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Concealed weapons: A revised reconstruction of the facial anatomy and life appearance of the sabre-toothed cat *Homotherium latidens* (Felidae, Machairodontinae)

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ABSTRACT

Homotherium is one of the sabre-toothed felid genera with a more extensive overlap in space and time with species of our own genus *Homo*, who must have been familiar with the animal, but now we only have its fossil remains to infer its life appearance. A revised reconstruction of the soft tissue and life appearance of *Homotherium latidens* is proposed here on the basis of new observations on the anatomy of extant carnivorans and a re-evaluation of the fairly preserved skull and mandible from the classical Late Pliocene site of Perrier (France). This fossil specimen provides some of the best information available about the morphology of the skull and mandible. Like other large early specimens of *Homotherium*, it has enormous upper canines relative to skull size and high-crowned enough to protrude beyond the lips in the living animal. On the other hand, observations of facial expressions in living big cats and dissected specimens show that, contrary to previous conclusions, the soft tissue around the mouth and the lower lip in particular can cover the upper canines of large felids, even when those are considerably high-crowned. Such observations lead us to propose a revised hypothesis about the life appearance of *Homotherium* and other sabre-toothed carnivorans, where the upper canines may have been covered in life when the mouth was completely closed.
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1. Introduction

Homotherium was the most widespread genus of sabre-toothed felids during the Late Pliocene and Pleistocene, overlapping extensively in range with several species of fossil hominins in Africa and Eurasia (Antón et al., 2005, 2014; Lewis and Werdelin, 2007; Werdelin and Lewis, 2005). In Europe, it is present at least until some 300 ka ago (Serangeli et al., 2015), and after that, the only confirmed presence is a mandible found at the North Sea and dated at some 28 ka ago (Reumer et al., 2003). The rich fossil record of *Homotherium* has allowed extensive studies on its anatomy, as well as inferences about its ecology and behaviour, indicating that this sabre-toothed felid was a specialized hunter of large herbivores, probably employing group action to take some of its prey, which apparently included juvenile proboscideans in at least some locations (Antón et al., 2005; Antón, 2021; Janssens et al., 2019; De Santis et al., 2021). Studies of its genetic material suggest that all post-Villafranchian *Homotherium* are very closely related and probably belonging to a single variable species, in turn, related to, but different from smilodontin sabretooths, and part of a Machairodontinae clade which diverged early from the lineage that led to extant felids (Widga et al., 2012; Paijmans et al., 2017). Genomic analyses suggest positive selection in several genes, including those involved in vision, cognitive function, and energy consumption, consistent with diurnal activity, well-developed social behaviour, and cursorial hunting (Barnett et al., 2020). The coexistence of *Homotherium* with early humans suggests the possibility of a whole range of possible interactions, from the likelihood of direct predation to the competition for resources, including aggressive scavenging by humans of the sabretooth's kills (Lewis, 1997). Other hypotheses include the possible use of *Homotherium* bones as tools, as observed at the Middle Pleistocene site of Schöningen (Germany) (Serangeli et al., 2015), or the possibility of representation in palaeolithic art (Mazák, 1970; Antón et al., 2009).

Life reconstructions of *Homotherium* are an integral part of the effort to formulate hypotheses about its biology and to visualize

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them. Such reconstructions improve continuously with the refinement of knowledge about the anatomy of modern relatives and with the finding of more complete or better-preserved fossils and the improved study of existing specimens. Our previous reconstructions (Antón et al., 2009; Antón, 2013) were based on a reasonably rich fossil record and also on a range of observations, mostly dissections, of modern carnivorans in general and big cats in particular. One of our conclusions at the time was that in the scimitar-toothed felids, the apical portion of the upper canine crown would protrude beyond the upper lip and sit outside the lower lip, thus being visible in life with the mouth closed and resembling the condition inferred in our previous studies for the sabre-toothed felid *Smilodon* (Antón et al., 1998). In the meantime, we have re-evaluated relevant fossils, which allow us to refine interpretations of the anatomy of *Homotherium*, while direct observations of wild animals in Africa and India have given us the opportunity to film and photograph free-ranging large felids in considerable detail. In view of this input, we find that some of our previous interpretations are in need of revision, which in turn made it advisable to conduct new dissections of extant felids. The combination of the results of all these observations allows a reappraisal of the reconstruction of the soft tissue and life appearance of *Homotherium* and other sabre-toothed felids.

2. Materials and methods

We studied the articulated skull and mandible (MNHN.F.PET 2000 a & b) of a single specimen of *Homotherium* from the Late Pliocene site of Perrier, housed at the Muséum national d'Histoire naturelle, Paris (France), both directly and through a CT-Scan performed at the AST-RX platform with a resolution of 0.19 mm, located at this same institution. Both the skull and mandible are almost perfectly preserved, and despite a very slight deformation, they can be articulated with a fair degree of anatomical accuracy.

Observations of free-ranging large felids took place in Northern Botswana in the years 2013–2019, and in Central India in 2018. The animals were filmed with full HD video cameras. Relevant footage shows lions (*Panthera leo*), leopards (*Panthera pardus*) and tigers (*Panthera tigris*) displaying a range of facial expressions with variable exposure of the upper canines, including relaxed mouth, yawning and growling. These observations provide a more complete information about the changing spatial relationship between the teeth and the oral soft tissue than we had previously gained from dissected specimens, where the behaviour of inert tissues differed from the condition of live animals in ways we could not fully assess at the time. Estimates of jaw gape aperture were obtained analysing the captured video frames with the software ImageJ 1.53k.

To complement the observations on the fossils and on the live animals, we conducted new studies on dead specimens that allowed us to check anatomical details of the structures filmed and photographed in the wild specimens. We performed a CT Scan of the intact head of an adult Sumatran tiger, *Panthera tigris* (MAR 6198) with remarkably long and intact upper canines, intact lower right canine, and broken lower left canine. We also examined existing CT scans of a leopard (*Panthera pardus*) and a jaguar (*Panthera onca*) previously performed at the Hospital Universitario de Valladolid (Spain), which allow general observations about bone-soft tissue relationship but only limited observations about the upper canine since the specimens' canines were broken and/or heavily worn. The CT scans of extant pantherin specimens were performed on a helicoidal CT scanner (Somatom, Siemens) at the Hospital Universitario de Valladolid with a resolution of 0.488 mm. After scanning, the tiger head was dissected and manipulated, which allowed us to observe the ability of the oral soft tissues to accommodate such large canines. The dissection was carried out at the department of Anatomy and Radiology, Faculty of Medicine, University of Valladolid, and it was documented through photographs and live sketches. We also examined comparative specimens from the collections of the MNCN-CSIC, including two adult individuals of *Panthera tigris* (MNCN-COMP 255) and *Panthera leo* (MNCN-COMP 254).

