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Evidence of intraspecific agonistic interactions in *Smilodon populator* (Carnivora, Felidae)

Preuve d'interactions agonistiques intraspécifiques chez Smilodon populator *(Carnivora, Felidae)*

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ABSTRACT

The saber-toothed cat *Smilodon* is a characteristic genus of the Pleistocene faunas of the American continent. *Smilodon* belongs to an extinct clade of felids that had hypertrophied blade-like upper canines. Because the length of the canines is so extreme, the killing bite of *Smilodon* is a hotly debated topic in vertebrate paleontology. Some authors have proposed that saber-toothed cats had a weak bite and their canines were fragile, not useful for attacking prey or penetrating bones. The aim of the present contribution is to describe two new specimens of *Smilodon populator* that have injuries on their skulls. Although it cannot be ruled out that the injuries were caused by a potential prey kicking the skull, the size, shape and general features of the injuries suggest that they were inflicted by the upper canines of another *Smilodon* individual during agonistic interactions.

RÉSUMÉ

Le chat à dents de sabre *Smilodon* est un genre caractéristique du continent Américain. *Smilodon* appartient à un clade éteint de félidés ayant des canines supérieures hypertrophiées en forme de lame. En raison de l'extrême longueur de ses canines, la morsure mortelle de *Smilodon* fait l'objet d'un vif débat en paléontologie des vertébrés. Certains auteurs ont suggéré que les chats à dents de sabre avaient une morsure faible et que leurs canines étaient fragiles et n'avaient pas d'utilité dans l'attaque des proies ou la pénétration de ces dents dans les os. Le but du présent article est de décrire deux nouveaux spécimens de *Smilodon populator* qui ont des blessures sur leur crâne. Bien qu'on ne puisse exclure

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le fait que les blessures aient été causées par une proie potentielle ayant donné des coups sur le crâne, la taille, la forme et les caractéristiques générales des blessures suggèrent que celles-ci ont été causées par les canines supérieures d'un autre individu *Smilodon* pendant des interactions agonistiques.

1. Introduction

The saber-toothed cat *Smilodon* is a characteristic genus of the ancient Pleistocene faunas of the American continents. *Smilodon* had a wide geographical distribution, from North America to the southern tip of South America (Prevosti et al., 2013). In South America, three species of the genus are recognized: *Smilodon fatalis* Leidy, 1878, from Peru, Ecuador, and Uruguay (Kurtén and Werdelin, 1990; Manzuetti et al., 2018); *S. populator*, recorded in Bolivia, Brazil, Uruguay, Argentina (Berta, 1985, 1987), and Venezuela (Rincón, 2006), and *S. gracilis* from Venezuela (Rincón et al., 2011).

The anatomy of *Smilodon* is well known because of its relatively high abundance (e.g., Berta, 1985, 1987; Kurtén and Werdelin, 1990; Merriam and Stock, 1932). Probably the most outstanding feature of *Smilodon* is the presence of hypertrophied upper canines that reach 28 cm in maximum crown height (Berta, 1985). The nature of the killing bite and bite mechanics of these felids remain under debate (Akersten, 1985; Bohlin, 1940; Christiansen, 2007; Emerson and Radinsky, 1980; Marinelli, 1938; Matthew, 1910; McHenry et al., 2007; Merriam and Stock, 1932; Miller, 1983, 1984; Simpson, 1941; Therrien, 2005; Turner and Antón, 1997; Warren, 1853; Wroe et al., 2005). Some authors (Miller, 1969, 1983; Moodie, 1923) described wounds in machairodontine skulls attributed to saber-toothed felids. Miller (1983) reported in detail these openings in *Smilodon fatalis* from the late Pleistocene of North America. Furthermore, Gillette and Ray (1981; see also Fariña et al., 2013) reported purported *Smilodon* canine wounds in a glyptodont skull. These consisted of two subparallel elliptical-shaped openings that match in size and contour those of *Smilodon* canines. These openings penetrate the frontal region of the skull of the glyptodont, and very likely were produced by a large machairodontine felid.

The aim of the present contribution is to describe two specimens of *Smilodon populator* that shed some light on the autoecology of the species and to discuss hypotheses regarding the utility of the upper canines in *Smilodon*.

