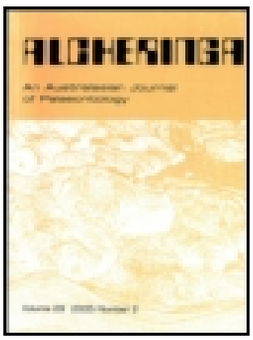

Alcheringa: An Australasian Journal of Palaeontology

ISSN: 0311-5518 (Print) 1752-0754 (Online) Journal homepage: https://www.tandfonline.com/loi/talc20

An extremely large saber-tooth cat skull from Uruguay (late Pleistocene–early Holocene, Dolores Formation): body size and paleobiological implications

Aldo Manzuetti, Daniel Perea, Washington Jones, Martín Ubilla & Andrés Rinderknecht

To cite this article: Aldo Manzuetti, Daniel Perea, Washington Jones, Martín Ubilla & Andrés Rinderknecht (2020): An extremely large saber-tooth cat skull from Uruguay (late Pleistocene–early Holocene, Dolores Formation): body size and paleobiological implications, Alcheringa: An Australasian Journal of Palaeontology, DOI: 10.1080/03115518.2019.1701080

To link to this article: https://doi.org/10.1080/03115518.2019.1701080

ALCHERINGA: AN AUSTRALASIAN JOURNAL OF PALAEONTOLOGY
https://doi.org/10.1080/03115518.2019.1701080

An extremely large saber-tooth cat skull from Uruguay (late Pleistocene–early Holocene, Dolores Formation): body size and paleobiological implications

Aldo Manzuetti, Daniel Perea, Washington Jones, Martín Ubilla, and Andrés Rinderknecht

ABSTRACT

Among the three recognized species of *Smilodon*, *S. populator* is the largest in size and has the widest distribution across South America. The present contribution describes an almost complete skull assigned to the aforementioned felid. The material was recovered from sediments of the Dolores Formation (Lujanian Stage/Age) from the southern part of Uruguay. This specimen is remarkable for its unusual craniodental measurements, indicating that it is one of the largest known specimens of the genus. Estimates of body mass indicate that this individual weighed over 400 kg. In addition, maximum prey size estimation greatly surpasses 1 t and approach nearly 3 t. Based on this, aspects of the paleobiology and paleoecology of *S. populator* are discussed. Undoubtedly, this kind of carnivorous mammal was at the top of the food chain, with clear adaptations for feeding upon the largest available herbivores, which potentially includes several megafaunal mammal species found in South America during the late Pleistocene.

ARTICLE HISTORY
Received 7 August 2019
Revised 24 October 2019
Accepted 2 December 2019

KEYWORDS
Dolores Formation; paleobiology; Quaternary; *Smilodon populator*; Uruguay

Aldo Manzuetti [aldomanzuetti@adinet.com.uy], Facultad de Ciencias (UdelaR), Iguá 4225, CP 11400, Montevideo, Uruguay; Daniel Perea [perea@fcien.edu.uy], Facultad de Ciencias (UdelaR), Iguá 4225, CP 11400, Montevideo, Uruguay; Washington Jones [wawijo@yahoo.com.ar], Museo Nacional de Historia Natural, 25 de Mayo 582, CP 11000, Montevideo, Uruguay; Martín Ubilla [ubilla@fcien.edu.uy], Facultad de Ciencias (UdelaR), Iguá 4225, CP 11400, Montevideo, Uruguay; Andrés Rinderknecht [apaleorinder@yahoo.com], Museo Nacional de Historia Natural, 25 de Mayo 582, CP 11000, Montevideo, Uruguay.

HYPERTROPHIED upper canines in carnivorous mammals evolved independently through time, both in placental mammals (Eutheria) and marsupials (Metatheria) (see Emerson & Radinsky 1980, Van Valkenburgh & Jenkins 2002, van den Hoek Ostende *et al.* 2006). Among the Machairodontinae (Carnivora, Felidae), those of the genus *Smilodon* Lund, 1842 stand out. This genus originated in North America in the late Pliocene and its record extended to the Pleistocene–Holocene boundary. By the time of their extinction, *Smilodon* inhabited vast areas of North and South America (Cordeiro de Castro & Cardoso-Langer 2008, Prevosti & Forasiepi 2018).

Currently, three species are recognized in this genus: *S. gracilis* Cope, 1880, *S. fatalis* Leidy, 1868 and *S. populator* Lund, 1842 (Kurtén & Werdelin 1990, Turner & Antón 1997, Antón 2013, Werdelin *et al.* 2018).