Life reconstructions of sabre-toothed felids were created with a combination of techniques including 3D modelling in BLENDER 2.77, and 2D drawing in pencil and in Adobe Photoshop Elements. We created a virtual, simplified 3D model of the skull and mandible of *Homotherium latidens* based on the Perrier specimen and other fossils, which has several advantages to serve as a basis for life reconstructions, including the restoration of an idealized symmetry and the possibility of rotating the mandible around the glenoid articulation to fit any angle of jaw aperture. Drawing of soft tissue layers on top of skeletal elements was done with vellum paper for traditional art and in separate layers for digital drawing. The reconstruction of head and neck muscles was based on the study of muscle attachment areas on the bone where available, while other soft tissues, like cartilage and skin, were restored on the basis of comparisons with closely related extant taxa and on the application of the Extant Phylogenetic Brackett methodology (Antón and Sánchez, 2004). The dissections, in combination with published descriptions of felid anatomy (Barone, 1967, 2010) allow us to establish the presence of osteological correlates of the soft-tissue elements that we intended to reconstruct in *Homotherium* (Antón et al., 2009). The process starts with the reconstruction of the muscles of mastication, which are the most important elements to restore the three-dimensional volumes of the living head, and whose attachment areas in the skull and mandible are clearly recognisable. In contrast, most facial muscles are thin and their attachment areas on the bone, when present, are not marked by such striking features as in the case of masticatory muscles, but their location on concrete areas of the skull and mandible is relatively constant in modern felids and other carnivores, so in order to reconstruct them we infer a similar location for their attachments in the case of *Homotherium*. Other soft tissue features which have osteological correlates include the cartilaginous ears, with the incisura intertragica located slightly dorsal to the external auditory meatus, and the cartilaginous nose, with the rhinarium placed rostro-dorsal to the premaxilla and the upper incisor row, as established in our previous dissections of felids (Antón et al., 1998, 2009). Reconstruction of different facial expressions and mandibular gapes was attempted with the help of the hand-sculpted virtual 3D model, which was rendered at different angles and with different gapes of jaw aperture to fit the different facial expressions observed in the modern pantherines that have served as reference for this study. Since the range of reconstructed gapes illustrated in this study reflects the jaw apertures displayed by the wild extant felids observed by us, even the relatively wide gape shown in the reconstructed yawn, is far from the maximum apertures inferred for sabre-toothed cats.

3. Results

3.1. Anatomy of Homotherium

The *Homotherium* skull from Perrier is among the largest specimens ever recorded (Koufos et al., 2020) (Fig. 1), and it broadly coincides in size and relative proportions with the larger,

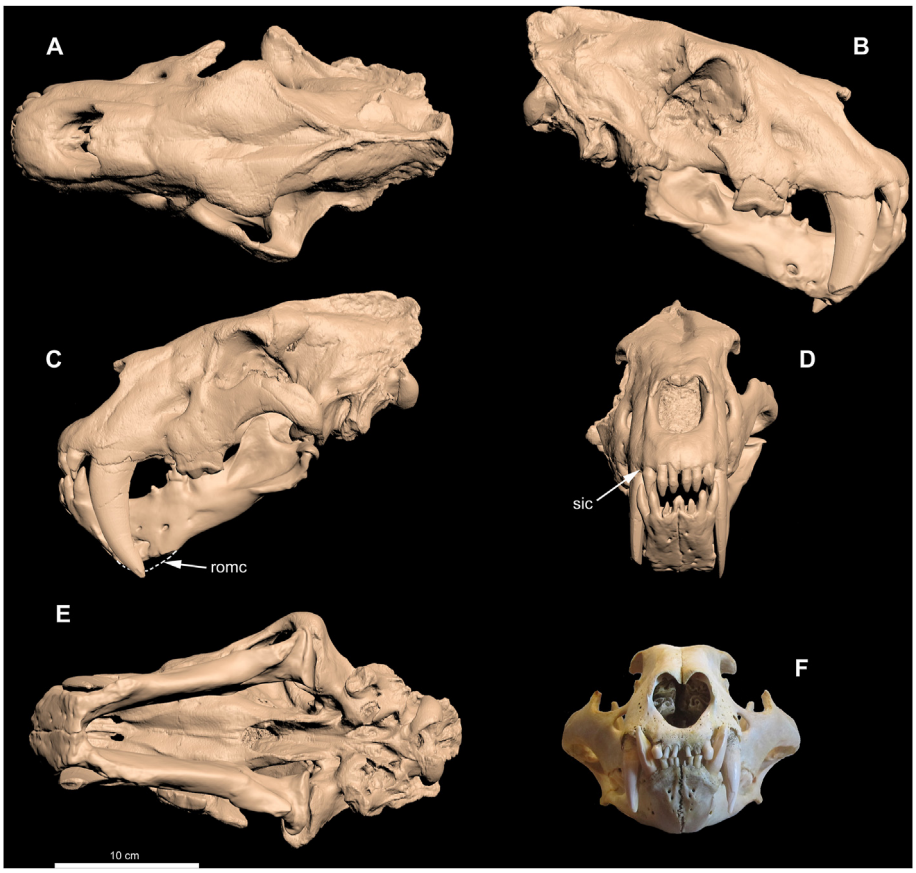

Fig. 1. 3D model based on CT Scan images of skull with associated mandible and cranial cervical vertebrae of *Homotherium latidens* (MNHN.F.PET 2000 a & b) from Perrier, in dorsal (A) right lateral (B), left lateral (C), rostral (D) and ventral (E) views, and (F) skull and mandible of tiger, *Panthera tigris* (MNCN-COMP-255) in rostral view; (sic) space between the upper third incisor and the upper canine (sic); (romc), reconstructed outline of mental crest.

presumably male skull IN-I-825 from the Early Pleistocene site of Incarcal (Spain) (Galobart et al., 2003), which is thus geologically younger (Table 1).

The size of the cervical vertebrae relative to cranio-mandibular dimensions in *Homotherium* is larger than in pantherin cats and indicates the presence of a long neck, as shown by the known cervicals yielded by the fossil sites of Senèze (France) (Ballesio, 1963) and Incarcal (Antón and Galobart, 1999), and also in line with the condition observed in the much earlier, late Miocene homotherin *Machairodus aphanistus* from Batallones-1 (Spain) (Antón et al., 2020). Such a proportionally long neck would be a noticeable feature in the living animal, with proportions intermediate between those of the relatively short-necked pantherins and the long-necked hyaenids.

