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Soft tissue reconstruction of *Homotherium latidens* (Mammalia, Carnivora, Felidae). Implications for the possibility of representations in Palaeolithic art $\stackrel{\leftrightarrow}{\sim}$

Reconstitution des parties molles d'Homotherium latidens (Mammalia, Carnivora, Felidae). Implications pour la possibilité d'une représentation dans l'art paléolithique

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Abstract

We reconstruct the life appearance of the head and body of the sabretoothed felid *Homotherium latidens* through the study of osteological correlates of soft tissue attributes, incorporating data from the dissection of several large felids and using the Extant Phylogenetic Bracket to infer the condition of unpreserved attributes where morphological evidence is inconclusive. Our reconstruction shows that *Homotherium* would have differed from modern felids in aspects of the general proportions of the head, having a straighter dorsal outline and a long, square muzzle with an angular "chin", although large pantherines may mimic to some degree the angular shape of the machairodontine mandibular symphysis with the growth of long hair in the chin area. The tips of the sabres of *Homotherium* would have been visible in life, protruding beyond the lips. Our reconstructed body proportions of *Homotherium* imply a sloping back. These conclusions contradict a previous proposal that postulated a different soft tissue anatomy for *Homotherium*, and which led to interpretation of a Palaeolithic figurine as a rendering of the sabretooth. Our results suggest that the figurine in question is a depiction of a cave lion, and that there is no single known representation of a machairodont in prehistoric art. The implications for our current understanding of the Late Pleistocene large-carnivore guild are discussed.

Keywords: Homotherium latidens; Reconstruction; Soft tissues; Isturitz figurine

Résumé

L'apparence naturelle de la tête et du corps du « tigre à dents de sabre » *Homotherium latidens* est reconstituée sur la base des corrélats ostéologiques des parties molles. Cette reconstitution prend en compte les données de la dissection de plusieurs grands félidés, en utilisant la méthode des « Encadrements Phylogénétiques Actuels » afin de déduire les caractéristiques non-préservées lorsque les données morphologiques sont insuffisantes. Notre reconstruction montre qu'*Homotherium* aurait été différent des chats modernes en termes de proportions générales du crâne, avec un profil dorsal plus droit, un museau carré et un menton plus angulaire, bien que les grands panthérinés puissent mimer d'une certaine façon la forme angulaire de la symphyse mandibulaire des machairodontes, du fait de la longueur des poils mentonniers. Les pointes des crocs d'*Homotherium* auraient été visibles, dépassant la base des lèvres. Notre reconstitution des proportions du corps d'*Homotherium* indique un dos assez arqué. Ces conclusions contredisent une proposition précédente relative aux parties molles d'*Homotherium*, à l'origine de l'interprétation

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d'une figurine paléolithique comme étant un « tigre à dents de sabre ». Nos résultats suggèrent que la figurine en question est l'image d'un lion des cavernes et qu'il n'y a aucune représentation connue d'un machairodonte dans l'art préhistorique. Les conséquences pour notre compréhension actuelle de la guilde des grands carnivores du Pléistocène terminal sont discutées.

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Mots clés : Homotherium latidens ; Reconstitution ; Parties molles ; Figurine d'Isturitz

1. Introduction

Homotherium was a widespread genus of sabretoothed felid that ranged throughout Eurasia, Africa and North America from the Early Pliocene to the Late Pleistocene (Kurtén, 1968; Turner and Antón, 1997, 1999; Antón et al., 2005). The timing of its extinction was different in each continent, so that while it disappeared first from Africa around 1.5 Ma, the last members of the genus became extinct in North America at the end of the Pleistocene. However, ideas about the extinction of the genus in Europe have changed through the years. During much of the 20th century, fossils of Homotherium latidens from British caves such as Kent's Cavern and Robin Hood's Cave were thought to indicate the presence of this cat in the Late Pleistocene of England (Kurtén, 1968), but later interpretations of the age of those deposits, and of the contexts of the specimens, pushed the extinction date as far back as half a million year, the age of the next youngest dated fossils (Cook and Jacobi, 1998; Turner and Antón, 1999). Arguments for a Late Pleistocene occurrence at Kent's Cavern have more recently been revived by Proctor et al. (2005), although they concede that the specimens, isolated teeth, could equally as well have been introduced into those deposits by Late Pleistocene humans, or even more probably could have been derived from the earlier, Middle Pleistocene deposits that are also present in the cave. In recent decades, fossils of homotheres have been found in slightly younger deposits, with records as recent as 400,000 yrs B.P. in sites such as level TD10 of Gran Dolina in Atapuerca, Spain (García, 2001), but not young enough to change the overall interpretation of extinction well within the Middle Pleistocene. However, recently published dates of about 28,000 yrs B.P. for a fossil specimen from the North Sea (Reumer et al., 2003; Mol et al., 2008) have once again raised the issue of later European survival of the species. Clearly, such a late appearance would raise a number of questions about the palaeoecology of the large predator guild in the later Pleistocene of Europe. We have discussed this matter in some detail in a previous work (Antón et al., 2005), and pointed out that even if the date of the specimen is correct then the animal must have led a very quiet existence, escaping incorporation into other deposits and suggesting that the lion was the dominant large felid in most if not all parts of Europe. In the face of a single dated specimen there appears to be little more that can currently be said on the topic of a late survival and its palaeoecological implications.

