and size in three species of machairodontine felids from the Pliocene and Pleistocene of Europe: **1** *Dinofelis diastemata*. – **2** *Megantereon cultridens*. – **3** *Homotherium latidens*. – All drawn to the same scale. Shoulder height of *Homotherium* about 1.1 m. – (Artwork M. Antón).

Fig. 4 Frames from videos of walking lions and spotted hyaenas in front view, showing differences in locomotion related to forelimb osteology: **1** lioness with left forelimb advanced and wrist flexed; notice that the forepaw is facing inwards and supinating. – **2** hyaena in the same stage of the walk; notice that the forearm and paw are aligned in the same vertical axis, with no appreciable supination of the paw. – **3** lioness with left forepaw just contacting the ground; notice that the forepaw is supinated so that the palm faces inward and the fifth digit touches the ground first. – **4** hyaena in the same stage of the walk; notice that the paw is not supinated so that the four digits contact the ground simultaneously. The intermediate forelimb morphology of *Homotherium* suggests that its locomotion would be somewhere in between the extremes shown in this figure. – (Filmed by M. Antón).

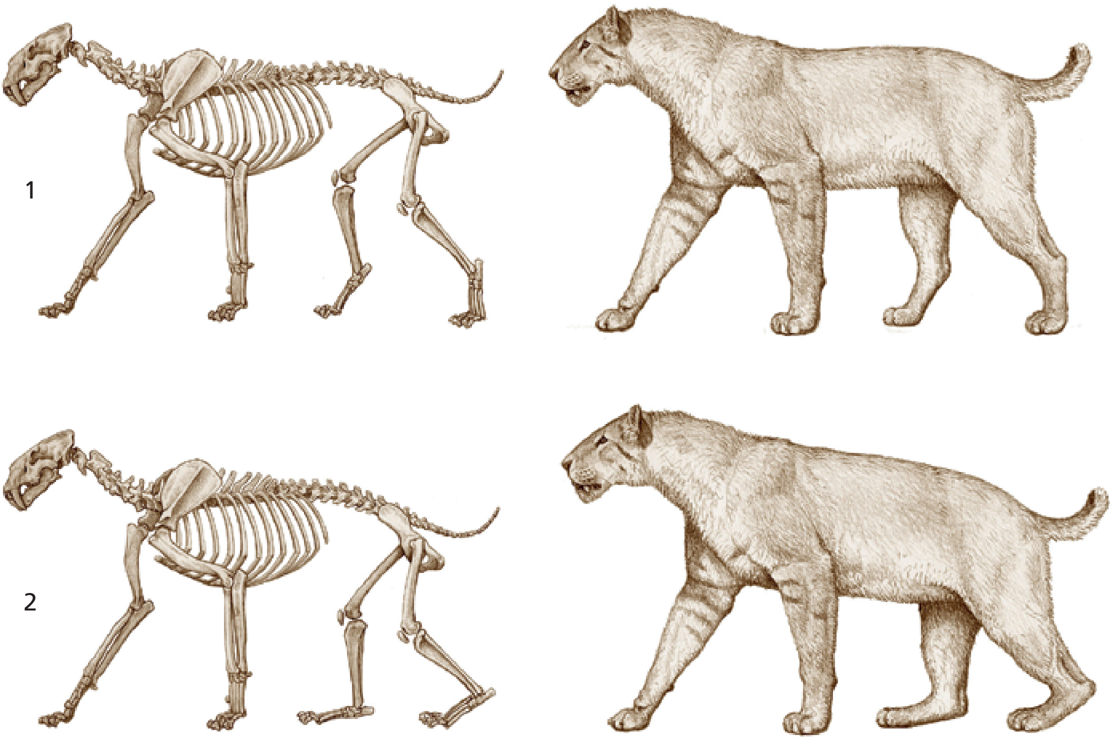

Fig. 5 Alternative reconstructions showing *Homotherium* as digitigrade and plantigrade: **1** digitigrade skeleton (left) and life appearance (right). – **2** plantigrade skeleton (left) and life appearance (right). Not only the morphology of the hind foot bones clearly indicates a digitigrade posture, but as the drawings show, the comparatively long (and undoubtedly digitigrade) forelimbs make it even more unlikely that the animal would walk on plantigrade hind limbs, since the steps of the hind limbs would become far shorter than those of the forelimbs. – (Artwork M. Antón).

Fig. 6 Reconstruction of a galloping *Homotherium latidens*. The animal's body proportions fit well with this kind of gallop or »canter« which is very efficient for covering long distances at moderate speeds. – (Artwork M. Antón).

