



RESEARCH ARTICLE

New evidence of the sabertooth cat *Smilodon* (Carnivora: Machairodontinae) in the late Pleistocene of southern Chilean Patagonia
Nueva evidencia del gato dientes de sable *Smilodon* (Carnivora: Machairodontinae) en el Pleistoceno tardío de Patagonia meridional chilena

ALFREDO PRIETO¹, RAFAEL LABARCA², * & VÍCTOR SIERPE¹

¹ Instituto de la Patagonia, Universidad de Magallanes, Casilla 113-D, Punta Arenas, Chile

² Programa de Doctorado Universidad Nacional del Centro de la Provincia de Buenos Aires, Av. Del Valle 5737, Olavarría, Argentina

* Corresponding author: r.labarca.e@gmail.com

ABSTRACT

Southern Patagonia is rich in late Pleistocene mammals, especially herbivores such as Camelids, Equids and Xenarthrans. Carnivores, on the other hand, are not commonly found in the paleontological record. One genus, *Smilodon*, is of particular interest because its presence in the region has not been demonstrated. In this paper, we present new fossil dental evidence that supports the presence of *Smilodon populator* (Lund) in the region. This evidence corresponds to the most southern record of the genus in the world, and the final step in the colonization of South America after the Great American Biotic Interchange. An AMS radiocarbon date on teeth indicates that the remains from Southern Chilean Patagonia are the most recent record for the genus in South America.

Key words: late Pleistocene, *Smilodon*, southern Patagonia, taxonomy.

RESUMEN

Surpatagonia es particularmente rica en mamíferos finiplesitocenos, particularmente camélidos, équidos y xenartros. Los carnívoros, por su parte, se encuentran representados en menor número en el registro paleontológico. Dentro de estos, el género *Smilodon*, es de particular interés debido a que su presencia en la región no ha sido convincentemente demostrada. En este trabajo presentamos evidencia dental que permite confirmar la presencia de *Smilodon populator* (Lund) en la región. Esta evidencia corresponde al registro más sureño de este taxón y al paso final en la colonización de América del Sur después del Gran Intercambio Biótico Americano. Un fechado radiocarbónico directo AMS indica que los restos de Patagonia del Sur corresponden a los registros más tardíos para este género en el subcontinente.

Palabras clave: Patagonia del sur, Pleistoceno final, *Smilodon*, taxonomía.

INTRODUCTION

The genus *Smilodon* (Felidae, Machairodontinae) is one of the most conspicuous representatives of the popularly known 'sabertooth cats'. It is an exclusively American group, whose first records come from the north-east area of the continent about 2.5 million years ago (Berta 1985, 1987, Turner & Antón 1997). Three species are distinguished from biometric and morphological attributes: *S. gracilis* (Cope, 1880), *S. fatalis* (Leidy, 1868) and *S. populator* (Lund, 1842) (Kurtén & Werdelin 1990).

The oldest sabertooth cat from South America comes from the Argentinian Ensenadian Land Mammal Age (Plio-

Pleistocene), around 2.0 million years ago, through the species *S. populator* (Berta 1985, Soibelzon & Prevosti 2007). Later, the nearctic taxon *S. fatalis* entered South America during the late Pleistocene (Kurtén & Werdelin 1990). The sabertooth cat findings in the subcontinent suggest that its distribution was allopatric, since *S. populator* inhabited the east slope of the Andes, according to fossil remains found in Venezuela, Brazil, Paraguay, Uruguay, Argentina, Bolivia and Chile. *S. fatalis* occupied the west side of the Andes, including Ecuador and Perú (Berta 1985, Kurtén & Werdelin 1990, Ubilla et al. 2004, Rincón 2006, Soibelzon & Prevosti 2007). Both species disappear at the Pleistocene-Holocene boundary (Lujanian-Platan).