However, in the course of their discussions, Reumer et al. (2003) and Mol et al. (2008) suggested that support for such a late appearance of *Homotherium* might be found in the form of a small Upper Palaeolithic-age figurine of a cat from the French

Pyrenean cave of Isturitz (Fig. 1). At a time when it was widely thought that the genus may have survived into the last glaciation, the Czech palaeontologist Vratislav Mazak (1970) had reviewed ideas about the figurine, which had been found at the site in 1896. The specimen was first described by Capitan et al. (1910), who cautiously suggested that although the stratigraphic provenance was uncertain it might be assigned what they termed an "Upper Aurignacian" age, corresponding to what would now be called Gravettian in the Isturitz sequence. The figurine had been lost during the intervening years so that Mazak could only study published depictions, but these did include a photograph (Rousseau, 1967a, 1967b). Mazak concluded that it was a representation of a sabretoothed cat, a view based as we shall show on debatable anatomical interpretations but at least supported by the then apparent coexistence of the felid and Aurignacian artists in Europe. However, when the supposed Late Pleistocene records of Homotherium were rejected, interest in Mazak's interpretation declined, and it was largely abandoned for three decades until being raised again by Reumer et al. (2003). Even if the dates are no longer seen as a problem based on the North Sea specimen, the interpretation of the animal depicted by the statuette must still stand or fall on the basis of its anatomical merits. We examine this identification in the light of our own reconstruction of the living appearance of Homotherium based on direct skeletal evidence and the comparative anatomy of living felids.

2. Previous work

Reconstructions of extinct animals have long been of interest to palaeontologists and archaeologists, but with the now ubiquitous use of computerized graphic images in television



Fig. 1. The palaeolithic statuette from Isturitz, variously interpreted as a representation of a cave lion (*Panthera leo spelaea*) or a sabretoothed cat (*Homotherium latidens*). Total length of original about 160 mm (artwork by M. Antón based on Mazak, 1970).

and cinematic productions they have increasingly come to the notice of the general public. Attention of specialists and public alike has understandably tended to centre on the bizarre and the exotic, and the machairodont or sabretoothed cats certainly fall into both of those categories. Unfortunately, the visual results of this interest have in our view ranged from the (rarely) good through the indifferent to the downright bad. Clearly, an excellent starting point for any reconstruction (short of a body preserved in ice) would seem to be the record of depictions left in the caves used by our prehistoric ancestors.

Mazak (1970) put forward a number of points in support of his interpretation of the Isturitz figure. First, he considered that the muzzle of the sculpted animal was too high and its outline was too square to be that of a true felin-that is a member of the tribe Felini within the subfamily Felinae, the living and fossil conical-toothed cats (Turner and Antón, 1997)-and he thought that such a shape was more consistent with the angular symphysis of sabretoothed cats, and of Homotherium in particular. Mazak noticed, however, that the figurine showed no trace of the upper canine tips, which would be expected to protrude beyond the upper lips in the extinct cat. In extant cats, the tips of the canines may be visible just beyond the upper lips even when the mouth is closed and relaxed, at least in individuals with particularly long fangs. But Mazak proposed that Homotherium would have differed from extant cats in the disposition of its lips, so that the lower lip would have covered the tip of the upper canines when the mouth was closed. He also thought that the figurine reflected other aspects of the anatomy of Homotherium, including the long legs, short body and short tail, although it is difficult to see that the figurine really shows evidence of elongated legs.