We know that modern hypercarnivores above a certain body size will tend to hunt prey as large or larger than themselves, for reasons of energy balance (Sunquist/Sunquist 1989). But risk of injury is a controlling factor, and that is one reason why solitary hunters take relatively small prey. For instance, the leopard takes prey averaging 25 kg, which is below the predator's own body size (Hayward et al. 2006), but it can and will take prey larger than that, and often heavier than the predator (**fig. 8**).

Prey size in solitary cats largely depends on the body mass of the individual cat and on its adaptations for handling and controlling that prey. Thus, cheetahs, although overlapping in body weight with leopards, concentrate on gazelle-sized prey and smaller (**fig. 9**), due in part to the reduced grasping ability of their forelimbs.

Prey size in social cats, on the other hand, is not limited by individual power. Recent observations are showing that lions take very large prey more often than usually thought (Power/Compion 2009), and have precise techniques for doing so (**fig. 10**). Such access to large prey species is a function of the lion's group hunting capability, no matter what hypothesis we accept to explain the evolution of such group life.

Also, we know that carnivores with lesser strength and flexibility in their forepaws must resort to group action when it comes to taking larger prey, as they are ill-equipped to take such prey individually. This happens of course to modern dogs and hyaenas, and it may have happened with any extinct large predator that has sacrificed grasping power for speed and endurance in locomotion.

Dogs and hyaenas share with *Homotherium* the possession of large incisors, arranged in an arc (**fig. 11**). This feature is related with the greater role of the

Fig. 7 A sequence of drawings showing the succesive steps of the hypothetical killing bite in *Homotherium*: **1** mandible wide open, upper and lower canine tips in contact with the body of prey, but given the huge gape the muscles of the mandible cannot close it strongly enough. – **2** the whole head rotates down relative to the first neck vertebrae thanks to the pull of powerful neck muscles, and the upper canine pierces the prey's skin and flesh. – **3** Once the upper canines sink, the mandibular gape is reduced, so now the muscles of the mandible can provide strength to further close the jaws and deepen the bite. – (Artwork M. Antón).

Fig. 8 Photograph of a female leopard with its impala kill in the Samburu National Reserve, Kenya. Although the average weight of the leopard's prey is said to be around 25 kg, these cats often hunt larger prey, and in this case the antelope is as heavy or heavier than the predator itself. – (Photo M. Antón).