In dorsal view (Fig. 1A) the skull from Perrier is narrower, relative to its length, than that of modern pantherins, especially at the level of the zygomatic arches. The muzzle is long, with the upper incisors projected in a wide arch and the upper canines separated by a relatively narrow distance; the sagittal crest is prominent and extends directly from the point where the post-orbital crests meet. In lateral view (Fig. 1B–C), the enormous development of the upper canines is noticeable; the dorsal outline of the skull is relatively straight, with the nasal bones and the sagittal crest almost in the same plane; the mastoid process is enlarged and projected rostroventrally while the jugular process has little prominence. In rostral view (Fig. 1D) the incisor row is wide, with the third incisor on each side obscuring from view part of the upper canine.

The mandible from Perrier displays a deep horizontal ramus, with a well-developed ventral symphyseal (or mental) crest (Fig. 1B–C), differing in this feature from other, generally smaller specimens, which tend to have lower rami and less developed mental crests (Antón et al., 2014). The margin of this crest is slightly damaged in the Perrier specimen but can be reconstructed confidently (Fig. 1C) with reference to other large specimens such as IN-I 1057 from Incarcal (Antón et al., 2014). When the mandible is

Table 1
Cranial measurements in mm of *Homotherium latidens* (Owen, 1846) from various Eurasian localities taken from Koufos et al. (2020).

Taxa	Skull basal length	Max breadth at zygomatic arches
Dafnero DFN3-152	251.5	140
Incarcal IN-I-929	305.0	175
Incarcal IN-I-825	287.0	195
Incarcal IN-II-37	260	170
Senèze FSL 210-991	275	185
Perrier MNHN.F.PET2000a	300	200

virtually articulated with the skull, the upper and lower incisors and cheek-teeth show a tight occlusion, suggesting that the relative positions of the maxilla, mandible and dentition are similar to their anatomical arrangement in life during mouth closure. In this position, the tips of the upper canines would protrude ventrally several millimetres below the ventral margin of the mental crests.

The interlocking of the upper and lower incisors is tight, with the lower canines becoming functionally part of the lower incisor battery. In rostral view it is evident that the upper canines occupy a position only slightly more lateral (buccal) than the lateral or third upper incisors, with the lingual side of the former being in a more lingual position than the buccal side of the third incisor, and thus actually overlapping. This is in contrast with the condition observed in modern pantherins (Fig. 1F) where the upper canine, as seen in rostral view, occupies a much more lateral position than the third incisor and is separated from it by a perceptible distance. This difference stems from the combination of a very wide incisor row and a narrow separation between the upper canines in *Homotherium*. A consequence of this conformation is the fact that the upper canine crowns are situated very close to the lateral side of the mandibular flange all along their length, leaving little room in between (Fig. 1D).

3.2. Observations of wild felids

Relevant video footage of wild pantherins includes an adult male African lion yawning and an adult female baring her canines during a growl, an adult female African leopard transitioning from relaxed face to yawn, and a female Indian tiger with a relaxed face. Frames of the video of the yawning lion show how the lower lip, stretched when the jaws are gaping with a gape of approximately 50° (Fig. 2A), actively contracts during the final stages of the yawn, thus enveloping the crown of the upper canine as the mouth closes (Fig. 2B). This observation contradicts our previous assumption, based on the observation of dead specimens, that the distal tip of the upper canine was always exposed laterally to the lower lip when the mouth was closed, and covered only by the overhanging upper lip. The video of a lioness growling further reveals that, as the lips contract after the growling gesture (Fig. 2C–D), the tip of the upper canine is first partly enveloped by a tongue-like fold of tissue adjacent to the margin of the lower lip, and then it is finally covered by the lower lip proper (Fig. 2E).

The video of the yawning leopard shows very clearly the structure of the relaxed lower lip previous to the yawn. One video frame (Fig. 2F) shows the two-layered structure of the lower lip, including an external, continuous layer which we can define as the margin of the lower lip proper, and an internal section that includes the tongue-like fold that envelopes the upper canine distally when the mouth closes. In a more relaxed position, with jaws slightly open, the margin of the lower lip hangs ventrally (Fig. 2G).

The video of the relaxed tigress shows more clearly the shape of the lower lip in rostrolateral and rostral views. In rostral view (Fig. 2H) the margin of the relaxed lip is seen to rest in a lateral position relative to the mandible, and it allows enough space, buccal to its external margin, for the crown of the upper canine to fit in once the jaw closes. In a rostrolateral view (Fig. 2I), this video shows the overlapping tips of the upper and lower canines, as well as the position of the relaxed upper lip that covers from view the entire upper canine crown.

3.3. CT scans of extant felids

The CT scan of the head of the adult Sumatran tiger shows the position of the oral tissues relative to the bone when the mouth is closed with the teeth in occlusion (Fig. 4). A thick mass of skin and connective tissue is apparent in a rostroventral position relative to the mental region of the mandible (Fig. 3A–B). With the jaws in occlusion, the crowns of the upper canines appear level to the ventral margin of the mandibular symphysis. In relation to the soft tissues, the upper canine crown is exposed when the lips are in the relaxed position shown in the scan. The rim of the lower lip hangs laterally and curves ventral to the canine tip (Fig. 3C).

The scanned specimens of *Panthera pardus* and *Panthera onca* (Fig. 4) have their canines broken and/or heavily worn, so that it is impossible to make comparably detailed observations about the relative positions of lower lip and upper canines. Otherwise, the observable disposition of the oral tissues relative to the bone appears similar to that seen in the tiger. Like the tiger, both specimens display a thick mass of connective tissue rostroventral to the mandibular symphysis.

3.4. Dissection

The dissection of the specimen of an adult Sumatran tiger allows us to observe and manipulate the oral tissues and to add detail to our previous observations of live animals. Relative to the position captured in the scan, it is possible to manipulate the rim of the lower lip in the still intact specimen (Fig. 5A), pulling it gently in dorsal direction until it covers from view the tip of the upper canine. Such a position of the lower lip is comparable to the one observed in the filmed lion (Fig. 5C) when the mouth is closed after yawning.

A detailed examination of the lower lip reveals its complex structure, especially around the area where the upper canine fits during closure of the mouth. In a lingual position relative to the margin of the lip there is a loose, tongue-like fold of flesh, which can be manipulated to be placed lingually or buccally relative to the upper canine when the mouth is closed (Fig. 5B). This fold of tissue corresponds to the structure observed in the living wild felids, and seen most clearly in the images of the growling lioness (Fig. 2D). When the skin is removed, the conformation of the lips and associated musculature is visible (Fig. 5C). As observed in the CT Scan, dissection confirms the presence of a thick layer of skin and connective tissue rostroventral to the mandibular symphysis (Fig. 5D).