2. Materials and methods

Here, two newly collected specimens of *Smilodon populator* are analyzed. Specimen MCA 2046 consists of a complete skull and mandible of an adult individual found at the cliffs of the Luján River, at Mercedes town, Buenos Aires province, Argentina (Fig. 1). The specimen comes from the upper Pleistocene Guerrero Member of the Luján Formation (see Dangavs and Blasi, 1995; Fidalgo, 1983; Mignone, 1941).

The second specimen, MRFA-PV-0564, was recovered by J.G.O. in sediments belonging to an unnamed lithostratigraphic unit of Pleistocene age (Luna and Cruz, 2014; Tauber et al., 2014). The fossil comes from the Corralito locality, Río Tercero department, Córdoba province, Argentina (Fig. 1). It consists of a skull belonging to an adult individual that lacks most of the rostrum (Fig. 2).

Institutional Abbreviations. MCA, Museo "Carlos Ameghino", Mercedes, Buenos Aires province, Argentina; MRFA, Museo Regional "Florentino Ameghino", Río Tercero, Córdoba province, Argentina.

3. Description

Both specimens, MCA 2046 and MRFA-PV-0564, show a similar opening located near the suture between the nasals and frontals, more precisely at mid-width within the rostral end of the frontals. In both specimens, the rostrocaudal length of the opening is 3 cm and their maximum width is 1.5 cm. In dorsal view, they are ogival in shape; the margins are sunken and lack osseous remodeling (Fig. 3).

In both specimens, the caudal half of the opening is slightly displaced toward the left side of the skull (Fig. 2) and the holes are surrounded by a depressed area of bone, but no distinct thinning of bone is evident. In MRFA-PV-0564, the skull shows a more recent (very probably taphonomic in origin) fracture on the left side of the original hole, resulting in a roughly heart-shaped injury. The opening in this specimen shows small depressed fractures surrounding the main hole, indicating that it may represents a peri-mortem damage, whereas MCA 2046 shows irregular and bulging trabecular bone on the margins of the hole, indicating bone healing, remodeling, and periosteal reactivity. The latter indicates that it was a pre-mortem damage and that the individual probably lived for a long time after the incident.

On the right margin of the hole, a small area presents vascular-like scarring characteristic of infection, but lacks hypervascularity in the form of small porous lesions. It lacks the projecting long and thin spicule bone formation ("sunburst" pattern) that characterizes some cancerous lesions, and also lacks a lumpy surface resulting from necrotic bone and an erosive surface typical of syphilis (Kaufman et al., 1997).

Specimen MCA 2046 shows a funnel-like extension at the right rostrolateral corner of the opening, surrounded by scarred margins of bone.

