

Pneumothorax as a predatory goal for the sabertooth cat (*Smilodon fatalis*)

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ABSTRACT

Smilodon fatalis was a large extinct felid distinguished by their two impressive maxillary canines and surprisingly low canine fracture rates. Previous theories regarding their attack strategy have suggested delivering damage by a bite with their maxillary canines. It has also been previously suggested that the canines could have been used to deliver a non-biting stab with an open jaw. It has been generally hypothesized that the attack was delivered to the neck of their large herbivore prey. *Smilodon fatalis* could have used their canines in a non-biting stab delivered with a closed jaw for the sole purpose of creating a pneumothorax. Creation of a pneumothorax would maximize immediate attack lethality, and minimize exposure of its canines to fracture.

Keywords: *Smilodon fatalis*; Sabertooth Cat; *Machairodontidae*; Pneumothorax

1. PERSPECTIVE

Smilodon fatalis (Sabertooth cat) was a large extinct felid easily distinguishable by the two elongated, curved, and laterally flattened maxillary canines called sabers. The canines of *S. fatalis* and the extant Bengal tiger (*Panthera tigris*) reflect the need for differing attack strategies (Figure 1). No extant cat with similar elongated canines survives in modern times leading to a debate on how *S. fatalis* used its canines. The robust nature of the *S. fatalis* maxillary canines with regards to their ability to generate force and resist torsional strain during a point-to-point bite or open-jawed stabbing action has been previously described [1-4]. It has also been suggested that *S. fatalis* used its maxillary canines to create a closed-jaw stab [5]. Manuscripts dating back to Warren in 1853 [6] have failed to consider whether creation of a pneumothorax in its prey could have been a predatory goal for *S. fatalis*. We propose that *S. fatalis* could have used its elongated canines in a closed-jaw fashion to cre-

ate deep paired punctures of the lateral aspect of the thoracic wall for the purpose of generating a lethal pneumothorax in its large herbivorous prey. The attack would have been quickly delivered, followed by a quick retreat after which the cat would wait for the prey to quickly asphyxiate (bilateral pneumothorax) or become partially incapacitated (partial/unilateral pneumothorax).

Pneumothorax is a pathophysiological condition characterized by the entry of air into the pleural cavity between lung and thoracic wall. An open pneumothorax occurs when a penetration of the thoracic wall reaches the pleural cavity and permits air to enter this space. The entry of air into the pleural cavity leads to a loss of negative pressure (vacuum) between lung and thoracic wall resulting in collapse of lung tissue. The collapse of all lung lobes (bilateral pneumothorax) leads to immediate asphyxiation, while partial collapse of some of the lung lobes (partial/unilateral) would lead to fractional losses in VO_2 max and a reduced ability to resist attack or flee from a predator.

The prey of *S. fatalis* included large herbivores such as *Equids* and *Bison*. *Equids* have a well known respiratory Achilles Heel consisting of an incomplete thoracic mediastinum across their pleural cavity such that a unilateral pneumothorax readily leads to bilateral lung collapse [7]. Native Americans of the Great Plains took advantage of a similar anatomical limitation in modern *Bison*, using an arrow delivered to the thoracic wall to create a pneumothorax in a manner similar to the human pathological



Figure 1. Representative images of cranium and mandible of sabertooth cat (*Smilodon fatalis*; left) and Bengal tiger (*Panthera tigris*; right).

condition called “Buffalo Lung” where unilateral pneumothorax leads to bilateral collapse [8]. The maxillary canines of *S. fatalis* extend far beyond the inferior aspect of the mandible when the jaw is closed. The maxillary canines in this condition could have been used to deliver paired deep punctures to the wide target area of a large herbivore’s mid-lateral thoracic wall for the explicit purpose of creating a pneumothorax.

The thorax of a large herbivore presents a large lateral surface with a thin wall that creates a large forgiving target for a penetrating blow delivered perpendicularly. In contrast, the carotid arteries of the neck represent a narrow target area and would require precise targeting [9]. The large barrel-shaped thorax of large herbivores provides inherent protection from biting or open jawed stabbing attacks.

Assuming 90 degrees of mandibular abduction, a bite or open-jawed stab across the wide angle of ribs cannot be delivered perpendicularly and would result in a glancing blow with a shallow angle of thoracic soft-tissue penetration due to obstruction of the mandibular incisors with the ribs. Obstruction of the mandibular incisors would make force-generation by a shearing point-to-point bite problematic and ever shallower as the radius of the thorax and size of these large herbivores increased [1]. If an open-jawed stab was delivered to the lateral thorax, once again the force delivered to the thorax would be glancing at best due to obstruction of the mandible and mandibular incisors resulting in at best shallow penetration and reduced opportunity to penetrate the pleural cavity. While the incisors of *S. fatalis* are robust [10], the incisors were probably used in a point-to-point bite only after the prey had been incapacitated (dead) as a result of a pneumothorax.

Breakage patterns suggest that the sabers of *S. fatalis* were used in a different fashion relative to other large predators that co-existed at the same time and are known to use their canines to deliver a classic point-to-point bite. *Panthera tigris* (Bengal tiger) is an extant cat well known to attack the neck and kill by applying a clamping point-to-point bite to the neck [11]. The cranially similar *Panthera atrox* (American lion), *Canis dirus* (dire wolf), and *Canis latrans* (coyote) were predators at the Rancho La Brea Tar Pits that lacked saber-shaped canines, and had canine fracture rates of 32%, 24%, and 18.8%, respectively. In contrast, *S. fatalis* at La Brea had a canine fracture rate of only 10% [12]. Delivery of the *S. fatalis* attack perpendicularly to the lateral aspect of the thoracic wall could have helped to protect their elongated canines from fracture by providing a larger and more forgiving area of lethality than the carotid area of the neck. This type of attack would potentially decrease the number of times a cat(s) might need to attack its prey, therefore reducing the number to times that the teeth could have

been exposed to potential fracture from prey torsion, bone contact or prey retaliation during an attack.