For 60 years, all late Pleistocene felid remains from southern Chile have been systematically assigned to an extinct subspecies of jaguar, known as *Panthera onca mesembrina* (Cabrera 1934) (Nami & Menegaz 1991, Latorre 1998, Massone 2004) until Canto in 1991, described a premaxillary from the paleontological site Cueva Lago Sofía 4, that corresponds to a *Smilodon* sp. (Canto 1991). From that moment on, earlier findings carried out in the area (e.g., Cueva del Milodón) and elsewhere were tentatively assigned to *Smilodon* or *Smilodon populator* (Mol et al. 2003, Barnett et al. 2005, Soibelzon & Prevosti 2007) without making any taxonomic comparisons.

This work discusses the presence of *Smilodon*, and particularly, *S. populator* during the late Pleistocene in the Chilean Patagonia, starting from fossils found in two well-known caves from the area, Cueva Lago Sofía 4 and Cueva del Medio.

Study sites

The specimens under study comes from the paleontological site of Cueva Lago Sofía 4 (CLS-4) and the archaeological/paleontological site of Cueva del Medio (CDM), both located to the northeast of Última Esperanza Province, Magellan Region in southern Chilean Patagonia

(Fig. 1). CLS-4 is a small cave (16 m long) situated in the foothills of Cerro Mocho, about 150 m above sea level. The cave floor consists mainly of a compact carbonated matrix, but in some areas there are layers of silty sand sediments as well. The *Smilodon* remains were recovered from the back of the cave after systematic excavations, around 70 and 30 cm deep. *Vicugna vicugna* (Molina, 1782) and *Mylodon darwini* (Owen, 1839) bones have been dated (^{14}C) from $13,545 \pm 100$ BP (Ua-36261) ($13,732$ - $14,625$ cal BP 2 sigmas) and $11,590 \pm 100$ BP (PITT-0940) ($13,255$ - $13,676$ cal BP 2 sigmas) (Borrero et al. 1997, Labarca & Prieto 2009). CDM is located in the east flank of Cerro Benítez, about 5 km to the southwest of CLS-4 (Fig. 1). The cave is 87 m long and 41 m wide. Archaeological excavations documented a late Pleistocene human occupation associated with extinct fauna (Nami 1987). The *Smilodon* material was recovered in a grey-yellowish sandy matrix about 90 cm deep. Dates (^{14}C) taken from charcoal and bone ranged from $9,595 \pm 115$ BP (PITT-0344) ($8,646$ - $9,266$ cal BP 2 sigmas) to $12,390 \pm 180$ BP (PITT-0343) ($11,968$ - $13,095$ cal BP 2 sigmas) (Nami 1987, Nami & Nakamura 1995). Also, in this research a direct *Smilodon* AMS ^{14}C date was obtained from the CEHA 29/12bN408 specimen (Table 1).

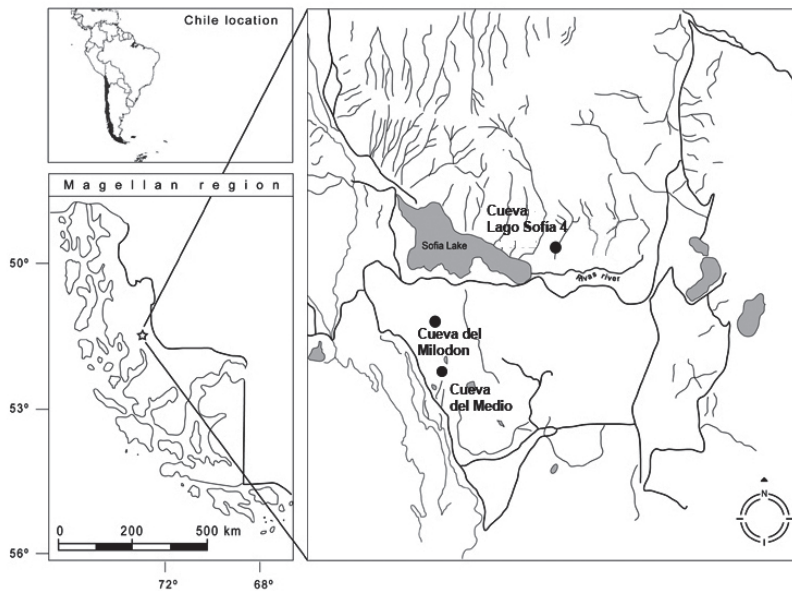


Fig. 1: Location of the archaeological and paleontological sites of Cueva Lago Sofía 4 and Cueva del Medio.