Resorting to archaeological evidence can be a useful way to complement our image of the appearance of an extinct species, but whenever the interpretation of that evidence is ambiguous the ultimate test has to be the study of anatomical evidence from actual remains. Is it possible to test the validity of Mazak's arguments from a purely anatomical and biological standpoint? We address this issue and propose an anatomically accurate reconstruction of the life appearance of the sabretoothed cat. For the reconstruction of the head of *Homotherium* we apply a methodology that we have developed over the last decade (Antón et al., 1998; Antón and Sánchez, 2004). We also offer a full body reconstruction based on our previous studies of the postcranial skeleton of *Homotherium* (Antón et al., 2005), which also allows us to test Mazak's assumptions about its body proportions.

3. Materials and methods

As a basis for our assessment of cranial morphology of *Homotherium* we have studied the excellent sample of skulls from the Spanish site of Incarcal (Antón and Galobart, 1999; Galobart et al., 2003). One of these skulls (IN-I 929) was digitized in 3D and served as the basis for a computerized model (Fig. 2). Composite reconstructions were created combining the best preserved parts of different individuals when necessary in order to obtain a picture of a complete,



Fig. 2. Digital 3D reconstructions of the skull and mandible of *Homotherium latidens* in antero-lateral view. **A.** Wireframe render. **B.** Surface render.

undamaged skull. We also considered the morphology of wellpreserved skulls from other sites such as Perrier (de Bonis, 1976), and Senèze (Ballesio, 1963). For soft tissue reconstruction we followed the methodology outlined in our previous works (Antón, 2003; Antón and Galobart, 1999; Antón and Sánchez, 2004; Antón et al., 1998; Turner and Antón, 1997). Deep muscles were restored on the basis of the morphology of muscle insertion areas (Barone, 1967; Bryant and Seymour, 1990), while for other soft tissues with less clear osteological correlates, including some muscles, cartilaginous structures, and skin, we followed the condition observed in related extant taxa, using the Extant Phylogenetic Bracket method (Witmer, 1995), and relevant functional considerations (Bryant and Russell, 1992) as a guide for restoration of unpreserved attributes. Data on the soft anatomy of extant large felids was collected during dissections of several species carried out during the last few years, including three adult tigers (*Panthera tigris*), one adult lioness (*Panthera leo*), one adult puma (*Puma concolor*), and one adult leopard (*Panthera pardus*). We made photographs and sketches during the successive stages of each dissection. During dissection of the head and neck, care was taken to leave one side of the animal intact so that it could be used as a reference for the position of the superficial soft tissue structures in relation to deeper ones and to the skull and mandible. For reconstruction of the complete skeleton of *Homotherium* we combined the Incarcal sample with information from specimens from other sites, especially the nearly complete skeleton from Senèze (Ballesio, 1963) and the sample from Hundsheim (Freudenberg, 1914).



Fig. 3. Dissected head of an adult tigress (*Panthera tigris*) in lateral view. A. After removal of masticatory muscles with attachment areas visible. B. Prior to removal of masticatory muscles. Abbreviations: d: muscle *digastricus*; m: muscle *masseter*; mf: masseteric fossa; t: muscle *temporalis*; tf: temporal fossa; z: zygomatic arch. Arrowheads show the anterior and dorsal margins of the attachment area of the muscle *masseter* in the zygomatic arch.

4. Results

4.1. Cranial bones and soft tissue in extant large felids

The following observations apply in general to the four species of large felids dissected, unless otherwise stated. Our dissections confirm the presence of discrete, recognizable areas for insertion of the main masticatory muscles, the masseter and temporalis in the temporal fossa of the skull, in the zygomatic arches and in the mandible (Fig. 3). These muscles not only fill the space between origin and insertion, but they also bulge out (especially when the mandible is adducted), considerably enlarging the outline of the head of the animal. As a consequence, the dorsal border of the sagittal crest occupies a slight groove between the masses of the temporalis muscles, especially when the jaws are closed. Several superficial muscles, including the frontoscutularis muscle, and in the mandible the mentalis muscle, have at least partial attachments on the bone, but we could not associate them with definite scars, although they are associated with certain osteological features such as the postorbital process of the frontal bone (Fig. 4). The orbicularis ori muscle and the lips follow the typical conformation seen in most carnivores, hanging from the maxilla over the upper incisors and canines, while in the mandible they are more tightly pressed against the bone and, as the mouth closes, the upper canines, if long enough, fit outside the lower lip (Fig. 5). The fibres of the digastric were observed to reach as far anteriorly as the symphyseal region of the mandible (Fig. 6).