4. Discussion

4.1. Skull morphology and evolution

The similarity in size and relative proportions of the skull of *Homotherium* from the Late Pliocene site of Perrier with the largest specimen from the Early Pleistocene locality of Incarcal, geologically younger (de Bonis, 1976; Antón and Galobart, 1999) indicates the persistence of such large, robust individuals for at least 2 million years in the fossil record, which suggests they are just at the extreme of the range of sexual and individual variation shown by this large machairodontine. The skull from Perrier displays proportionally and absolutely huge upper canines, which are in contrast with the very specialized but rather small ones observed in late Pleistocene specimens, especially those coming from North

Fig. 2. Frames of videos of wild pantherins showing different facial expressions. Lion yawning: (A), with jaws at wide gape and lips distended (lm, lip margin); (B), jaws almost closed, lips contracted, upper canine tip already enveloped by lower lip margin; Lioness growling: (C), jaws moderately open, canine crowns slightly overlapping, tongue-like fold of tissue (tf) covering diastema; (D) jaws closing, canine crowns overlapping extensively, tip of upper canine partly covered by tissue flap; (E) jaws closing further, upper canine tip covered by outer margin of lower lip (lm); Leopard yawning: (F), jaws gaping, lower lip margin (lm) distended, tissue fold (tf) showing buccal to lip margin; (G) moderate gape, lip margin (lm) less distended. Relaxed tigress: (H), frontal view, jaws moderately open, relaxed lower lip with outer margin (lm) hanging ventrolaterally, allowing visible space between the lip margin and the side of the mandible; (I) rostrolateral view, showing slight overlap between upper and lower canine tips (ct) and relaxed, hanging upper lip (ul) covering the upper canine from view from the sides.

America and included in the species *Homotherium serum*. The morphology of the Perrier mandible, with very high ramus and symphyseal region, also resembles the large specimen from Incarcal, suggesting that such mandibular shape can be related with large size and large upper canines.

Earlier, large members of the homotherin clade show a gradual evolution of the morphology of the mesial dentition, premaxilla and symphyseal region, starting with the Vallesian species *Machairodus aphanistus,* which had small upper and lower incisors arranged in a row, relatively large lower canines, and an angular symphysis but hardly any flange (Antón et al., 2004). In the geologically younger *Amphimachairodus giganteus* the incisors are larger and arranged in a protruding arch, the lower canines are smaller, and the flange is more pronounced (Sotnikova, 1992). *Homotherium* culminates the trend, with a more exaggerated rostral projection of the incisors, reduction of the lower canines, and presence of a marked mental flange.

4.2. Soft tissue structure

Our films of facial expressions in wild felids reveal a greater versatility of the oral soft tissue, and of the lower lip in particular, than we had assumed based on our previous observations, largely of dissected specimens. The footage of the yawning lion shows how the action of muscles pulling the lips backward and those closing them around the oral cavity allow the animal to expose or cover its teeth and, more specifically, its upper canines, at will. When the mouth is closing, the tips of upper canines are seen to be covered by the lower lip as it contracts, an effect visually comparable to that of a knife being sheathed. This action is probably powered by the contraction of the orbicularis oris muscle, but it involves more complex movements, such as those of the tongue-like flap on the lingual part of the lower lip. This structure is seen to adapt in different ways to the proximity of the upper canine crown, adopting either a lingual or a buccal position.

4.3. Anatomical reconstruction

The anatomy of the Perrier skull agrees with that of other specimens of *Homotherium* in the configuration of the major muscle attachment areas, supporting our previous reconstruction of the musculature of the head and neck (Antón et al., 2009). The high sagittal crest contributes to provide the large attachment area for the temporalis muscle, while the reduced coronoid process of the mandible houses the attachment of both temporalis and masseter, the latter muscle extending from the ventral rim of the

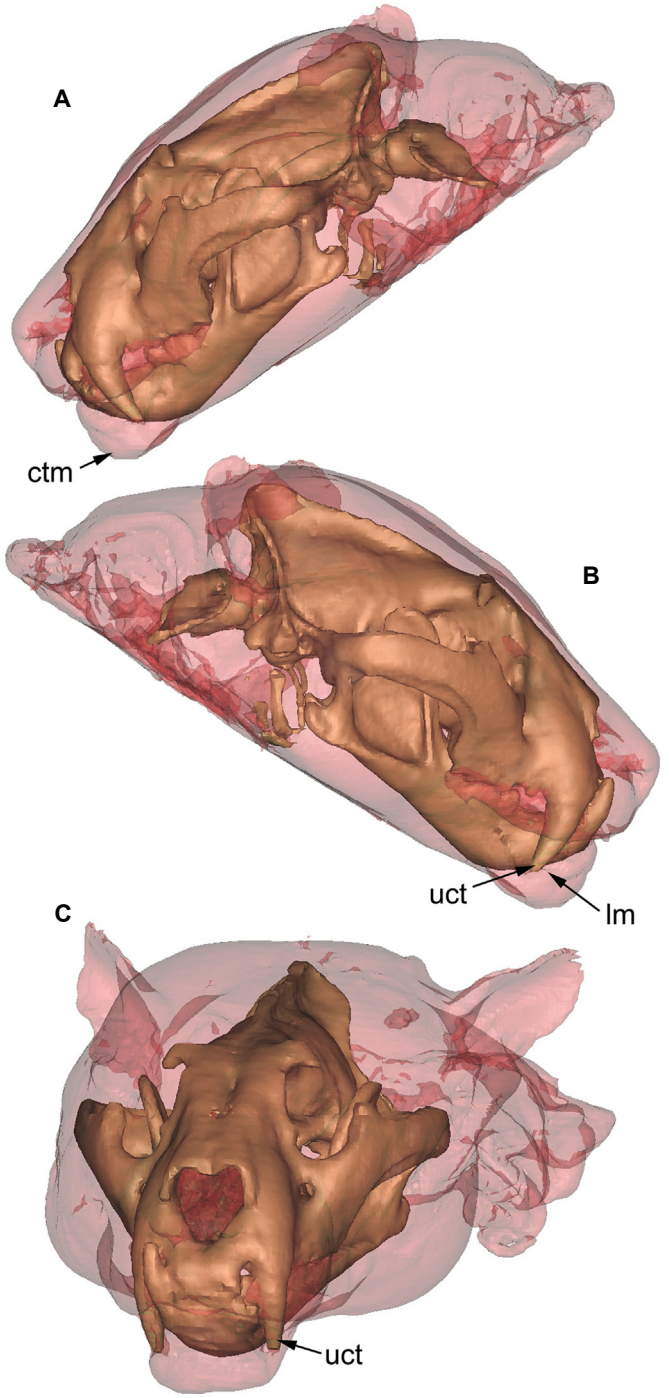

Fig. 3. 3D model based on CT Scan images of the head of an adult male Sumatran tiger (*Panthera tigris*). (A), left lateral view; (B), right lateral view; (C), rostrolateral view. Note the connective tissue mass (ctm) rostroventral to the mandibular symphysis, and the lower lip margin (lm) folded ventral to the exposed upper canine tip (uct).