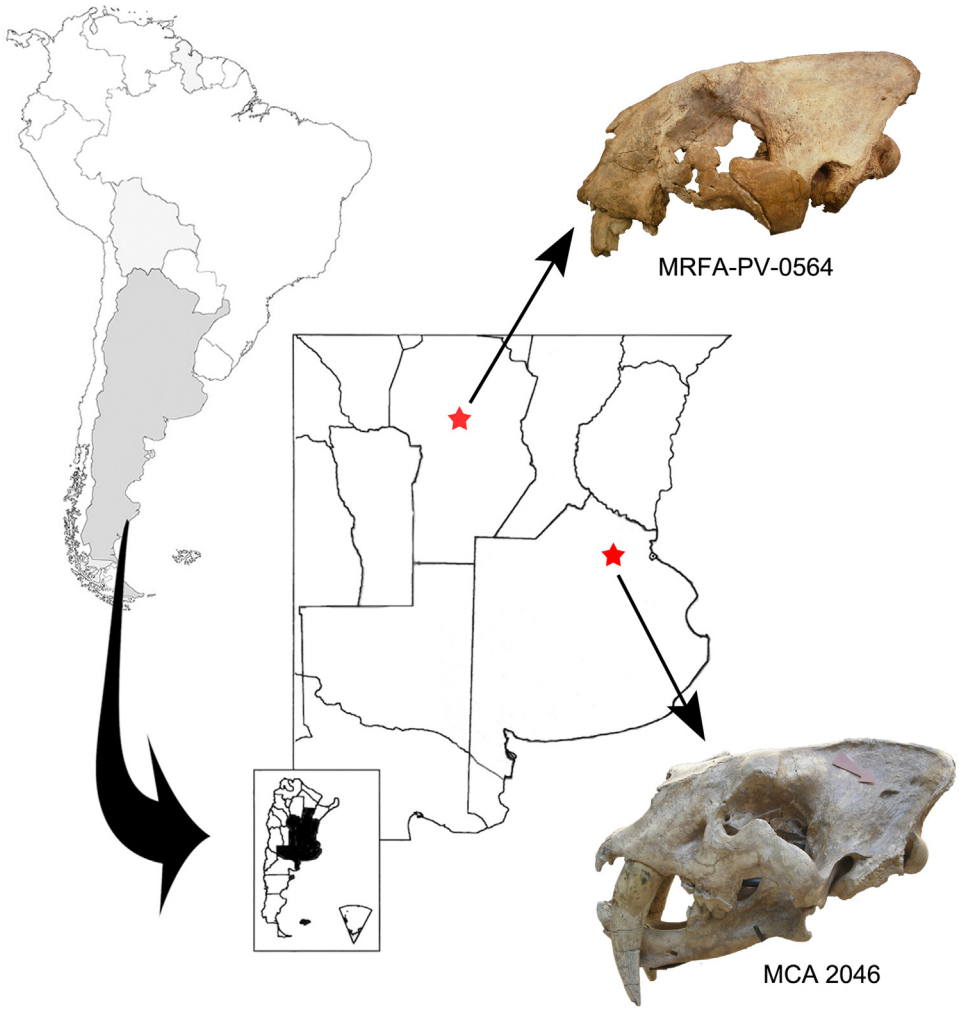

Fig. 1. Map showing fossil localities mentioned in the text.
Fig. 1. Carte montrant les localités fossilifères mentionnées dans le texte.

4. Discussion

The size, shape, and general features of the opening in the frontal region of specimens MCA 2046 and MRFA-PV-0564, together with the consistent presence of similar-shaped injuries reported by other authors (Fariña, 2002; Fariña et al., 2013; Miller, 1969, 1983; Moodie, 1923), suggest that taphonomic processes can be ruled out as the producer of the damage. In addition, in specimens MCA 2046 and MRFA-PV-0564, the bone lacks the typical surface pattern that characterizes some cancerous lesions or other kind of illness (see Kaufman et al., 1997).

Thus, because of the strong similarities in size and shape, the only agent that may stand as the possible producer of these injuries is another large animal with the capability to injure saber-toothed skulls. Because in both specimens the hole is single and elliptical, it is unlikely that the holes are the result of kicking of a three-toed litoptern, a four-toed toxodont, a two-toed large artiodactyl, or a transversely-broad toed horse. Bears, canids and other carnivores have conical canines that are subcircular in contour, resulting in round holes different from the ellipsoidal-shaped holes reported here (see Diedrich, 2011). Our findings support Moodie's (1923) and Miller's (1969, 1983) proposal and are consistent with those of Gillette and Ray (1981).

Large-clawed giant ground-sloths could be other potential producers of the injuries described here. Most ground-sloths have sharp claws, especially on digit III of the manus and pes. However, these claws are transversely broad and have lateral and ventral longitudinal keels that should have resulted in very different injuries from those reported here (Bargo et al., 2000; Morgan et al., 2011; White, 1997).

The size and general contours of the injuries present in specimens MCA 2046 and MRFA-PV-0564 are consistent with the size and contours observed in the upper canines of *Smilodon*. In fact, when a blade-like upper canine of a *Smilodon* specimen is inserted through the described opening, both perfectly match in size and shape (Fig. 3). As indicated above, it is unlikely that the wounds were