Among non-muscular structures, the postorbital ligament is a prominent feature bridging the space between the postorbital process of the frontal and zygoma (Fig. 7). The cartilaginous



Fig. 4. Dissected head of an adult tigress (*Panthera tigris*) in lateral view, showing superficial musculature. Abbreviations: **fs**: muscle *frontoscutularis*; **nc**: nasal cartilage; **o**: muscle *orbicularis oris*; **p**: platisma; **z**: muscle *zygomaticus*.



Fig. 6. Dissected head of an adult tigress (*Panthera tigris*) in ventral view. Abbreviations: **d**: muscle *digastricus*; **m**: muscle *masseter*.



Fig. 7. Dissected head of an adult puma (*Puma concolor*) in lateral view. Abbreviations: **ac**: auricular cartilage; **lnl**: muscle *levator nasolabialis*; **pol**: postorbital ligament.

ear or pinna emerges from the external auditory meatus, and extends upwards toward the midline of the head. Its morphology is consistent with that of primitive feliformia such as viverrids, with a conspicuous bursa (Fig. 7). The cartilaginous nose extends from the anterior margin of the nasal bones to a point ahead of the upper incisors. This is true in all the large felid species dissected, ranging from the lion, where the distance between both points is largest, to the puma, where that distance is smallest (Fig. 5).

4.2. General skull morphology in Homotherium

Compared with modern large felids, the skull of *Homotherium* displays all the set of morphological differences that make up the so-called machairodont complex (Turner and



(A)

Fig. 5. Head of an adult lioness (*Panthera leo*) in lateral view. **A**. Skull superimposed on head outline. **B**. Intact head before dissection. Abbreviations: **uct**: upper canine tip.

uct



Fig. 8. Skulls of felids in dorsal view. A. Sabretoothed cat (*Homotherium latidens*) specimen IN-1929 from Incarcal (Spain). B. Lion (*Panthera leo*). Skulls figured to the same size; basal length of the *Homotherium* skull = 305 mm.

Antón, 1997; Antón and Galobart, 1999; Antón et al., 2004). Some of these features are especially likely to influence the general proportions and external appearance of the head in the living animal. The skull of *Homotherium* is generally narrower and more elongated than those of pantherines (Fig. 8). It has a straighter dorsal outline, an elevated snout, and a high sagittal crest. Apart from the presence of the large upper canines, the incisor battery differs from that of pantherines in being enlarged and protracted anteriorly, which creates a greater distance between the anterior border of the nasal bones and the incisors, giving the impression of retracted nasals (Fig. 9). The symphyseal region of the mandible is more angular and higher in lateral view. Other differences include the short coronoid process in the mandible (Fig. 9).

4.3. Osteological correlates of soft tissue in Homotherium

The insertion areas for the temporalis and masseter muscles clearly define the location and development of these muscles (Fig. 9), although we cannot recognize clear marks in the bone



Fig. 9. Skulls of felids in lateral view. **A**. Sabretoothed cat (*Homotherium latidens*), composite of skull IN-I 929 and mandible IN-I 826 from Incarcal (Spain). **B**. Lion (*Panthera leo*). Skulls figured to the same size; basal length of the *Homotherium* skull = 305 mm.

that correspond to the insertions of facial muscles and these have to be reconstructed by assigning to their insertions a similar anatomical position as in the extant relatives. The external auditory meatus provides a clear indication of the position of the pinna, whose insertion would look marginally lower than in modern cats. The large distance between the anterior border of the nasal bones and the anterior border of the premaxilla would be filled by the nasal cartilage, as we have previously shown in the case of the large American machairodont cat *Smilodon* (Antón et al., 1998). In terms of the Extant Phylogenetic Bracket, such an inference is strongly supported by the widespread presence of the same condition not only in extant felids, but also in the vast majority of living Carnivora (Antón et al., 1998).