Ubicación de los sitios arqueológicos y paleontológicos de Cueva Lagos Sofia 4 y Cueva del Medio.

TABLE 1

Smilodon bone/tooth AMS radiocarbon dates from southern Chile. Radiocarbon dates were calibrated using Calib 5.1 software (Stuiver & Reimer 1993).

Fechados radiocarbónicos por AMS en huesos/dientes de *Smilodon* del sur de Chile. Los fechados radiocarbónicos fueron calibrados usando el software Calib 5.1 (Stuiver & Reimer 1993).

Site	Lab code	Radiocarbon date	Calibrated age (2 sigmas)	Reference
Cueva del Medio	Ua-37622	11,100 ± 80	10,935 - 11,209 cal BP	This work
Cueva del Milodón	IB-249	11,420 ± 50	11,437 - 11,240 cal BP	R Barnett, personal communication, 2010
Cueva del Milodón	IB-247	11,265 ± 45	11,300 - 11,131 cal BP	R Barnett, personal communication, 2010

METHODS

For the morphological analysis, the remains were compared with (1) modern dental pieces of *Puma concolor* (Linnaeus, 1758) stored at Centro de Estudios del Hombre Austral, Universidad de Magallanes (CEHA), Punta Arenas, Chile; (2) fossil material from *Smilodon populator* stored at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN) and Museo de La Plata (MLP), La Plata, Argentina; and (3) a resin replica of *Smilodon fatalis* from Rancho La Brea stored at CEHA. Osteological terminology from Merriam and Stock (1932) was used for the description. In order to compare the size of the *Smilodon* specimens from Southern Chile with those found in other parts of America, we conducted an analysis of logarithmic distances¹, using metrical data from Merriam & Stock (1932), Berta (1985, 1987), Kurtén & Werdelin (1990), as well as personal data gathered at MLP and MACN, and unpublished data from F. Prevosti (personal communication, 2008) (Appendix A and B). Measurements are in millimeters with 0.1 mm accuracy.

The specimens under study are housed at the Centro de Estudios del Hombre Austral, Universidad de Magallanes (CEHA) in Punta Arenas, Chile.

RESULTS

Systematic palaeontology

Order Carnivora (Bowdich, 1821)
 Suborder Feliformia (Kretzoi, 1945)
 Family Felidae (Gray, 1821)
 Subfamily Machairodontinae (Gill, 1872)
 Tribe Smilodontini (Kurtén, 1963)
 Genus *Smilodon* (Lund, 1842)

Smilodon populator (Lund, 1842) (Fig. 2A)

¹ MEADOW R (1987) Techniques for comparing bones measurement data from small samples. Northeastern faunal analysis conference Storrs, Connecticut, USA.

Referred specimen

CLS-4: UMAG 86661(i-08) fragment of a left-upper canine.

Description and comparison

The piece UMAG 86661(i-08) corresponds to a proximal portion of a large left-upper canine. According to Berta (1985, 1987), the upper canine from *Smilodon* genus has unusual growth, lateral compression, acuminate morphology, curved towards its distal end and fine serrations on the edges. The piece from Lago Sofia 4, although it was fractured, has dimensions matching *Smilodon* (Appendix A) with a laterally compressed cross-section and a slight curvature. The specimen is only a root, so there is no distal serration. Despite the fact that it is incomplete, it is possible to obtain the maximum mesiodistal length (L) and maximum buccolingual width (W) (Appendix A).

Berta (1985) as well as Kurtén and Werdelin (1990) state that *S. populator*, particularly the Lujanian form is the largest species within the genus. Berta (1985, 1987), nevertheless, mentions that a classification based exclusively on size is not reliable because of sexual dimorphism and/or typical variations of animals with wide geographical distribution (i.e., "Bergmann's rule"). Kurtén and Werdelin (1990), however, have demonstrated that although there was some degree of sexual dimorphism in *Smilodon*, this was less than in other widespread felids (e.g., *Puma concolor*). The analysis of logarithmic distances using the canine buccolingual maximum width and taking MLP-83-I-15-3 as reference (Appendix A) indicates that the CLS-4 tooth has a size compatible only with *S. populator* (Fig. 3A).