The first species, *S. gracilis*, was restricted mainly to the late Pliocene–middle Pleistocene of North America (Berta 1985, 1987, 1995, Kurtén & Werdelin 1990), but has also been recorded in early–middle Pleistocene sediments in northern South America (Venezuela) (Rincón *et al.* 2011). *Smilodon fatalis*, is typically known from the mid–late Pleistocene of North America, but has also been found in late Pleistocene sediments in northwestern South America (Coralito in Ecuador and Talara in Peru) (Kurtén & Werdelin 1990); recently it was recovered from the southeast part of the South American continent (late Pleistocene of Uruguay, Sopas Formation) (Manzuetti *et al.* 2018a). Finally, *Smilodon populator*, endemic to South America, is most frequently found from Ensenadan to Lujanian deposits (early Pleistocene to early Holocene), particularly toward the center and eastern parts of the continent (Brazil, Bolivia, Paraguay, Venezuela, Argentina, Uruguay, southern Chile and eastern Peru) (Berta 1985, Kurtén & Werdelin 1990, Rincón 2006, Soibelzon & Prevosti 2007, 2013, Shockey *et al.* 2009, Prieto *et al.* 2010).

This study describes a near-complete skull that belonged to the saber-toothed cat *Smilodon populator*. The material was found in sediments of the Dolores Formation (Lujanian Stage/Age) from southern Uruguay (Limetas Creek, Department of Colonia) (Fig. 1). Given the unique size and proportions of this new skull, which indicate that it is one of the largest known specimens of the genus, implications for its paleobiology and paleoecology will be discussed.

Geological setting

The Dolores Formation, mainly located in western and southern Uruguay (Ubilla *et al.* 2011, Ubilla & Martínez 2016), is comprised of silty claystones and siltstones, clay deposits, sandstones, and gravel (mudstone). It is generally brownish in color, with gray-green local shades, and a maximum of 10 m thickness. It was deposited in semi-arid and cold climatic conditions (Martínez & Ubilla 2004, Corona *et al.* 2013). Several absolute dates based on radiocarbon and OSL/TL methods were obtained for the Dolores Formation, with ages ranging from 30,100–27,000 to 11,150–10,480 years before present (BP) (Ubilla *et al.* 2011

Supplemental data for this article is available online at https://doi.org/10.1080/03115518.2019.1701080.