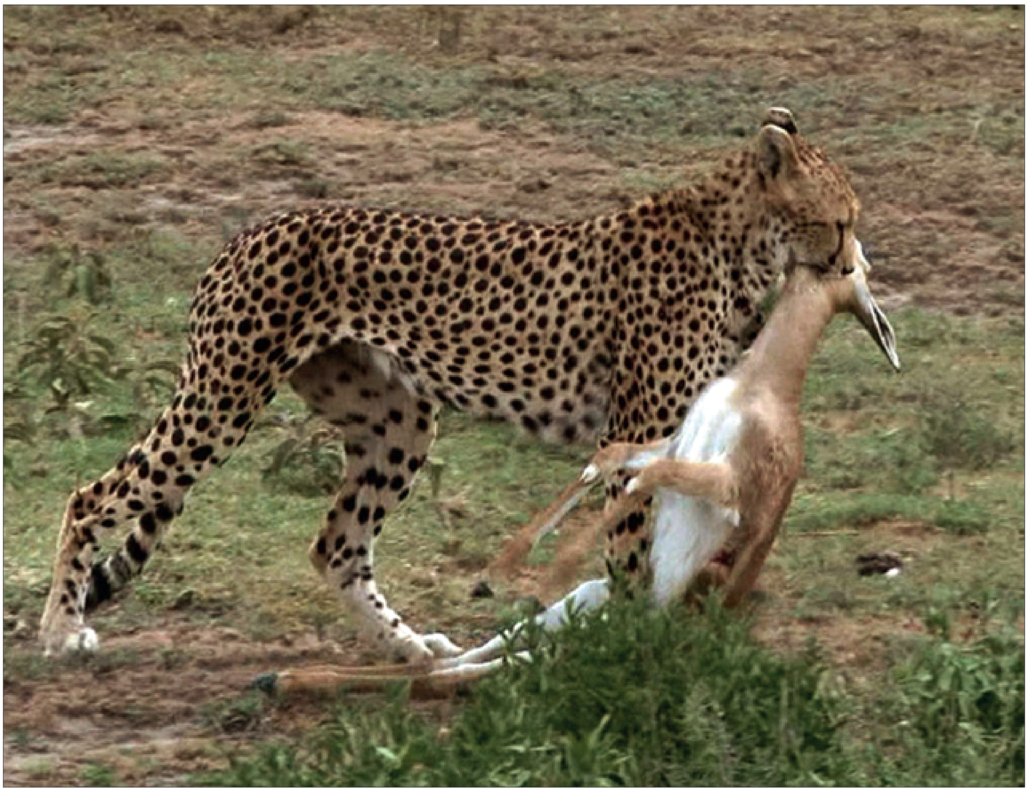

Fig. 9 Video frame of a female cheetah killing a young gazelle in the Ngorongoro Conservation Area, Tanzania. Although cheetahs overlap in weight with leopards, they rarely take prey heavier than themselves and can be seen as essentially »gazelle specialists«. The adaptations of the cheetah for speed imply a partial loss of the grasping ability of its forelimbs, something that contributes to limit the size of the prey it can hunt. – (Filmed by M. Antón).

Fig. 10 Photograph of lionesses feasting on their giraffe kill in the Chobe National Park, Botswana. Although lions are the largest cats in Africa, hunting such enormous prey would be impossible for them without group action. – (Photo M. Antón).

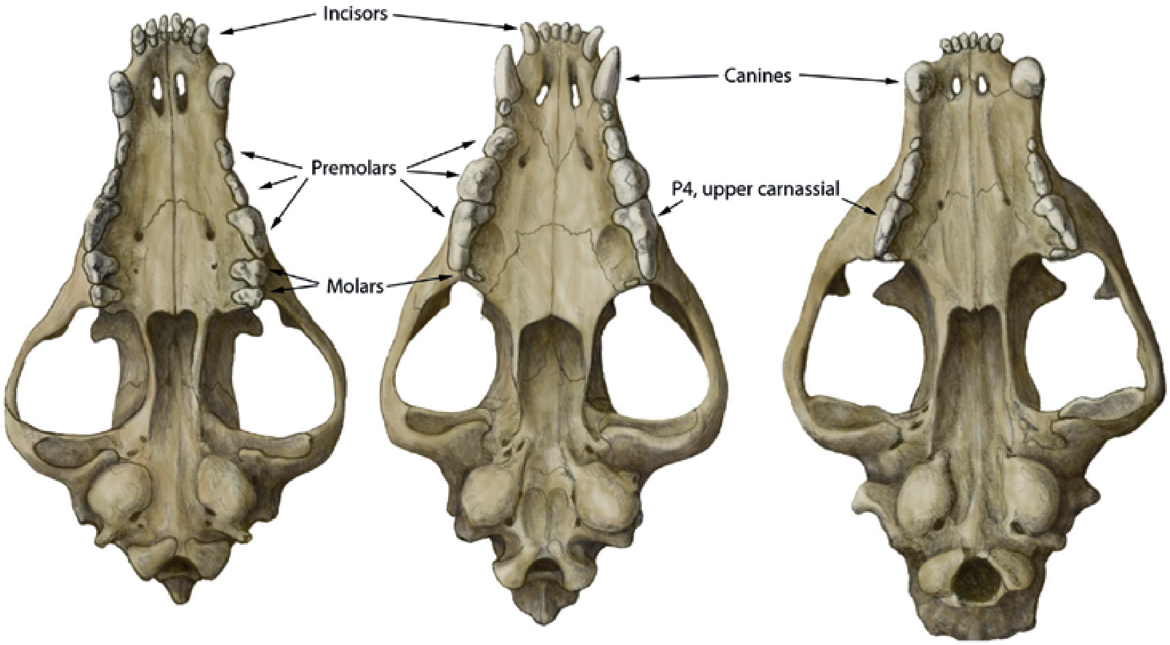

Fig. 11 Comparison between the skulls of three carnivore species in palatal (ventral) view, showing the differences in their dentitions. From left to right: wolf (*Canis lupus*), spotted hyaena (*Crocuta crocuta*) and leopard (*Panthera pardus*). Notice how the incisors of the wolf and hyaena are porpotionally larger and arranged in an arc, while those of the leopard are smaller and arranged in a row. This difference reflects the fact that in dogs and hyaenas the incisors play an important role in prey capture, while in felids that function is largely taken by the forelimbs. *Homotherium* had large, projecting incisors, suggesting some role in the capture of prey. – (Artwork M. Antón).

Fig. 12 Photograph of a group of cheetahs chasing zebra in the Maasai Mara Reserve, Kenya. The third member of the cheetah coalition was involved in the chase but is out of the frame. The targeted zebra foal was large enough to be outside the prey size range for solitary cheetahs, but coalitions do take such large prey. – (Photo M. Antón).

incisors for grasping prey, as compared to the felines where the grasping function is mostly taken by the forelimbs.