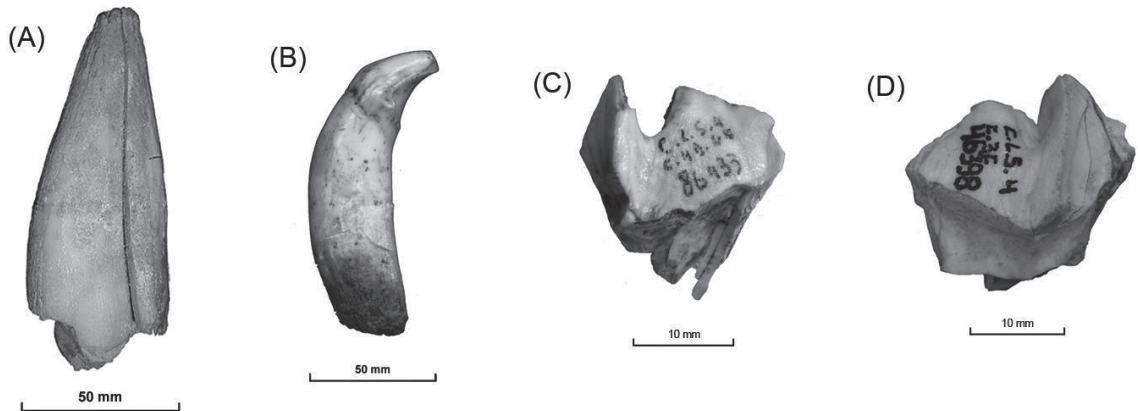


Fig. 2: Dental remains of *Smilodon* of CLS-4 and CDM. *Smilodon populator*: (A) Fragment of a left-upper canine (UMAG 86661[i-08]), buccal view; *Smilodon* cf. *S. populator*: (B) Right-upper third incisor (UMAG 29/12bN408), buccal view; (C) Fragment of a left-upper fourth premolar (UMAG 86433), lingual view; (D) Fragment of a right-upper fourth premolar (UMAG 46388), buccal view.

Restos dentales de *Smilodon* de CLS-4 y CDM. *Smilodon populator*: (A) Fragmento de canino superior izquierdo (UMAG 86661[i-08]), vista bucal; *Smilodon* cf. *S. populator*: (B) Tercer incisivo superior derecho (UMAG 29/12bN408), vista bucal; (C) Fragmento de cuarto premolar superior izquierdo (UMAG 86433), vista lingual; (D) Fragmento de cuarto premolar superior derecho (UMAG 46388), vista bucal.

Smilodon cf. *S. populator*

Referred specimens

CDM: UMAG 29/12bN408 right-upper third incisor (Fig. 2B); CLS-4: UMAG 86433 (Fig. 2C) fragment of a left-upper fourth premolar; UMAG 46388 (Fig. 2D) fragment of a right-upper fourth premolar.

Description and comparison

The piece UMAG 29/12bN408 is a large right-upper third incisor. It has a great development of the main cusp, an oval section, a slight compression in its lateral section, and is curved towards its distal end. Its medial side has a groove that runs from the tip of the crown to its base. The enamel on its lateral side is fractured. Both sides of the lingual section show two slightly flattened posterior tubercles separated by a "U" shaped notch. It is worn on its occlusal surface. The big size of this tooth (Appendix B), the presence of a prominent root and posterior tubercles are features of *Smilodon* (Merriam & Stock 1932). The logarithmic distances using the third incisor bucolingual maximum width (W) taking the MLP 10-2 specimen as reference (Appendix B) shows that the UMAG 29/

12bN408 tooth has dimensions similar to the largest specimens of *S. fatalis* from the Rancholabrean of North America and *S. populator* of Lujanian of South America (Fig. 3B, Appendix B), suggesting that this tooth does not have a specific taxonomic value. However, it is assigned to *Smilodon* cf. *S. populator* due to its morphological and size features, chronological contemporaneity, geographical proximity and faunal composition between CDM and CLS-4. The fact that *S. fatalis* and *S. populator* have an allopatric distribution in South America supports this assignation (Kurtén & Werdelin 1990).