zygomatic arch to the masseteric fossa (Fig. 6B and C). These two muscles would largely define the three-dimensional volumes of the head of the living animal, while the digastric ran between the ventral side of the mandible and the jugular process of the skull. Other, thinner muscles of the head leave little or no recognisable marks on the bone, and in order to reconstruct them it is necessary to transfer the condition observed in modern relatives. One muscle

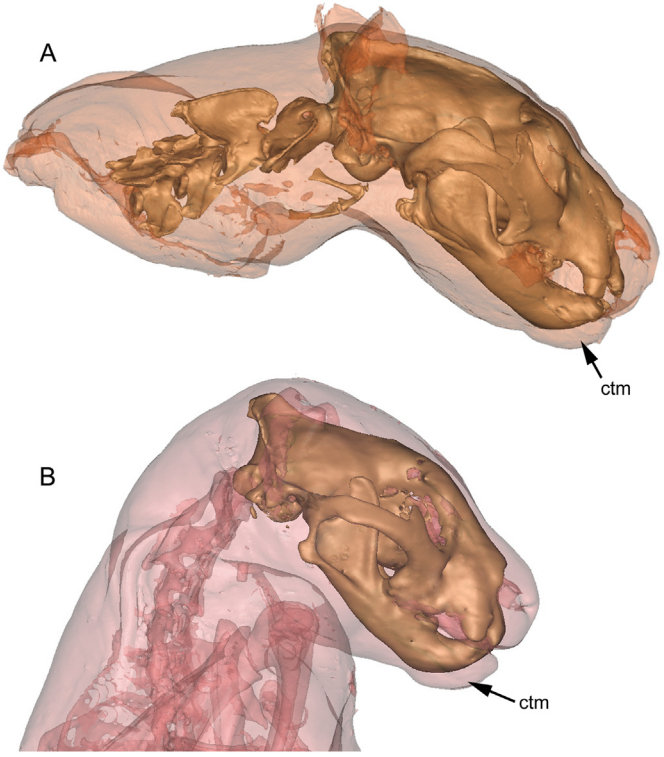

Fig. 4. 3D model based on CT Scan images of the heads of extant pantherins. (A), adult jaguar (*Panthera onca*), (B), adult leopard (*Panthera pardus*). Note the presence of a thick mass of connective tissue rostroventral to the mandibular symphysis in both animals.

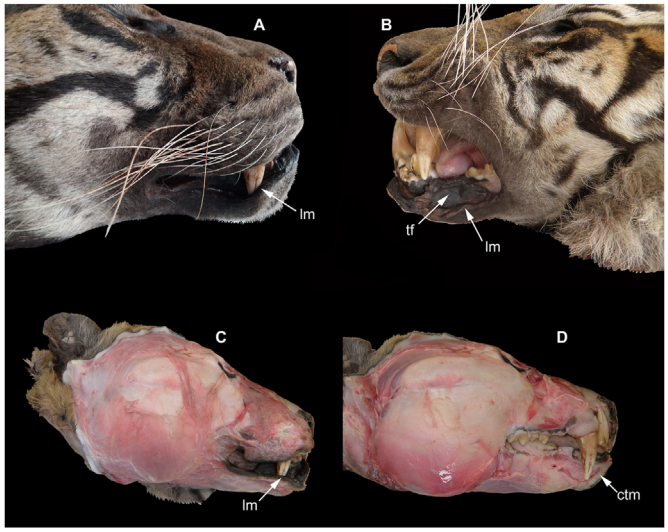

Fig. 5. Photographs of the dissected head of an adult male Sumatran tiger (*Panthera tigris*). (A), right side view of the intact specimen showing how the margin of the lower lip (lm) can envelope the tip of the upper canine crown; (B), left side view of the intact specimen, showing the relaxed lower lip that reveals its complex structures, including the external margin of the lip proper (lm) and the internal tongue-like fold of tissue (tf); (C), right side view of the head after removing skin from that side, with the lower lip (lm) still in place and covering the tip of the upper canine; (D), right side view of the head after removing the skin and lips from that side. The thickness of skin and connective tissue on the chin, still in place on the left side (ctm), is visible cranioventrally to the mandibular symphysis.

that is especially relevant for the reconstruction of the range of positions and expressions of the soft tissue of the face and mouth is the levator nasolabialis, which in modern felids attaches to the area immediately rostral to the orbits, its fibres extending rostroventrally and interlacing with those of the orbicularis oris. We infer a similar position for the attachment of this muscle in *Homotherium* (Fig. 6B, D). Non-muscular soft tissue structures also relevant for reconstruction include the cartilaginous nose, which in modern felids extends rostrally from the nasal bones to a point in front of the premaxilla (Fig. 6C), and the mass of connective tissue rostroventral to the mental area of the mandible, which we reconstruct in *Homotherium* with a position and thickness comparable to that observed in the dissected felids (Figs. 5D and 6C). Regarding the oral muscles and lips, our detailed observations about the position of the mesial dentition and the morphology of the maxilla and mandible suggest a different arrangement than initially thought. The extent and general conformation of the orbicularis oris muscle would follow the pattern observed in modern pantherines and transferred by us to *Homotherium* in previous works (Antón et al., 2009), but with a relevant difference: given the tight fitting of the upper canines relative to the mandible, it seems unlikely that the fibres of that muscle and the soft tissues of the lip would fit in that narrow space during mouth closure. Combined with our observations about the fitting of the upper canines within the lower lip in living pantherins, this suggests that when the mouth of *Homotherium* was closed, the upper canines could be covered by the lower lips (Fig. 6D–E, and 7A-B). Additionally, if a thick layer of skin and connective tissue was present rostroventrally to the mandibular symphysis in *Homotherium*, as observed in the dissected tiger, this could add to the ventral depth of tissue providing more room to fit the apical portion of the upper canine crown during mouth closure. We infer a similar absolute thickness for this layer of tissue in *Homotherium* as in *P. tigris* (Fig. 5D), given the similar body size of both animals and the lack of clear osteological indications for a difference in its thickness.