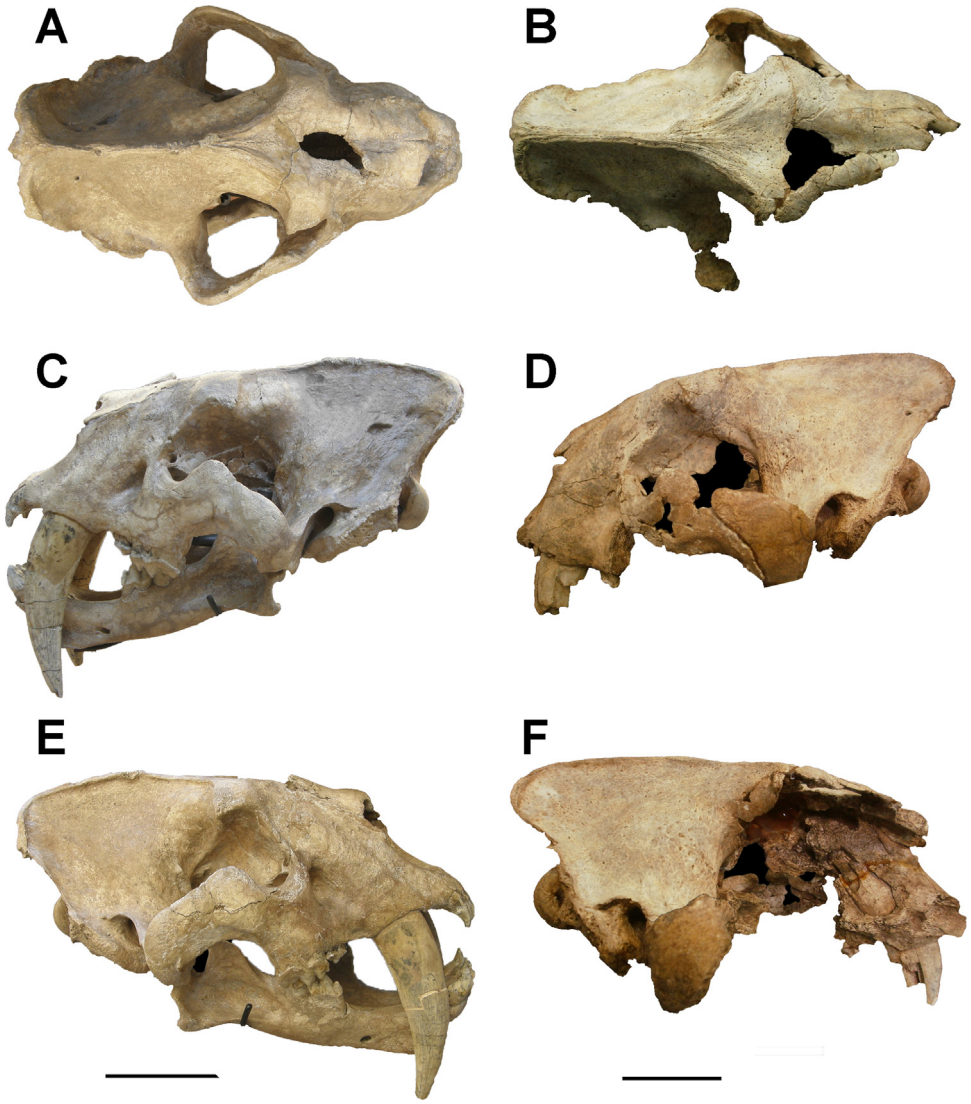

Fig. 2. Skull of different *Smilodon populator* specimens in **A, B,** dorsal; **C, D,** left lateral; and **E, F,** right lateral views. **A, C, E,** specimen MCA 2046; **B, D, F,** specimen MRFA-PV-0564. Scale bar: 10 cm.
Fig. 2. Crâne de différents spécimens de *Smilodon populator* en vues dorsale (**A, B**) ; latérale gauche (**C, D**) et latérale droite (**E, F**). **A, C, E**, spécimen MCA 2046 ; **B, D, F**, spécimen MRFA-PV-0564. Barre d'échelle = 10 cm.

produced by any other element of the South American Pleistocene fauna. As a result, we suggest that they were done by the upper canines of another *Smilodon* specimen during agonistic interactions. Also, skull injuries similar to those reported here have been described in the machairodontine *Machairodus* by Geraads et al. (2004), who described a hole between the orbits at the level of the frontals that caused the death of the animal. This hole is congruent in size and shape with the hypertrophied upper canines of *Machairodus*. This indicates that intraspecific combat was probably widespread in machairodontines.