As we have seen, there are some similarities between the limb skeletons of *Homotherium* and the cheetah, especially in the shape and function of the wrist and forefeet. But these do not imply that the former was a sprint hunter, because other features of its anatomy, such as the comparatively short back and hind limbs, are poorly suited for quick acceleration or extreme top speeds, and fit better with efficient running at moderate speeds for relatively long distances (Antón et al. 2005). And yet, we may still learn from those similarities. The cheetah's physique is perfectly suited for taking medium-sized prey (gazelles) through solitary hunting. But cheetahs have a social system where male siblings often remain together through adult life, forming coalitions. Those coalitions are seen as an adaptation for the defence of territory and for easier access to transient females. However, during a trip to Kenya, I was able to film a coalition of three cheetah males attempting to hunt a large zebra foal, a bigger prey than any solitary cheetah could hope to catch (**fig. 12**). The cheetahs managed to bring down the foal, but it was rescued by a protective adult zebra in the last moment. Such observations may seem anecdotal, but they clearly show that even if group life is not originally and adaptation for the hunting of larger prey, it allows such predation when opportunities arise.

Fig. 13 Hypothetical scene set in the Pleistocene of Spain, showing a pair of *Homotherium* about to capture a large bovine. Group action would make it far easier to capture and control such large and powerful prey. – (Artwork M. Antón).

GROUP LIVING AND GROUP HUNTING

Do we have any reason to suspect that *Homotherium* would have a social structure independently of its hunting needs? In fact, studies of modern predators indicate that any large mammalian land carnivore living in relatively open environments, which it shares with an inflated large carnivore guild that includes lions and giant hyaenas, will be strongly pressed to become social in order to defend its resources such as territory, cubs, females and kills (Packer et al. 1990; Sunquist/Sunquist 1989). It may not react to all of these pressures, but if it reacts to just one of them, it will become social. And then a whole range of prey will become available: large bovids, for instance, can be taken (**fig. 13**), and the same happens with juvenile proboscideans (**fig. 14**).

Taking the young of large, aggressive herbivores is made easier by distracting maneuvers, something that group hunters such as modern wolves often do (**fig. 15**). *Homotherium* would obviously benefit from such strategies, a possibility that was poetically elaborated by Kurtén in his novel »Dance of the Tiger«.

The cheetah relies on its superb efficiency to make new kills if kleptoparasites rob from it, and its superior speed allows it to flee from any competing predator that could kill or maul it. So its strategy is to keep a low profile. But in the case of *Homotherium*, large body mass and moderate speed made those strategies less likely. In the face of aggression from competitors, it needed to stand its ground, and the best way to do this would be through strength by numbers.

So we see a number of reasons why it would be advantageous for *Homotherium* to live and hunt in groups, although obviously there is a large component of speculation.

Fig. 14 Hypothetical scene set in the Pleistocene of Spain, showing a group of *Homotherium* in the process of killing a juvenile mammoth. Again, group action would be required to bring down such prey, but also in order to keep other herd members at bay. – (Artwork M. Antón).

Fig. 15 Hypothetical scene set in the Pleistocene of Spain, showing an individual *Homotherium latidens* trying to capture a juvenile hippopotamus while a second cat distracts the mother. – (Artwork M. Antón).

SABERTOOTH CAT ECOMORPHS: SABERTOOTH DIVERSITY REVISITED

After looking at all those aspects of sabretooth functional anatomy and behaviour, we can look again at the diversity of body sizes and proportions among the sabretooth species from the Plio-Pleistocene of Europe. *Dinofelis* for instance could be compared with the modern jaguar in terms of body size and proportions, which could also imply a preference for wooded habitats. Moderate sabretooth adaptations might imply taking marginally larger prey than in the case of the modern jaguar. Its heyday in Europe coincides with a great extension of tropical and subtropical forests during the Early and Middle Pliocene. During the Late Pliocene there is evidence of a greater mosaicism, and during that time *Dinofelis* disappears, giving way to *Megantereon* and *Homotherium* during and after the Villafranchian.

Megantereon overlapped with the leopard in terms of body size although some specimens, such as the Senèze skeleton, are larger than any leopard, and are more like jaguars. Body proportions suggest a closed habitat, as in the case of *Dinofelis*, but more extreme sabretooth adaptations in the neck and skull suggest larger prey relative to body size. Smaller size than *Dinofelis* could help *Megantereon* to partition resources with the larger *Homotherium*. Frequent coexistence of *Megantereon* and *Homotherium* at Villafranchian fossil sites points to a mosaic of vegetation at those areas, and at their ability to hunt different prey at different times of day and/or in different sections of the habitat.