The reconstruction of different facial expressions and mandibular gapes was attempted with the help of the hand-sculpted virtual 3D model, rendered at different angles and with different gapes of jaw aperture to fit the facial expressions observed in the modern pantherins that have served as reference for this study. The illustration of *Homotherium* in a relaxed attitude (Fig. 7C, F), shows how the hanging tissues of the relaxed lower lip could reveal much of the crown of the upper canine given a moderate gape, comparable to that of the relaxed tigress (Fig. 2I–J). During a yawn, with a gape similar to that in the male lion from Fig. 2A, *Homotherium* (Fig. 7G) would reveal the full size of its upper canines. In a snarling gesture (Fig. 7H), the tip of the upper canines crown would be already covered by the lower lip proper, while the tongue-like fold of flesh would be pressed against the buccal and distal edge of the tooth.

Concerning the possibility that a Palaeolithic statuette from Isturitz is a representation of *Homotherium*, as discussed in a previous work (Antón et al., 2009), our new results lead us to reconsider our conclusions from that time. While some objections stand, especially those concerning body proportions as depicted in the sculpture, our previous arguments about the visibility of the upper canines in the living animal are clearly put in question by our current observations.

4.4. Comparison with other machairodontines

Some of the osteological features discussed here in relation with the reconstruction of life appearance differ among the different taxa of machairodontine felids. For instance, the width of the premaxilla between the upper incisors in *Homotherium* is very large compared to the moderate width of the maxilla between its upper canines. In the smilodontin genus *Smilodon* however, the upper incisor row and the premaxilla are relatively narrower (Fig. 8A–B), resembling to some degree the condition observed in pantherin cats (Merriam and Stock, 1932). The relatively larger width of the maxilla in *Smilodon*, combined with a narrow symphyseal region in the mandible, allows for more space between the lingual side of the upper canines and the lateral margin of the mandible, giving room for the lips and the orbicularis muscles to run buccal to the upper canine crowns. In ventral view, the rostral part of the mandible of *Homotherium* is wide and almost rectangular, while in *Smilodon* it is narrow and distinctly V-shaped (Fig. 8C–D). These differences fit well with the hypothesis of exposed canines in *Smilodon* (Antón et al., 1998). Among extant mammals, taxa with hypertrophied upper canines that are exposed in life with the mouth closed such as walruses, musk deer or mouse deer all have narrow symphyseal areas separated widely from the buccal side of the upper canines, leaving ample space for lower lips and associated soft tissues (see below) (Terai et al., 1998; Kastelein, 2009; Meijaard, 2011).

The cranial morphology of homotherin felid genera from the Late Miocene, such as *Amphimachairodus* and *Machairodus*, agrees more with that of *Homotherium*, suggesting in turn the presence of upper canines covered in life.

Members of the smilodontin genus *Megantereon* display a diversity of morphologies with varying degrees of mental projection. A trend toward a more reduced projection may be present, leading to the morphology of early *Smilodon* taxa like *S. gracilis* where the upper canines are too high-crowned and the mental flange too reduced to fit with each other. Examples of possible transitional stages could be found among Chinese specimens attributed to *M. nihowanensis*, including an associated skull and mandible from Longdan figured by Lewis and Werdelin (2009), where the upper canines are so long that they appear to protrude well below the ventral margin of the mental flanges. Another skull recently described from Chongzuo in Southern China (Zhu et al., 2020) displays excellent three-dimensional preservation and reveals a wide maxilla with ample space between the upper canines, and a relatively narrow incisor row, features that resemble *Smilodon*. Ultimately, only a detailed study of skulls and mandibles with good three-dimensional preservation will allow to establish if at least in some species of *Megantereon* there would be enough space between canines and flanges to fit the lips when the mouth was closed.

Other carnivorans that have convergently evolved sabre-tooth morphologies include the Nimravidae and the Barbourofelidae. In both families, taxa with very high-crowned canines also display mental projections to match. In view of our observations about *Homotherium*, it is feasible that in those taxa the lower lip could cover the upper canine tips in life when the mouth was closed. It appears feasible that the presence of deep mental flanges is indicative of an anatomical adaptation to keep the oral cavity sealed in animals with high-crowned canines which grow vertically (leaving insufficient space for the lips between the canines and the