Published online 02 Mar 2020

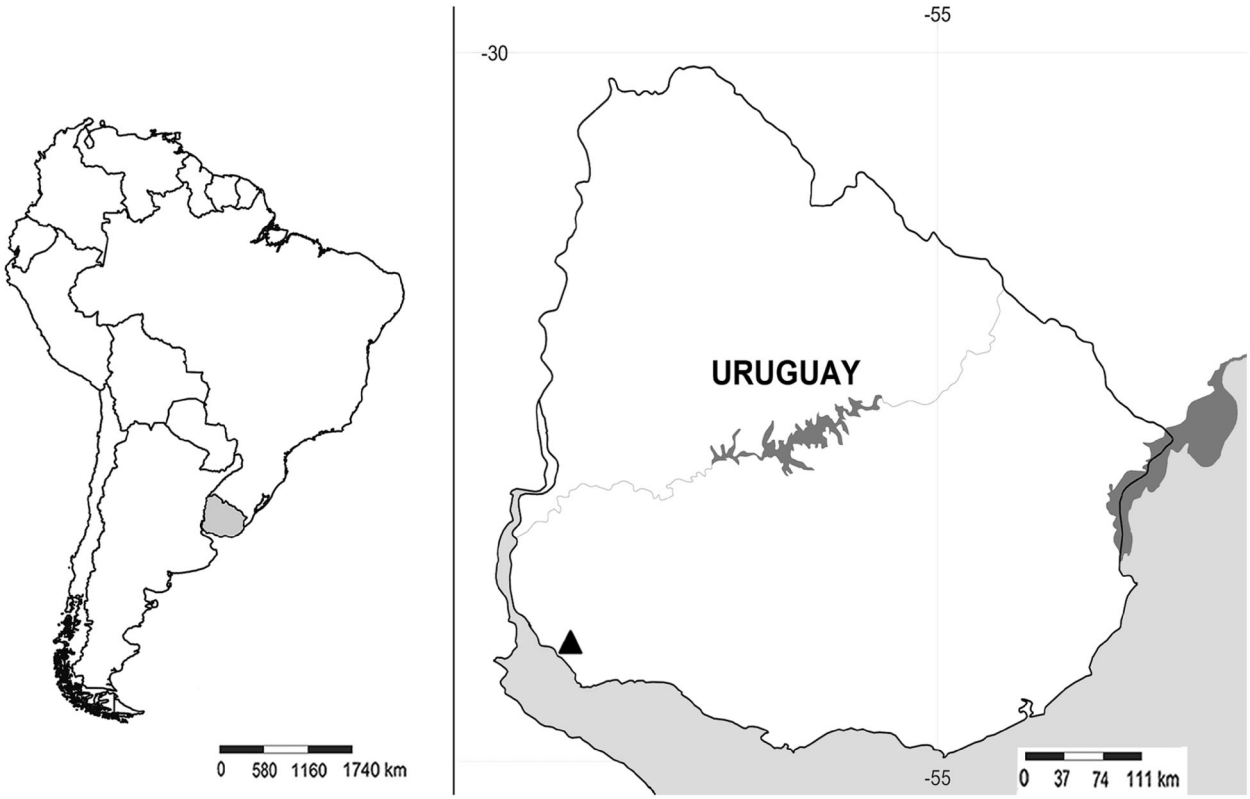

Figure 1. Map of Uruguay showing the approximate geographic location where the *Smilodon populator* skull (MNHN-P 957) was found (black triangle): Limetas Creek (Department of Colonia), Dolores Formation.

and references therein, Ubilla *et al.* 2018). Based on the mammalian assemblage, this unit is correlated with the Lujanian Stage/Age (late Pleistocene–early Holocene) (Ubilla *et al.* 2011 and references therein). This unit yields several taxa of the order Carnivora, and among the largest carnivores registered were *Arctotherium tarijense* Ameghino, 1902, *Panthera onca* (Linnaeus, 1758) and *S. populator* (Ubilla *et al.* 2011, Ubilla & Martínez, 2016, see also Manzuetti *et al.* 2018b). The area studied (Limetas Creek) is remarkable for the diverse mammalian taxa found there such as *Toxodon platensis* Owen, 1837, *Glossotherium* Owen, 1839, *Hemiauchenia* Gervais & Ameghino, 1880, *Lestodon armatus* Gervais, 1855, *Ctenomys praderii* Mones & Castiglioni, 1979, *Catagonus* Ameghino, 1904, *Glyptodon* Owen, 1839, *Hippidion* Roth, 1899, and the frog *Ceratophrys* Wied-Neuwied, 1824 (see Mones & Francis 1973 and references therein, Rinderknecht 1998). However, Limetas Creek lacks any record of carnivorous mammals except for the material here described.

Material and methods

Institutional abbreviations

MNHN-P, Museo Nacional de Historia Natural, Departamento de Paleontología, Montevideo, Uruguay; FC-DPV, Facultad de Ciencias-Colección Paleontológica (Vertebrados Fósiles), Montevideo, Uruguay; CBM, colección particular Brum-Martínez, Montevideo, Uruguay.

For comparative analysis, skeletal material of *Smilodon populator* housed in the FC-DPV and the MNHN-P and material of *S. fatalis* stored in the CBM were used. Published literature on *S. gracilis*, *Smilodon fatalis* and *S. populator* from Merriam & Stock (1932), Méndez-Alzola (1941), Churcher (1967), Berta (1985, 1987, 1995), Kurtén & Werdelin (1990), Rincón *et al.* (2011) and Manzuetti *et al.* (2018a) were also used. Dental nomenclature follows Berta (1987).

Body mass estimates were made based on allometric equations formulated for extant felids (Van Valkenburgh 1990) using measurements of the skull, limited only by preservation of the material. Body mass estimates of the typical prey species available to *S. populator* and maximum prey size were calculated using equations formulated for extant felids by Prevosti & Vizcaíno (2006), and Prevosti & Martin (2013) (Appendix 1). To infer maximum prey size, the average body mass estimate of the carnivore was used. For all of the equations, the mean absolute value of percent prediction error (%PE) and the coefficient of correlation (r) were used as comparative indicators of the accuracy of the prediction of the study variables.

Bivariate graphs were used to highlight quantitative differences among taxa, using the statistical program PAST Version 2.09 (Hammer *et al.* 2001). The data for *Smilodon gracilis*, *S. fatalis* and *S. populator* came from the literature (Merriam & Stock, 1932, Méndez-Alzola 1941, Churcher 1967, Berta 1987, 1995, Kurtén & Werdelin 1990, Prieto *et al.* 2010, Rincón *et al.* 2011, Manzuetti *et al.* 2018a) (Appendix 2).

All measurements on skull MNHN-P 957 were taken by one of us (A.M.) following Méndez-Alzola (1941), Churcher (1967) and von den Driesch (1976). Measurements were