Homotherium, in turn, overlapped with the lion in body size and our own comparisons of post-cranial, and especially appendicular morphology, suggest that it was a relatively light animal, certainly lighter than the large Pleistocene lions that shared its habitat. Marked sabretooth specializations allowed the taking of large prey, while adaptations for long-distance running limited their prey-handling abilities, but allowed the animal to range across large territories and maybe even to follow migrating prey for part of their seasonal trips.

CONCLUSIONS

In conclusion, although broad parallels can be established with modern felines, sabretooth species were no exact ecological equivalents of jaguars, leopards or lions, as further demonstrated by the fact that they coexisted with those species at various points in space and time. They were unique products of evolution with their own answers to the challenges of hunting large prey.

Homotherium itself was a broadly lion-sized sabretooth cat, which combined a craniodental and cervical complex specialized for the killing of large prey, with relatively long limbs adapted for running at moderate speeds for long distances. Such locomotor adaptations implied reduced individual power for subduing prey. *Homotherium* likely used the open sections of its habitat and foraged widely, probably following migratory prey. In order to catch prey of the right size for its killing weapons it may have needed to hunt in groups. As a large felid living in open habitats with »crowded« large carnivore guilds, it had additional reasons to become social: protection of territory, of females, of cubs and of prey.

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SUMMARY / ZUSAMMENFASSUNG

Behaviour of *Homotherium* in the Light of Modern African Big Cats

In order to reconstruct the appearance and behaviour of the sabretoothed felid *Homotherium* we combine the study of its functional anatomy with various complementary sources of information, including the comparative anatomy, the dissection of extant carnivores and the observation of living felines in the African wilderness. The results of these comparative studies reveal *Homotherium* as a lion-sized sabretooth, much lighter in build than its Pleistocene relatives such as the *Smilodon*. Compared to extant and fossil lions, *Homotherium* had a longer and more muscular neck; a shorter back and tail; narrower forearms and less powerful forepaws with smaller and less retractable claws, with the exception of a huge dewclaw. These features suggest that *Homotherium* would target large ungulates as prey, but in order to bring down animals the size of a buffalo and larger, the loss of strength and of the prehensile abilities of its forepaws would pose a limitation, and make group action necessary. Body proportions and morphology suggest an adaptation to relatively open environments, and given this and the cat's body size there could be ecological pressures to evolve group living, in order to defend territory, cubs, and kills. In turn, we know from the observation of living felines that group-living, even if originally developed as a response to ecological pressures, increases the likelihood of group hunting.

Das Verhalten von *Homotherium* im Lichte der modernen afrikanischen Großkatzen

Um das Aussehen und das Verhalten des Säbelzahntigers *Homotherium* zu rekonstruieren, kombinieren wir die Untersuchung seiner funktionellen Anatomie mit verschiedenen ergänzenden Informationsquellen, darunter die vergleichende Anatomie, die Sektion lebender Raubtiere und die Beobachtung lebender Raubkatzen in der afrikanischen Wildnis. Die Ergebnisse dieser vergleichenden Studien zeigen, dass *Homotherium* eine löwengroße Säbelzahnkatze ist, die viel leichter gebaut ist als ihre pleistozänen Verwandten wie der Smilodon. Im Vergleich zu heutigen und fossilen Löwen hatte *Homotherium* einen längeren und muskulöseren Hals, einen kürzeren Rücken und Schwanz, schmalere Unterarme und weniger kräftige Vorderpfoten mit kleineren und weniger einziehbaren Krallen, mit Ausnahme einer großen Afterkralle. Diese Merkmale deuten darauf hin, dass *Homotherium* große Huftiere als Beute ins Visier nahm, aber um Tiere von der Größe eines Büffels und größer zu erlegen, würde der Verlust der Kraft und der Greiffähigkeit der Vorderpfoten eine Einschränkung darstellen und Gruppenaktionen erforderlich machen. Die Körperproportionen und die Morphologie deuten auf eine Anpassung an relativ offene Umgebungen hin, und angesichts dessen und der Körpergröße der Katze könnte ein ökologischer Druck bestehen, ein Gruppenleben zu entwickeln, um Territorium, Jungtiere und Beute zu verteidigen. Im Gegenzug wissen wir aus der Beobachtung lebender Katzen, dass das Leben in der Gruppe, selbst wenn es sich ursprünglich als Reaktion auf ökologischen Druck entwickelt hat, die Wahrscheinlichkeit der Gruppenjagd erhöht.