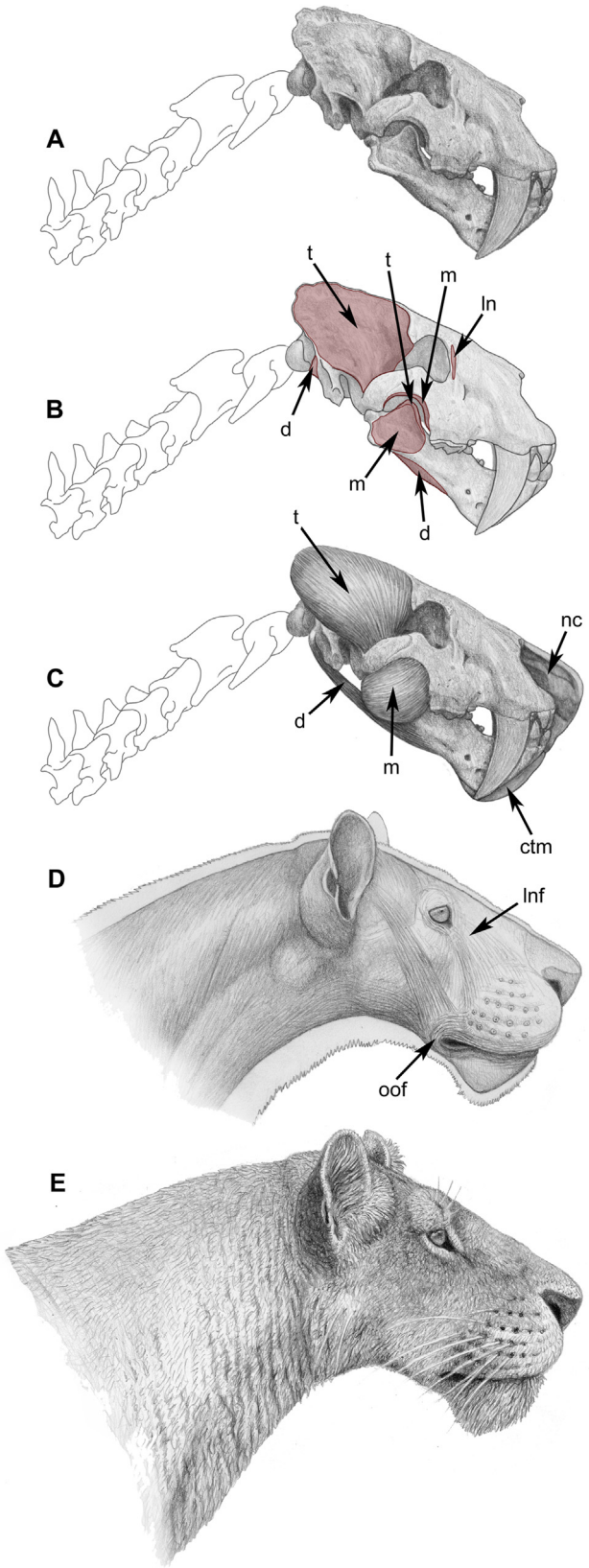

Fig. 6. Reconstruction of *Homotherium latidens* based on the fossil specimen MNHN.F.PET 2000 a & b from Perrier: (A), lateral view of skull and mandible with slight restoration of the ventral outline of the mental crest, and cervical column (this latter a schematic outline based on fossils from Senèze and Incarcal); (B), outline of cranio-cervical skeleton, showing the attachment areas of selected muscles including the temporalis (t), masseter (m), digastric (d) and levator nasolabialis (ln); (C), reconstruction of selected elements of soft-tissue anatomy including the muscles temporalis (t), masseter (m) and digastric (d), as well as the bisected nasal cartilage (nc) and the bisected mass of connective tissue rostroventral to the mental region of the mandible (ctm); (D), reconstruction of the superficial craniocervical musculature, showing fibres of the levator nasolabialis muscle (lnf) and of the orbicularis oris (oof); (E), reconstructed external appearance of the head and neck (Artwork by M. Antón).

mandible) and in which the canines are not used with the mouth closed. The flanges provide a rigid surface against which canines get sheathed without piercing dangling soft tissues. Sabre-toothed predatory mammals, not only carnivorans, but also creodonts and even metatherians, display mental flanges broadly matching the height of the upper canine crowns, but there is a range of differences in the fit between the flanges and the upper canines that suggest potentially different arrangements of the corresponding soft-tissue structures. For instance, the symphyseal region of the mandible appears constricted at the level of post-canine diastema in all sabre-toothed carnivorans when seen in occlusal view, which is logical since the upper canines fit there during occlusion. But in some taxa, like for instance in derived members of the Barbourofelid genus *Barbourofelis*, that constriction appears to be so pronounced as to suggest that it might allow to fit the lips and orbicularis muscles between the mandible and the upper canines (Schultz et al., 1970). Again, as in the case of *Megantereon*, only a careful study of well-preserved skulls and mandibles can tell us more about the possible conformation of the associated soft tissues in those taxa. Within the herbivore order Dinocerata, the genus *Uintatherium* displays vertically oriented enlarged upper canines with mental flanges to match (Marsh, 1884). Among living mammals, long-tusked ruminants like musk deer (genus *Moschus*), and chevrotains (genera *Tragulus*, *Hyemoschus* and *Moschiola*) have long, subvertical upper canines which protrude outside the oral cavity and are used by males for intraspecific combat with the mouth closed (Meijaard, 2011). In these animals, the mandibular symphysis is much narrower than the maxilla, leaving ample space for soft tissue between the upper canines and the side of the mandible. A similar conformation is observed in the walrus, which also uses its enormous canines with closed mouth, and which also has a mandibular symphysis that is much narrower than the space between the upper canines (Kastelein, 2009).

5. Conclusions

A revised reconstruction of the soft tissue and life appearance of the sabre-toothed felid *Homotherium latidens* is proposed on the basis of the study of the anatomy of extant carnivorans and iconic fossil finds such as that from the Late Pliocene site of Perrier (France). The new study of this specimen provides revealing information about the morphology of the skull and mandible. Like other large, early specimens of *Homotherium* it has very large upper canines relative to skull and mandible size, and high-crowned enough to protrude beyond the lips in the living animal. When articulated, their occlusion reveals the tight interlocking of the mesial teeth and the mandible. This arrangement leaves only a very narrow space between the upper canines and the mental flanges of the mandible, making it unlikely that the lower lip and other oral soft tissues could fit in that space. On the other hand, observations of facial expressions in living big cats and dissected specimens show that, contrary to previous observations, the soft tissue around the mouth and the lower lip in particular can cover the upper canines of large felids, even when those are considerably high-crowned. This combined evidence leads us to hypothesize that, in life, the upper canines of *Homotherium* would be covered by the lower lips when the mouth was completely closed. This was the