Smilodon fatalis preyed upon the extinct paleolithic bison (*i.e.* *Bison occidentalis*), so examination of a fresh carcass to determine if the maxillary canines could penetrate deeply enough to enter the pleural cavity and create a pneumothorax is impossible. As a substitute, carcasses of modern North American bison (*Bison bison*; 3 steers and one cow; 418 ± 98 kg; 2-year-old) were examined at a local abattoir (Ledebuhr Meats, Goodview, Minnesota, USA) to estimate the distance the canines would need to penetrate in order to create a pneumothorax in its prey. The distance across skin and intercostal muscles to the pleural cavity between ribs 7 and 8 was 19.2 ± 2.7 mm. A canine of *S. fatalis* has been observed to penetrate 85 mm into another *S. fatalis* skull in an attack that probably required a closed jaw [5]. A similar depth of penetration to the thoracic wall would create a 66 mm deep laceration (85 mm - 19 mm) within the spongy lung tissue of the pleural cavity.

Smilodon fatalis would have needed to avoid canine-bone contact in order to reduce the risk of canine fracture. In modern bison, the lateral thorax between ribs 5 and 9 is associated with the thinnest thoracic wall. A representative skeleton of a large extinct *Bison occidentalis* (Science Museum of Minnesota, St Paul, MN, USA) had an average rib width of 3.3 ± 0.3 cm (T5-T9), and the space between the medial surfaces of the two maxillary canines of *S. fatalis* was 8.0 ± 1.8 cm ($n = 4$; images obtained from Science Museum of Minnesota, St. Paul, MN and George C. Page Museum, Los Angeles, CA, USA). This would allow the canines to straddle a rib with 130 degrees of rotational error where no tooth-rib contact would occur. The gap between bison ribs (4.4 ± 1.4 cm) would permit 2 cm of error on the anterior/posterior axis if a rib was straddled perpendicularly. These predator-prey characteristics would reduce the chance that a canine would strike bone (rib) during the closed-jaw stab and this would have reduced the chance of canine fracture as was mentioned previously [12].

Smilodon fatalis was a cat with exceptional forearm strength that was probably used to knock down its prey prior to using its canines [13]. Making prey stationary in this manner could arguably improve the ability of the cat to aim its strike at the narrow carotid region of the neck, however it would dramatically improve the ability to strike at the larger more forgiving thorax. This would improve visual targeting to the soft-tissue between the ribs, compressing the underlying lung tissues, improving tissue penetration, and minimizing risk of damage to their canines. *S. fatalis* canine width was 31.9 ± 0.8 mm on the anterior-posterior axis at the midpoint between tip and alveolar margin ($n = 4$). Assuming a conservative 30 mm of additional cutting across the cutting edges of the

sabers on the angle of entry/exit, rather sizable paired openings (60 mm) to the thorax wall and underlying lungs would result in an open pneumothorax.

Homo sapiens is the only extant mammal that specifically uses the creation of a pneumothorax as a primary attack goal during predation of large herbivorous prey. The disappearance of *S. fatalis* and many of the large herbivores from North America paralleled the rise of the Clovis people 13,000 years ago who developed long fluted spear points [14] for the purpose of creating a pneumothorax. Modern broadhead arrows have a 30 mm cutting path that is commonly used to create a fatal pneumothorax in large herbivores. Paired closed-jaw stabs to the lateral thoracic wall by *S. fatalis* would, at a minimum, cause dramatic reductions in lung ventilation and VO₂ max, after which attack to the contralateral thoracic wall could occur with a greatly diminished ability to repel subsequent attacks and reduced risk of canine fracture, perhaps explaining the discrepancy in canine fracture rate observed by Valkenburgh & Hertel (1993) [12]. In a perfect attack on an *Equid*, a single strike to one lateral aspect would result in paired thoracic punctures and a bilateral pneumothorax that would be fatal in a matter of minutes.

Other predators with enlarged canines and cranial features with varying degrees of anatomical similarity to *S. fatalis* include the *Homotherium*, *Barbourrofelini*, *Hoplophoneus*, and *Thylacosmilus* to name a few. Their use of pneumothorax as an attack goal or the evolution of cranial morphologies leading to *S. fatalis* is of course beyond the scope of this brief manuscript. Shorter canines and mandibular phlanges could have obviously limited the potential to create a pneumothorax in the manner described. It is also known that younger members of *S. fatalis* had shorter and less elongated maxillary canines, as well as deciduous and adult canines in the same immature skull. Therefore, pneumothorax as an attack goal in younger members of *S. fatalis* would have been improbable. These younger cats were presumably, as with modern lions, dependent on other adults for food during their rise to hunting self-sufficiency [15].

In conclusion, it is surprising that to our knowledge no prior investigator has suggested that *S. fatalis* could have used its elongated canines for the purpose of creating a pneumothorax as an attack goal. Delivery of the stab with a closed jaw would be associated with a length of canine that would be sufficient to enter the thoracic wall and create a pneumothorax. Attack in this fashion could have reduced the duration of time that the canines of *S. fatalis* were exposed to prey retaliation, canine torsion, and fracture. This might help explain why the fracture rate of *S. fatalis* canines was lower than the fracture rate of other larger predators found at the La Brea Tar Pits. While it remains possible that the canines were used to

deliver point-to-point bites or open jawed-stabs as described by the many prior investigators, it is also very logical to propose that the attack goal could have been the creation of deep, paired thoracic wall punctures leading to bilateral pneumothorax and prey death.

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