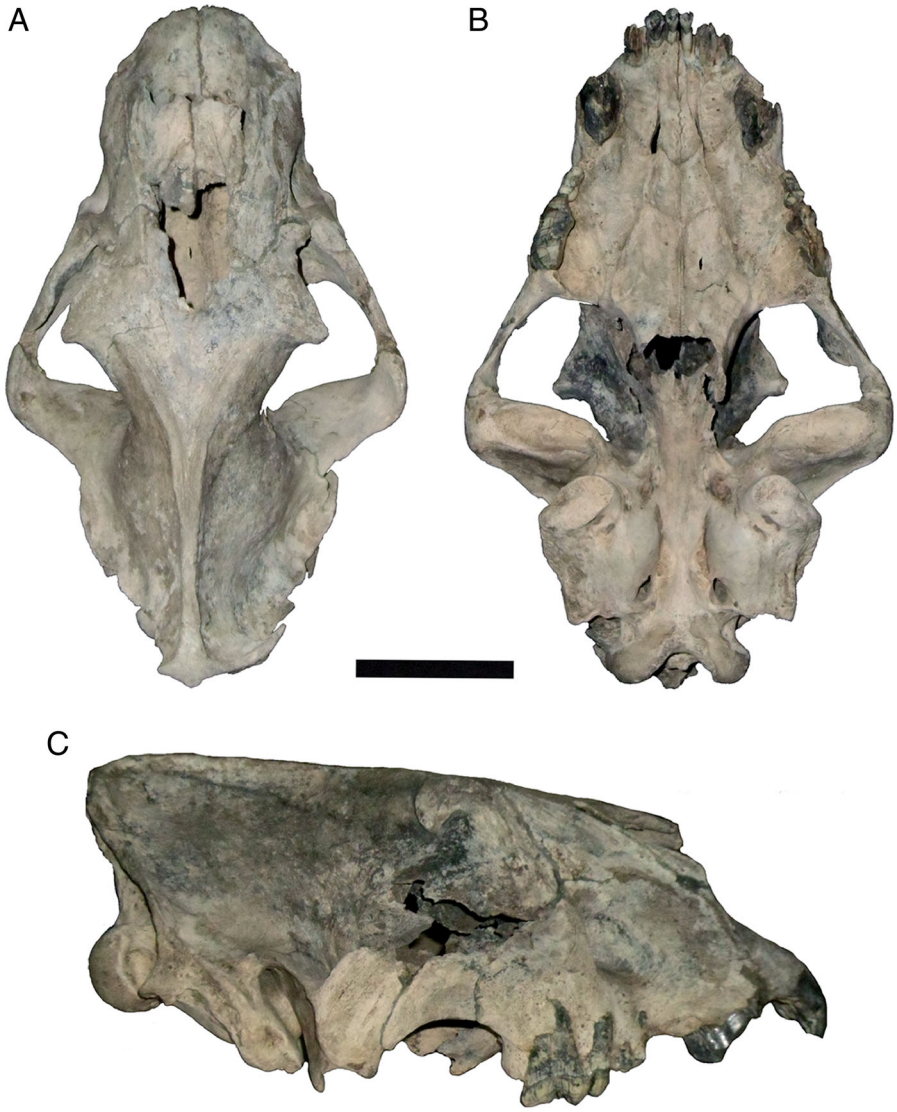

Figure 2. *Smilodon populator* skull MNHN-P 957. **A**, dorsal view; **B**, ventral view; **C**, lateral view. Scale bar 10 cm.

acquired using manual calipers accurate to 0.1 mm and expressed in millimeters (Appendix 3).

Skull measurements: TL, total length; CBL, condylobasal length; OOL, orbito-occipital length; ZW, zygomatic width; RW, rostral width; IOW, interorbital width; PCW, width at the post-orbital constriction; GBM, greatest mastoid breadth; GBC, greatest breadth at the occipital condyles; FMB, greatest breadth of the foramen magnum; FMH, height of the foramen magnum.

Dental measurements (right side): TRL I1-PM4, tooth row length I1-PM4; Diast, diastema canine-PM3; CAP, anteroposterior diameter of the canine; CML, transverse diameter of the canine; PM3AP, anteroposterior diameter of the PM3; PM3ML, transverse diameter of the PM3; PM4AP, anteroposterior diameter of the PM4; PM4ML, transverse diameter of the PM4.

Systematic paleontology

ORDER CARNIVORA Bowdich, 1821
FAMILY FELIDAE Fischer von Waldheim, 1817
SUBFAMILY MACHAIRODONTINAE Gill, 1872
TRIBE SMILODONTINI Kretzoi, 1929
Smilodon Lund, 1842

Smilodon populator Lund, 1842

Referred material. MNHN-P 957, almost complete skull (Fig. 2).

Geographic and stratigraphic location. Limetas Creek (Department of Colonia, Uruguay), Dolores Formation, late Pleistocene–early Holocene.

Comparative description. Dorsal view: elongated and rather narrow skull, according to the disposition of the zygomatic arches. There is an opening in the frontonasal region of the skull. Lateral view: the nasals are high and the large lambdoid crest forms a marked angle where it meets the mastoid process as evidenced in *Smilodon populator* and differing from *S. fatalis* (Kurtén & Werdelin 1990). Ventral view: enlarged

Table 1. Body mass estimation (in kg) for the *Smilodon populator* skull MNHN-P 957.