UMAG 86433 and UMAG 46388 correspond to left and right fourth premolar fragments, respectively. Both are fractured in a very similar way, retaining the upper portion of the crown. The specimen UMAG 86433 has an almost complete metacone with a small lingual portion of the paracone. It also has a fragment of the principal root, and shows intensive occlusal wear exposing the dentine. The specimen UMAG 46388 also retains the distal section of the crown conserving a large mesial portion of the metacone and the distal portion of the paracone. The deep depression that divides both sections is complete. It has a very advanced occlusal wear on the lingual side. The similarities in occlusal wear and general

size between both premolars, suggests that they probably came from the same individual. Due to the fragmentary nature of the specimens, it is impossible to obtain reliable measurements, however, the very prominent metacone and a marked depression between the metacone and the paracone are distinctive features of the genus *Smilodon* (Merriam & Stock 1932). Due to extensive fragmentation, UMAG 46388 and UMAG 86433 cannot be specifically assigned, however their stratigraphic relationship with UMAG-86661(i-08) permits their inclusion with the other *Smilodon* cf. *S. populator* material.

DISCUSSION

Remains of *Smilodon populator* have been documented in Venezuela, Brazil, Paraguay, Uruguay, Argentina, Bolivia and Chile (Berta & Marshal 1978, Berta 1985, Kurtén & Werdelin 1990, Ubilla et al. 2004, Rincón

2006). Not counting the Patagonian findings, the southernmost record of *Smilodon* comes from the late-Pleistocene (Lujanian-Platan) in Central Argentina (Soibelzon & Prevosti 2007). The radiocarbon date of the *Smilodon* tooth from Cueva del Medio corresponds to the most recent record of this taxon in South America and the southernmost occurrence. The date is slightly younger than those obtained from Cueva del Milodon (Table 1).

The paleoclimatological data of the area shows that when the now extinct megafauna was alive, the climate was very cold and the landscape vegetation was more open (Heusser 1995, Cárdenas 2006, Villa-Martínez & Moreno 2007). This agrees with the faunal assemblages identified in CLS-4 and CDM, since *Smilodon populator* remains were found along with remains of the common grazers of open landscapes such as *Myiodon darwini*, *Hippidion saldiasi* (Roth, 1899), *Lama guanicoe* (Müller, 1776) and *Vicugna vicugna* (Nami & Mengaz 1991, Borrero et al. 1997).

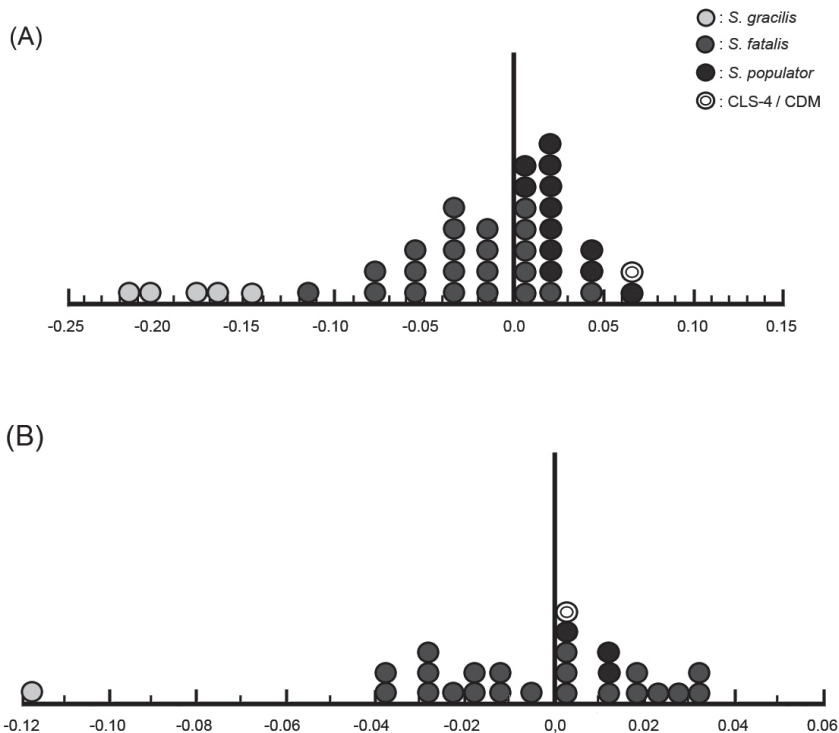


Fig. 3: Logarithmic distances of dental pieces of *Smilodon* genus. (A) C¹, taking as a reference the piece MLP-83-I-15-3 (Appendix A); (B) I³, taking as a reference the piece MLP 10-2 (Appendix B).