Smilodon belongs to the machairodontines, an extinct clade of felids having hypertrophied, blade-like upper canines (Christiansen, 2007). Some authors have proposed that saber-toothed cats had a weak bite (Bohlin, 1940; Kurtén, 1952) and their canines were not useful for prey attack, but for intraspecific display. In this line of thought, Akersten (1985) stated that although *Smilodon* canines are heavier than a knife, they are slender and probably breakable structures. Thus, several authors consider that the upper canines of *Smilodon* were too fragile to be used on bony areas of their prey (Akersten, 1985; Emerson and Radinsky, 1980; Martin, 1980). In this regard, Akersten (1985) proposed that the throat and abdomen of the prey may be suitable areas for the *Smilodon* bite, being zones in which bone would not be encountered (see also Bohlin, 1940; Emerson and Radinsky, 1980; Martin, 1980; Matthew, 1910; Merriam and Stock, 1932; Turner and Antón, 1997; Therrien, 2005). Furthermore, Fariña et al. (2013) proposed that *Smilodon* could have used its strong forelimbs to seize and immobilize prey in a way that the teeth would have been able to penetrate tissues without

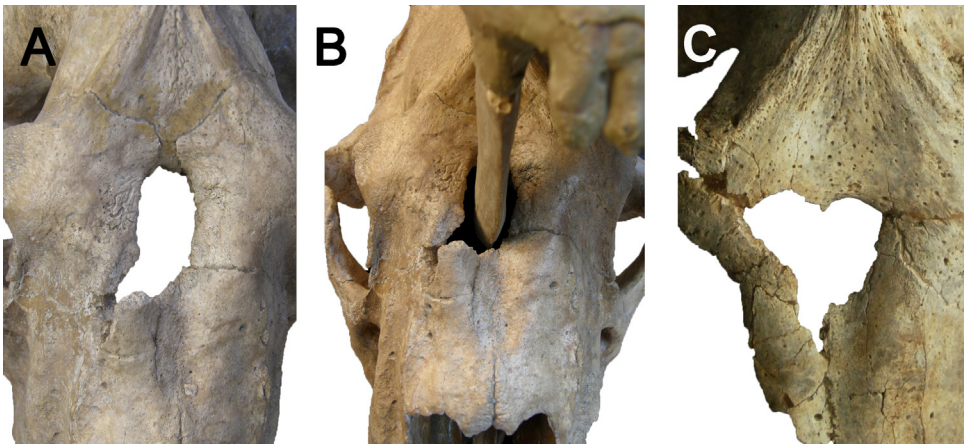

Fig. 3. A. Detail of the injury of *Smilodon populator* specimen MCA 2046. **B.** Detail showing the canine of another *Smilodon* specimen inserted through the opened injury. **C**. Detail of the injury of specimen MRFA-PV-0564. Not to scale.
Fig. 3. A. Détail de la blessure de *Smilodon populator*, spécimen MCA 2046. **B.** Détail de la canine d'un autre spécimen de *Smilodon*, insérée dans la blessure ouverte. **C.** Détail de la blessure du spécimen MRFA-PV-0564. La figure n'est pas à l'échelle.

the risk of breaking the canines. Recent studies indicate that derived sabercats, such as *Smilodon*, were capable of high force outputs at the jaw and carnassials (Christiansen, 2011; Therrien, 2005).

Our present report counters previous hypotheses on *Smilodon* predatory behavior and indicates that *Smilodon* canines could have been effectively employed on intraspecific and interspecific (in the case of glyptodonts; Fariña et al., 2013) fighting, and were strong enough to penetrate bone.

It is worth mentioning that intraspecific injuries similar to those reported here for *Smilodon populator* are common in living felids (e.g., *Leopardus pardalis, Puma concolor, Acinonyx jubatus, Panthera onca*; Azevedo et al., 2010; Galantine and Swift, 2007; Thompson, 2011). These injuries are the result of agonistic interactions between males and occasionally females (Emmons, 1988) and frequently result in the death of one of the individuals (see Lourenço et al., 2014; see also Hunter and Skinner, 1995; Amstrup et al., 2006).

We propose here that the injuries described on specimens MCA 2046 and MRFA-PV-0564 belonging to *S. populator* are the result of intraspecific agonistic interactions. In addition, it implies that *Smilodon* probably possessed social behavior, including intraspecific combat between males for territory or access to mates, and consequent death of injured individuals, as observed in living Felinae.

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