4.4. Reconstruction of soft tissue in Homotherium

The reconstructed appearance of the head of *Homotherium* in lateral view reflects the major features of cranial morphology mentioned above. As a first step, the large masses of the masticatory muscles are set in place (Fig. 10, top), which does not alter the outline of the skull to any great extent. When the nasal cartilage is drawn in its logical position above the incisor arcade (Fig. 10, middle), it adds considerably to the long-muzzled appearance of the animal, emphasizing its difference from pantherine cats. The restoration of the cartilage also adds to the straight appearance of the dorsal outline of the head, again different from the gently convex profile of pantherine cat heads. A pinna or ear cartilage of medium size is added, in the

(A) (B) (C)

Fig. 10. Sequential reconstruction of the head of the sabretoothed cat *Homo-therium latidens*. **A**. Skull and mandible with selected deep muscles. **B**. Head and anterior neck with superficial musculature. **C**. Hypothetical life appearance (artwork by M. Antón).

logical anatomical position indicated by the location of the external auditory meatus. Its insertion is located lower relative to the dorsal outline of the skull than in pantherine cats, as a consequence of the ventral position of the meatus in *Homotherium* and of its high sagittal crest. However, the ear tips would still normally protrude above the head outline when in an alert position as depicted here (Fig. 10, middle and bottom).

We reconstruct the lips with the same general morphology seen in all living felids and most Carnivora, with the upper lip overhanging the lower one, which in turn is shown tightly pressed against the mandible. This implies that the tips of the elongated upper canines would show when the animal had its mouth closed, at least in any individual with canines long enough to project beyond the margin of the overhanging upper lips. The finishing touch to the life restoration is the hair, and both the patterns of colouration and of hair length distribution are built upon patterns that are widespread among the extant relatives of machairodont cats. The models used have been not only the extant cats (which are the closest related taxa and thus the first choice for a reference), but also members of the related families Viverridae and Hyaenidae. We have shown *Homotherium* with relatively long hairs in the anterior throat region, as well as behind the masseter area and under the chin, a pattern borrowed from modern cats, but observed in other Carnivora, including dogs.

4.5. Postcranial skeleton and body proportions

The full body reconstruction of *Homotherium latidens* and the comparison with the lion offered in Fig. 11 show the differences in body proportions revealed by our previous studies of postcranial anatomy in the species (Antón et al., 2004). Apart from the differences in the shape of the head discussed above, the neck of *Homotherium* is longer, its back and tail are shorter, and the forelimbs are longer relative to the hindlimbs than in the lion. Apart from these differences in relative proportions, the general body build of *Homotherium* is similar to or lighter than that of the lion, and the back is sloping, although not nearly so much as in extant hyaenids.

5. Discussion

Transferring the features observed in modern felids to Homotherium involves varying degrees of inference. While the placement of the main masticatory muscles is indicated by clear features of the skull and mandible, the more superficial or thinner facial muscles are placed by assuming that they were associated with the same anatomical features as in the case of their extant relatives. Such associations are in the great majority of cases very constant and widespread, not only among the extant members of the family Felidae (Barone, 1967) but also among the rest of the Feliformia and even across the whole order Carnivora, which tends to make their assumption in Homotherium a safe one. These safe inferences include the position and overall morphology of the nasal and ear cartilages, and the position of the lips relative to the dentition (Antón et al., 1998). It is worth noting here that in higher primates (which are of course far removed from felids and from the Carnivora in general), the presence of lower lips that cover the tips of upper canines is a widespread feature, even in animals with impressive canines such as baboons (Jablonski et al., 2002, 2008). The fact that lemur and other primitive primates show the same lip morphology as Carnivora (or as ruminants and even opposums, for that matter) indicates that the presence of a lower lip that envelopes upper canine tips is a synapomorphy of the primate infraorder Simiiformes. If we stick to the logic of the Extant Phylogenetic Bracket, then the only sensible option when reconstructing an extinct felid is to transfer the condition that is widespread, not to say universal, among the order Carnivora. This is especially so since there is no single piece of evidence in the fossil record, nor any kind of functional



Fig. 11. Skeletons and reconstructed life outlines of Pleistocene felids. A, B. Sabretoothed cat (*Homotherium latidens*). C, D. Cave lion (*Panthera leo spelaea*) (artwork by M. Antón). Scale bar represents 25 cm. Modified from Antón et al. (2005).

argument, to suggest that the lips of *Homotherium* or any other machairodont cat would have had to be built like those of a higher primate (Antón et al., 1998).

A higher level of inference is needed for reconstructing such external features as fur length and colour patterns, which are entirely based on phylogenetic and functional reasoning as explained elsewhere in our previous methodological discussions (Antón et al., 1998; Antón and Sánchez, 2004). The inference of a pattern of hair length in *Homotherium* similar to that of its living relatives affects the general outline of the head in two ways. First, it makes the ventral back part of the head and the throat look thicker, making it similar to modern cats. Second, it makes the shape of the chin even more pointed and protruding.