Measure	CBL	OOL
Body mass estimation[a]	436.1	379.1
%PE	38	37
r	0.92	0.92

[a]Mean body mass 407.6. Body mass equations from Van Valkenburgh (1990). Abbreviations: CBL, condylobasal length; OOL, orbito-occipital length.

mastoid process; anteroposteriorly elongated and transversely compressed auditory bullae.

The tooth rows are very well preserved but lacking M1; canines are cracked and broken. The incisors are slightly recurved posteriorly, the PM3 is tricuspidate and slightly oblique with respect to the corresponding PM4. The PM4 is secodont and has the typical configuration of the genus (Berta 1987), the secondary ectoparastyle is anterior to the parastyle, and the protocone is reduced. Judging from the degree of wear of the teeth, specially PM4, and the level of fusion of the cranial sutures, the specimen MNHN-P 957 is from an adult individual.

Remarks. The body mass estimations, using equations for extant felids based on measurements of the skull, provide an average value above 400 kg (Table 1). Based on that average body mass, the typical prey size must have greatly exceeded 1 t, and the maximum prey size was around 3 t (Table 2). Bivariate analysis based on measurements of the skull and dentition (Figs 3 and 4) shows significant differences between *Smilodon gracilis* and *S. fatalis*, and in some ways with *S. populator* too. In terms of absolute size, the specimen MNHN-P 957 is larger than *S. gracilis* (Berta 1987, 1995), *S. fatalis* (Merriam & Stock 1932, Kurtén & Werdelin 1990) and even the sample of specimens of *S. populator* used here (Figs 3 and 4A) (Méndez-Alzola 1941, Churcher 1967, Kurtén & Werdelin 1990). The only exception is the biplot of the PM4, which falls within the size variability of the largest *S. fatalis* and *S. populator* (Fig. 4B).

Measurements (in mm). Skull measurements: TL, 392; CBL, 379; OOL, 242; ZW, 240; RW, 119; IOW, 112; PCW, 100; GBM, 152; GBC, 83; FMB, 35; FMH, 32. Dental measurements (right side): TRL I-PM4, 168; Diast, 22; CAP, 52; CML, 24; PM3AP, 19; PM3ML, 12; PM4AP, 44; PM4ML, 18.

Discussion

Body mass and size

Body mass has an important relationship to several aspects of the biology of a species. Estimating this parameter is important for understanding and making inferences about the ecology of the taxa of the past (Soibelzon & Tarantini 2009, Elissamburu 2012, Ghizzoni 2014). The best body mass predictors in most mammal groups are based on measurements of the long bones, because these skeletal elements directly bear the weight of the animal (Hemmer *et al.* 2011 and references therein; see also Losey *et al.* 2017). In other cases, estimates are calculated using other parameters (skull measurements, dental measurements, among others). In any case, all estimations of body mass made for extinct taxa should be considered with caution and taken as approximate, rather than absolute values (Prevosti & Vizcaíno 2006, Losey *et al.* 2017).

Table 2. Body mass estimation (in kg) of the typical prey (TPM) and maximum prey (MPM) for the specimen MNHN-P 957 (range of estimation between parentheses).

Parameter	TPM[a]	MPM[a]	TPM[b]	MPM[b]
Estimation (range)	1303.3 (1477.9–1138.9)	2768.2 (3020.4–2521.1)	1258.2 (1396.2–1125.3)	1996.3 (2135.9–1856.8)
%PE	77.73	15.2	54.55	35.02
r	0.9	0.88	0.9	0.88

[a]According to equations of Prevosti & Vizcaíno (2006).
[b]According to equations of Prevosti & Martin (2013).

According to body size estimates based on measurements of long bones, *Smilodon gracilis* (range of 55–100 kg) was similar in mass to the extant jaguar, *Panthera onca*, (Christiansen & Harris, 2005). *Smilodon fatalis* had a mass similar to that of the largest extant felid, the Siberian tiger (*P. tigris altaica* Temminck, 1844), of 160–280 kg. Finally, *S. populator* is estimated to be the largest species of the genus. With an average body mass of approximately 220–360 kg, some unusually large individuals could exceed 400 kg.

The *Smilodon populator* skull MNHN-P 957 has a size far from average, being an extremely large representative of the species and may have weighed up to 436 kg. Van Valkenburgh (1990) noted that for carnivorous mammals over 100 kg, the equation based on the CBL metric would have a smaller %PE (~26), and thus would have a better prediction range than the equation based on the OOL metric (~28), which implies that the estimation of 436 kg may actually be most reliable.

Certainly, *Smilodon populator* was among the largest carnivorous mammals in South America during the late Pleistocene (Werdelin *et al.* 2018). These very large saber-toothed cats were surpassed in body mass only by the short-faced bear *Arctotherium* Burmeister, 1879 (Soibelzon & Tarantini 2009, Prevosti & Martin 2013, see also Soibelzon & Schubert 2011).