Distancias logarítmicas de las piezas dentales del género *Smilodon*. (A) C¹, tomando como referencia la pieza MLP-83-I-15-3 (Apéndice A) (B) I³, tomando como referencia la pieza MLP 10-2 (Apéndice B).

During the late Pleistocene, *Smilodon populator* was at the top of the foodweb. Prevosti & Vizcaíno (2006) suggest that *S. populator* could have captured an animal of 1,871 kg. For this reason, all the Pleistocene mammals recorded in southern Patagonia were potentially prey. In this scenario, *S. populator* competed against other large carnivores, such as *Arctotherium tarijense* (Ameghino 1902) and *Panthera onca mesembrina*. The morphology of the limbs suggests that *Smilodon* was not able to run long distances and accelerate quickly, thus, its hunting strategy most likely focused on ambush instead of pursuit in relatively closed environments (Gonyea 1976, Turner & Antón 1997). Given the large areas of open landscape in southern Patagonia, *S. populator* may have complemented its hunting strategy by incorporating pursuit at least occasionally. The presence of this sabertooth at the very tip of South America demonstrates the high adaptability of the species.

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APPENDIX A

Upper-left canine measures (mm) of *Smilodon* genus.Medidas (mm) de caninos superiores izquierdos del género *Smilodon*.

Repository code	Taxa	L	W	Reference
CEHA-86661(i-08)	<i>S. populator</i>	43.6	25.1	This work
MLP 10-2	<i>S. populator</i>	43.5	21.3	This work
MLP 10-2	<i>S. populator</i>	43.1	21.6	This work
MLP 98-II-20-1	<i>S. populator</i>	45.4	23.3	This work
MLP 83-I-15-1	<i>S. populator</i>	42.1	21.5	This work
MLP 83-1-15-3	<i>S. populator</i>	-	22.2	This work
MLP 55-VIII-12-1	<i>S. populator</i>	44.5	20.7	This work
CM La Plata	<i>S. populator</i>	44.5	20.7	Kurtén & Werderlin 1990
CM Arroyo Pergamino	<i>S. populator</i>	44.3	22.1	Kurtén & Werderlin 1990
CM La Plata	<i>S. populator</i>	45.9	21.8	Kurtén & Werderlin 1990
CM Lapa Escrivania	<i>S. populator</i>	49.2	25	Kurtén & Werderlin 1990
CM Lapa Escrivania	<i>S. populator</i>	44.3	22.3	Kurtén & Werderlin 1990
CM Lapa Escrivania	<i>S. populator</i>	44.7	22.8	Kurtén & Werderlin 1990
ROM 2121	<i>S. fatalis</i>	43.3	15.5	Kurtén & Werderlin 1990
2001-24	<i>S. fatalis</i>	46.1	22.9	Merriam & Stock 1932
2001-230	<i>S. fatalis</i>	44	21.7	Merriam & Stock 1932
2001-225	<i>S. fatalis</i>	43.7	24.1	Merriam & Stock 1932
2001-151	<i>S. fatalis</i>	41.7	22.2	Merriam & Stock 1932
2001-77	<i>S. fatalis</i>	41.4	18.8	Merriam & Stock 1932
2001-111	<i>S. fatalis</i>	41.9	22.3	Merriam & Stock 1932
2001-132	<i>S. fatalis</i>	44.1	22.6	Merriam & Stock 1932
2001-288	<i>S. fatalis</i>	45.6	21.4	Merriam & Stock 1932
2001-16	<i>S. fatalis</i>	41.5	21.4	Merriam & Stock 1932
2001-181	<i>S. fatalis</i>	43	21.2	Merriam & Stock 1932
2001-19	<i>S. fatalis</i>	42.1	20.5	Merriam & Stock 1932
2001-65	<i>S. fatalis</i>	46.1	20.4	Merriam & Stock 1932
2001-2	<i>S. fatalis</i>	45	23	Merriam & Stock 1932
2001-5	<i>S. fatalis</i>	43.5	21	Merriam & Stock 1932
2001-307	<i>S. fatalis</i>	38.1	21.7	Merriam & Stock 1932
2001-311	<i>S. fatalis</i>	40	20.1	Merriam & Stock 1932
2001-302	<i>S. fatalis</i>	42.2	19.8	Merriam & Stock 1932
2001-90	<i>S. fatalis</i>	41	19.3	Merriam & Stock 1932
2001-131	<i>S. fatalis</i>	43	19.7	Merriam & Stock 1932
2001-4	<i>S. fatalis</i>	42.2	19.7	Merriam & Stock 1932
2001-256	<i>S. fatalis</i>	36	18.8	Merriam & Stock 1932
2001-113	<i>S. fatalis</i>	38.6	16.6	Merriam & Stock 1932
2001-76	<i>S. fatalis</i>	39	18	Merriam & Stock 1932
2001-148	<i>S. fatalis</i>	38.8	18	Merriam & Stock 1932
ANSP 47	<i>S. gracilis</i>	26.8	13.3	Berta 1987
ANSP 46	<i>S. gracilis</i>	25.9	13.1	Berta 1987
ANSP 44	<i>S. gracilis</i>	35.5	15.2	Berta 1987
F:AM 95525	<i>S. gracilis</i>	29.7	14.2	Berta 1987
F:AM 95526	<i>S. gracilis</i>	31.4	14.4	Berta 1987