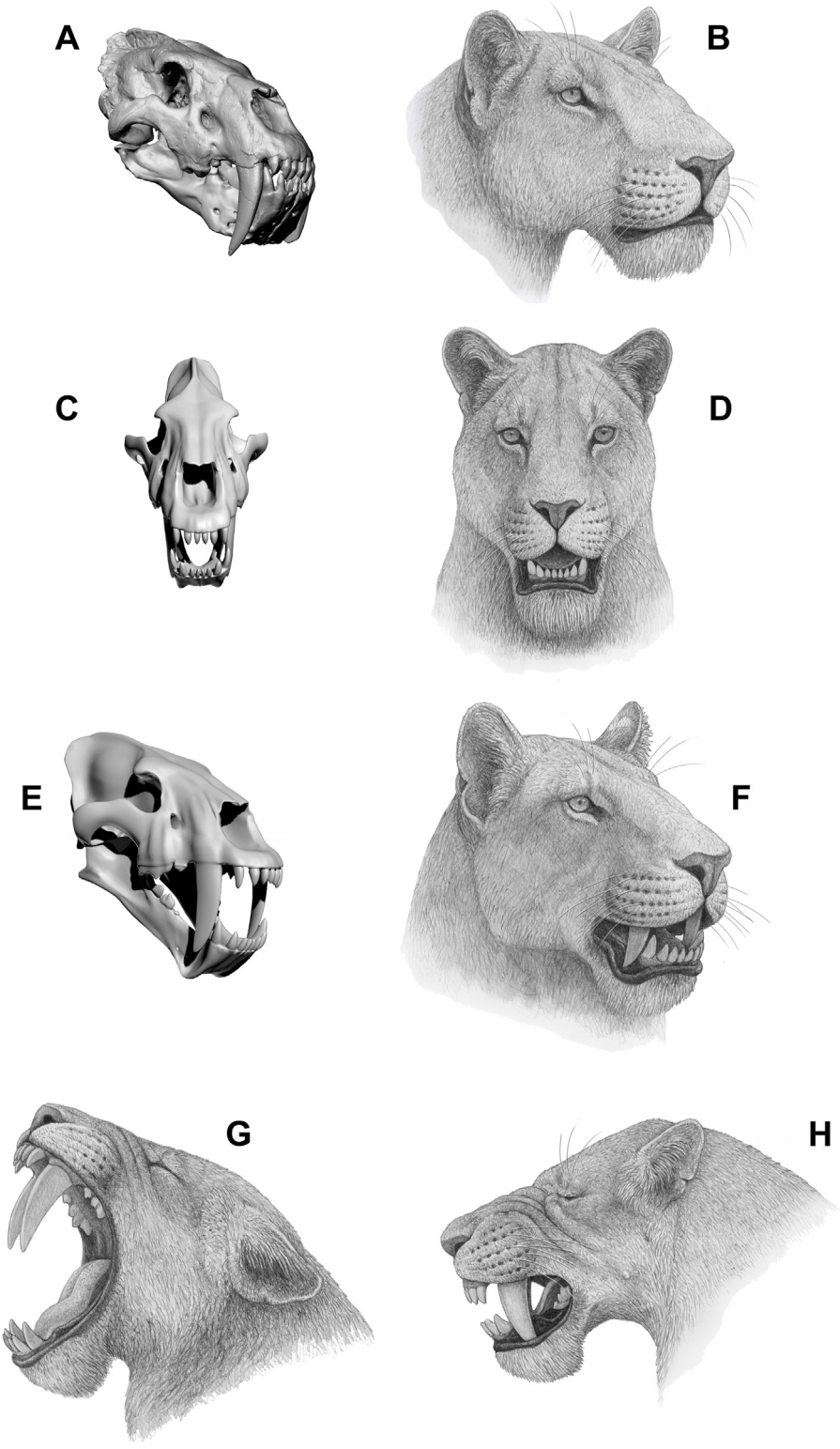

Fig. 7. Reconstruction of *Homotherium latidens* based on the fossil specimen MNHN.F.PET 2000 a & b from Perrier: (A) and (B), perspective view of skull from CT scan, and reconstructed head; (C) and (D), frontal view of idealized virtually sculpted skull and reconstructed head (Artwork by M. Antón). (E) and (F), perspective view with a relaxed expression comparable to that observed in modern tiger (*Panthera tigris*) shown in Fig. 2J; (G), lateral view of a yawning animal comparable to that observed in modern male lion (*Panthera leo*) shown in Fig. 2A; (H), lateral view of animal with slightly open jaws and lips contracted in a growling gesture comparable to that observed in modern lioness (*Panthera* leo) shown in Fig. 2D (Artwork by M. Antón).

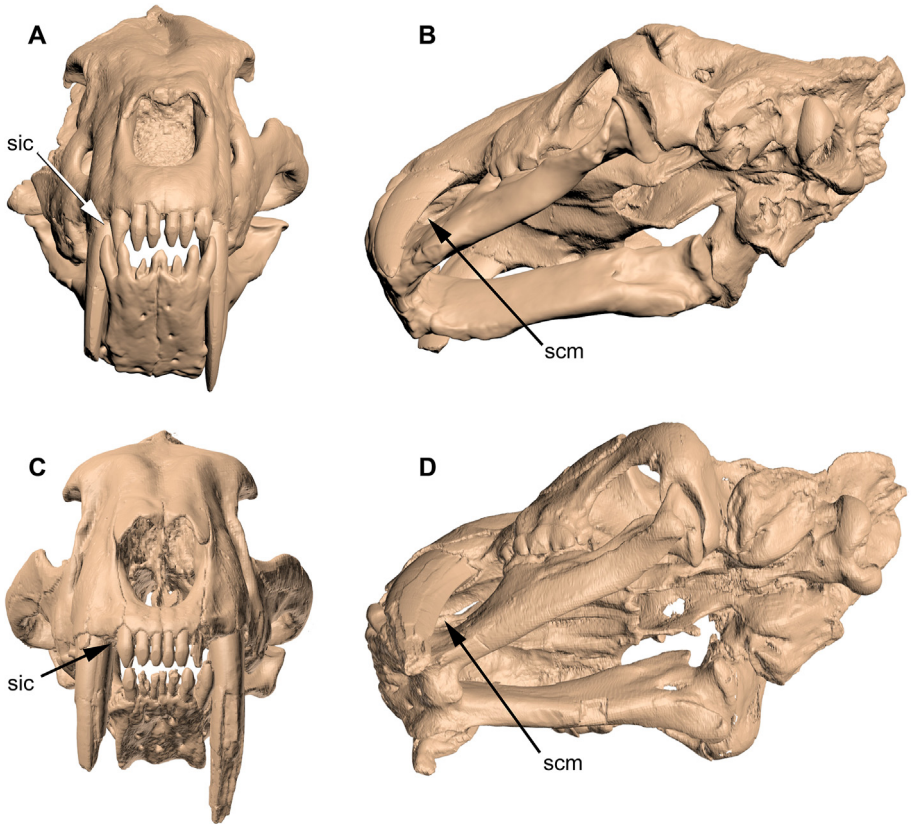

Fig. 8. Skull and mandible of *Homotherium latidens* (MNHN.F.PET 2000 a & b) from Perrier (A, rostral view; C, lateroventral view), and *Smilodon fatalis* (F:AM 14349) from Rancho La Brea (B, rostral view; D lateroventral view). Note the greater space between upper third incisor and upper canines (sic) in *Smilodon*, the greater space between the upper canines and the mental flange of the mandible (scm) in *Smilodon*, and the V-shape of the symphyseal region in lateroventral view in *Smilodon* in contrast to the subrectangular shape in *Homotherium*.

likely condition of other sabre-toothed felids where the mandibular flanges matched the crown height of the upper canines and were tightly fitting against their buccal side. In the case of *Smilodon*, with reduced flange and a less tight fit, it is likely that the upper canines would be exposed in life, even with a closed mouth. This new vision completely changes our image of the life appearance of the sabre-toothed felids, solves some anatomical incongruencies inherent to the previous hypothesis of exposed upper canines, and reinforces the necessity for anatomical studies on extant species in order to obtain physiological and structural data that support our interpretations on the paleobiology of fossil taxa.

Credit author statemenst

Mauricio Antón: Conceptualization, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Gema Siliceo**: Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Visualization, Review and editing. **Juan Francisco Pastor**: Data curation, Investigation, Validation, Review and editing. **Manuel J. Salesa**: Conceptualization, Formal analysis, Funding acquisition, Investigation, Resources, Supervision, Review and editing.

Data availability

Datasets related to this article can be found at the AST-RX platform, Muséum national d'Histoire naturelle (Paris, France) (http://www.ums2700.mnhn.fr/ast-rx/presentation) (for *Homotherium*), and www.morphosource.org/media/000009730, F:AM 14349, © American Museum of Natural History (for *Smilodon*).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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