Potential prey size (typical and maximum prey)

The ability to prey on megamammals (body mass equal to or greater than 1 t) would be limited by the size of the carnivore and its hunting strategy. It also depends upon the size and type of prey and whether the prey species has some kind of defense mechanism that would provide protection against predation (such as body armor and sharp claws, or gregarious social behavior forming group defenses), and the age and health of the prey animals (Prevosti & Vizcaíno 2006 and references therein). It is well established that *Smilodon* was a large, powerful hunter that specialized in preying upon megaherbivores that were considerably larger and heavier (Prevosti & Forasiepi 2018 and references therein). Published values of the typical prey size for *S. populator* are 760–880 kg while maximum prey size is estimated at 1540–1870 kg (Prevosti & Vizcaíno 2006, Prevosti & Martin 2013). The new estimates reported here for both typical and maximum prey size highly exceed those values, the latter reaching near 3 t.

During the late Pleistocene, potential prey species may have included large camelids and equids, giant armadillos and small glyptodonts, and also megamammals (ground sloths), among

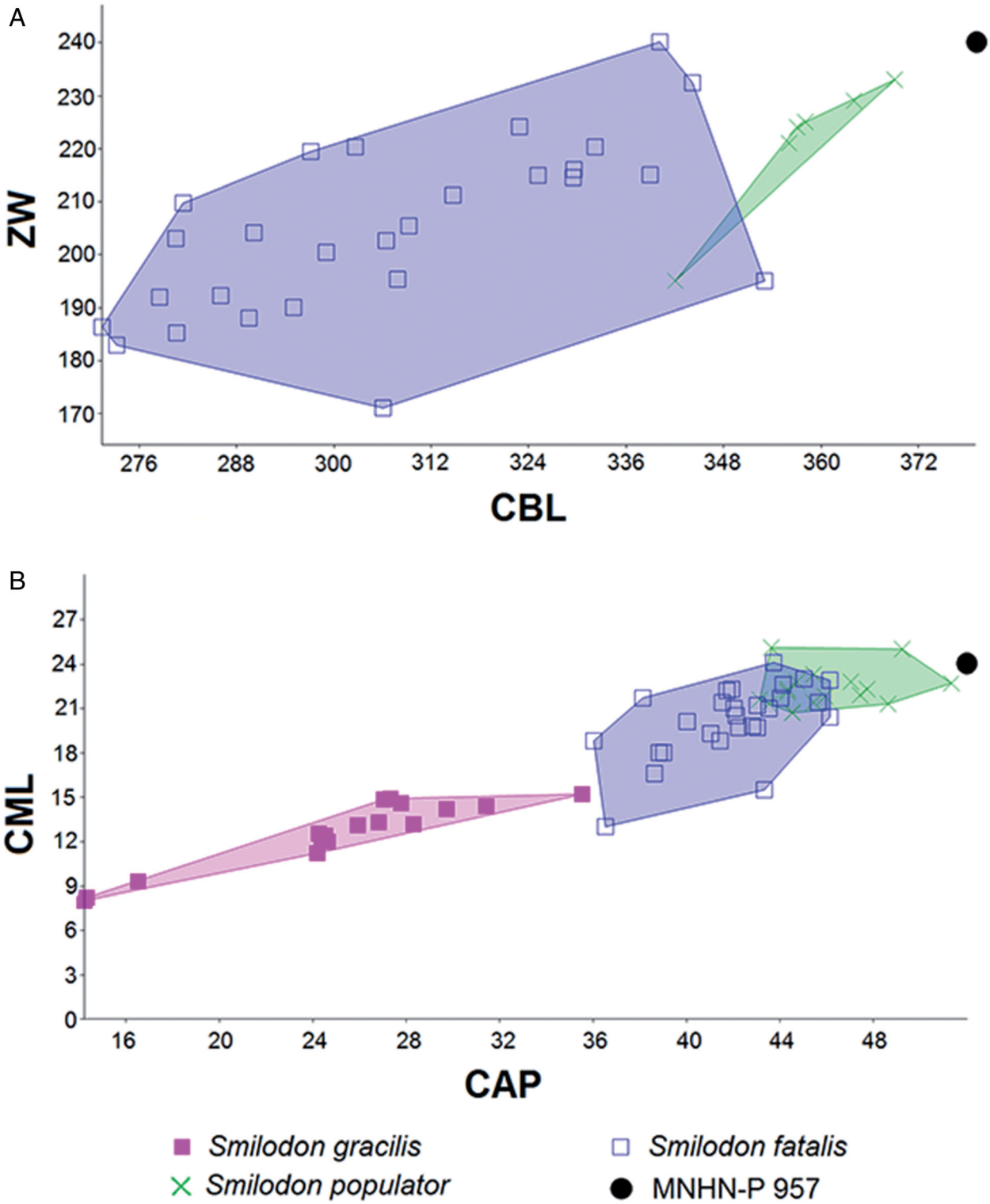

Figure 3. Bivariate graphs for the *Smilodon populator* specimen MNHN-P 957. **A**, zygomatic width (ZW) versus condylobasal length (CBL); **B**, canine transverse diameter (CML) versus canine anteroposterior diameter (CAP). Data from different sources (see Material and methods).