The picture resulting from this reconstruction of the head shows *Homotherium* having had a straighter dorsal outline, a longer muzzle, and a higher and more angular chin than in a lion or tiger. In an adult animal with average-sized upper canines the tips of the latter would certainly have shown even when the mouth was closed, and would have been prominent in older individuals, especially in males.

The image of the living *Homotherium* is completed by the reconstruction of its body proportions, which show it as an animal with a longer neck and forelimbs and shorter hindlimbs, back and tail than lions or tigers. The overall build of the animal would be similar to or lighter than in lions, but the appearance of the animal could change with the seasons in populations living in temperate or cold latitudes, so that it would look stockier with its winter coat. We cannot stress enough that *Homotherium* and other machairodont cats (Salesa et al., 2005,

2006) were different in their bodily proportions from living feline cats (Turner and Antón, 1997), and none of them can be depicted as a lion or a tiger with simply elongated upper canines as some reconstructors have been content to do.

With these considerations in mind, we can return to the Isturitz statuette shown on Fig. 1 and check how well it fits with the anatomical reconstruction of Homotherium. We immediately see that several features of the statuette differ markedly from our restoration, even making the most generous assumptions about the intentions of the sculptor. It has a head with a convex dorsal outline, the ears are placed in a very dorsal position, there is no evidence of protruding upper canine tips, the neck is not especially long, the hindquarters appear to be as high as or even higher than the forequarters, and the back is correspondingly straight or even ascending towards the rear. These two latter characters cannot be an artifact of the broken legs of the statuette, since the orientation of the legs suggests that it is posed more or less correctly, although it is hard to see that the legs can be said to be long even in relation to the short body.

The high, angular chin of the statuette, mentioned by Mazak as evidence that it could not be the depiction of a lion, is actually entirely compatible with the fact that lions and tigers have long hair on their chins, accidentally mimicking the angular shape of the anterior mandibles of sabretooth cats. Mazak's assertion is probably derived from his comparison of the shapes of the bare bones without knowledge of the influence of soft tissues on the external appearance of the living animals. One interesting detail is that the eyes of the statuette are proportionally very large, while all machairodont cats have relatively smaller eyes than a feline of comparable size. Some specimens of *Homotherium* have relatively large orbits for a sabretooth, but even so they are always relatively smaller than in a lion or tiger. The eyes of the sculpture are in fact too large even for an adult lion, a feature which, combined with the relatively large head, suggests to us that the artist may have wanted to depict a lion cub. Palaeolithic depictions of adult lions, such as those from Chauvet (Clottes, 2001) show eyes of correct size. Finally, there is no strong evidence to prove that the short tail of the statuette is its original condition and not simply the consequence of a breakage.

6. Conclusions

In summary, we find that all available evidence is compatible with the interpretation of the Isturitz statuette as the representation of a lion, perhaps even a juvenile in view of the proportionally large head and eyes, and there is no strong argument to defend it as a depiction of Homotherium. Although the discovery of a Homotherium mandible in the North Sea dated to 28,000 yrs B.P. has brought back the possibility of coexistence of sabretooths and modern humans in Ice age Europe, it remains true that a single dated fossil is scant evidence to put against the overwhelming dominance of the lion in Late Pleistocene deposits all over Eurasia (Antón et al., 2005). Even if Homotherium were indeed there, it must have been a rare animal and any encounter with humans equally rare. Furthermore, recent reviews of the effect of better pre-treatment on the results of AMS carbon 14 dating of bone make it advisable to accept dates, or even series of dates, with renewed caution. Improved procedures to purify bone collagen by ultrafiltration of the prepared gelatine samples in order to eliminate contamination are now able to separate out smaller and lower molecular weight fractions that seem to have been a major source of more recent organic contamination by humic acids, organic salts or heavily degraded collagen in the samples (Bronk Ramsey et al., 2004). Application of such techniques to bone samples from British assemblages have led to significant alterations in inferred age, and even in some cases to placing specimens beyond the range of carbon 14 dating (Jacobi et al., 2006). It would seem appropriate to suggest submitting the North Sea Homotherium to such refined analysis at a second laboratory. At any rate, while it remains an open question whether sabretoothed cats inhabited Europe in any numbers during the later Pleistocene, it seems most likely that the Isturitz statuette was not a portrait of one of them.

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