APPENDIX B

Right-upper third incisor measures (mm) of *Smilodon* genus.Medidas (mm) de terceros incisivos derechos del género *Smilodon*.

Repository code	Taxa	W	Reference
UMAG 29/12bN408	CDM	12	This work
MLP 10-2	<i>S. populator</i>	12	This work
MLP 55-VIII-12-I	<i>S. populator</i>	12.4	This work
MACN 18057	<i>S. populator</i>	12.3	F. Prevosti pers comm.
2001-24	<i>S. fatalis</i>	13	Merriam & Stock 1932
2001-230	<i>S. fatalis</i>	12.9	Merriam & Stock 1932
2001-225	<i>S. fatalis</i>	12.4	Merriam & Stock 1932
2001-151	<i>S. fatalis</i>	12.5	Merriam & Stock 1932
2001-111	<i>S. fatalis</i>	11.2	Merriam & Stock 1932
2001-132	<i>S. fatalis</i>	11.6	Merriam & Stock 1932
2001-288	<i>S. fatalis</i>	12.5	Merriam & Stock 1932
2001-16	<i>S. fatalis</i>	11.5	Merriam & Stock 1932
2001-181	<i>S. fatalis</i>	11	Merriam & Stock 1932
2001-19	<i>S. fatalis</i>	12.6	Merriam & Stock 1932
2001-2	<i>S. fatalis</i>	12	Merriam & Stock 1932
2001-5	<i>S. fatalis</i>	12.8	Merriam & Stock 1932
2001-307	<i>S. fatalis</i>	11.5	Merriam & Stock 1932
2001-311	<i>S. fatalis</i>	11.9	Merriam & Stock 1932
2001-302	<i>S. fatalis</i>	11.3	Merriam & Stock 1932
2001-90	<i>S. fatalis</i>	11.6	Merriam & Stock 1932
2001-131	<i>S. fatalis</i>	11.4	Merriam & Stock 1932
2001-4	<i>S. fatalis</i>	11.3	Merriam & Stock 1932
2001-256	<i>S. fatalis</i>	11.1	Merriam & Stock 1932
2001-113	<i>S. fatalis</i>	11.7	Merriam & Stock 1932
2001-76	<i>S. fatalis</i>	12	Merriam & Stock 1932
ANSP 44	<i>S. gracilis</i>	9	Berta 1987