others (Prevosti & Vizcaíno 2006, Prevosti & Martin 2013, Bocherens *et al.* 2016, Prevosti & Forasiepi 2018, Werdelin *et al.* 2018). Moreover, as was already pointed out by Bocherens *et al.* (2016), if *Smilodon* used social-hunting behavior, then it is possible that they were able to kill larger prey, as occurs in large extant felids (Schaller 1972, Christiansen & Harris 2005, Sunquist & Sunquist 2009, Power & Compion 2009). In this context, and keeping in mind the maximum prey size estimation presented in this paper, it is not unreasonable that both *Megatherium* Cuvier, 1796 (body mass 6073 kg) and *Stegomastodon* Pohlig, 1912 (body mass 7580 kg) (Prevosti & Vizcaíno 2006) could be hunted by *Smilodon*, even in the adult stage (Werdelin *et al.* 2018 and references therein).

Others carnivorous mammals that potentially could have preyed upon the Lujanian South American large prey and megafauna (or at least juvenile individuals) include the felids

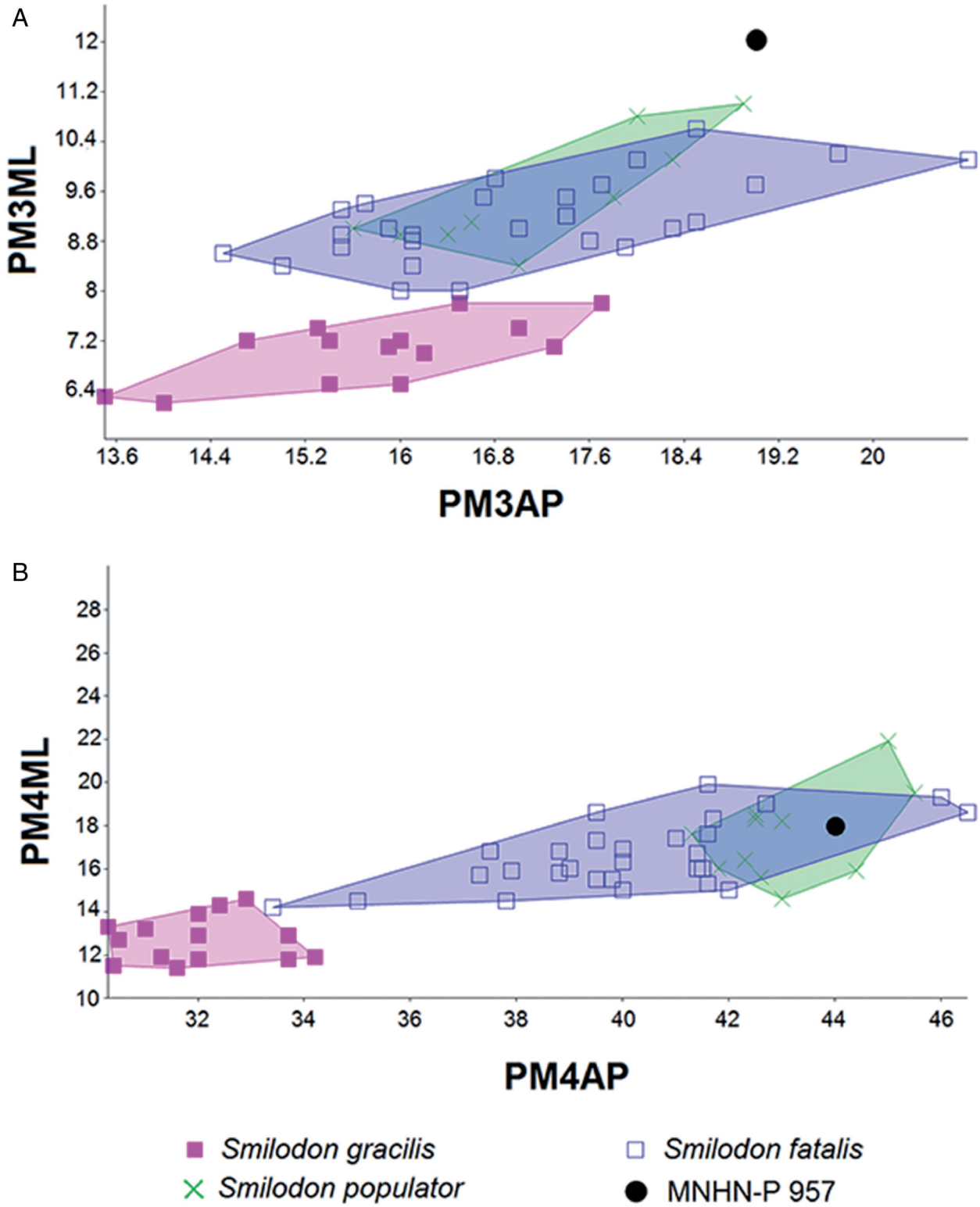

Fig. 4. Bivariate graphs for the *Smilodon populator* specimen MNHN-P 957. **A**, PM3 transverse diameter (PM3ML) versus PM3 anteroposterior diameter (PM3AP); **B**, PM4 transverse diameter (PM4ML) versus PM4 anteroposterior diameter (PM4AP). Data from different sources (see Material and methods).

Smilodon fatalis, *Panthera onca*, and *P. atrox* Leidy, 1853; some canids that were probably pack-hunters (*Canis nehringi* Ameghino, 1902, and *Protocyon troglodytes* (Lund), 1838) and the short-faced bear *Arctotherium* (see Prevosti & Vizcaíno 2006, Prevosti *et al.* 2009, Prevosti & Martin 2013, Bocherens *et al.* 2016, Chimento & Agnolin 2017, Manzuetti *et al.* 2018a). However, trophic segregation could be inferred based on the differences in body mass between each carnivore species (Prevosti & Martin 2013). If so, it is possible that only *Smilodon* preyed consistently on the larger herbivores and megaherbivores within this fauna (Prevosti & Vizcaíno 2006, Prevosti & Martin 2013, see also Bocherens *et al.* 2016). Finally, although speculative, the presence of other individuals of *Smilodon populator* of such large size cannot be ruled out.

In this way, the opening observed in the frontonasal region of the skull resemble to those described by Chimento *et al.* (2019; see also Antón, 2013 and references therein), thus could be tentatively assigned to signs of attack by another *Smilodon* individual as a result of an intraspecific agonistic interaction. So, the impact of this large-bodied predator on the late Pleistocene fauna is not yet be fully understood.

Conclusions

The skull herein described (MNHN-P 957) corresponds, both in anatomical and morphometric characteristics, to an extremely large individual of *Smilodon populator*. This skull is one of the largest specimens ever recovered and studied of this species. Its estimated body mass exceeds 400 kg and may have weighed as much as 436 kg. *Smilodon populator* preyed on herbivorous animals much larger than the predator. Prey mass calculations average above 1 t and approach a maximum of 3 t. It is clear that *S. populator* was at the top of the food chain and without doubt could have fed on the wide variety of megamammals (juvenile and adult) present during the late Pleistocene of South America. More material and additional studies are necessary to better understand the overall ecological impact of this large-bodied predator on the faunas of the past.

Acknowledgements

We thank Alejandra Rojas (FC-DPV) and family Brum-Martínez (CBM) for the fossil comparative remains of *S. populator* and *S. fatalis*, respectively, in the collection under their care. Two anonymous reviewers and the Associate Editor made suggestions that significantly improved the manuscript. Margaret Lewis, Christopher Shaw and Kevin Seymour also provided constructive criticisms and kindly helped with language issues. This paper is a contribution to ANII project POS_NAC_2018_1_151199 (A. Manzuetti).

Disclosure statement

No potential conflict of interest was reported by the authors.

References

Ameghino, F., 1902. Notas sobre algunos mamíferos fósiles nuevos o poco conocidos del valle de Tarija. *Anales del Museo Nacional Buenos Aires 3*, 225–261.

Ameghino, F., 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina 57*, 162–341.

Antón, M., 2013. *Sabertooth: Life of the Past*. Indiana University Press, Indiana, 269 pp.

Berta, A., 1985. The status of *Smilodon* in North and South America. Natural History Museum of Los Angeles County. *Contributions in Science 370*, 1–15.

Berta, A., 1987. The sabercat *Smilodon gracilis* from Florida and a discussion of its relationships (Mammalia, Felidae, Smilodontini). *Bulletin of the Florida State Museum Biological Sciences 31*, 1–63.

Berta, A., 1995. Fossil carnivores from the Leisey Shell Pits, Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History 37*, 463–499.

Bocherens, H., Cotte, M., Bonini, R., Scian, D., Straccia, P., Soibelzon, L. & Prevosti, F., 2016. Paleobiology of sabretooth cat *Smilodon populator* in the Pampean Region (Buenos Aires Province, Argentina) around the Last Glacial Maximum: Insights from carbon and nitrogen stable isotopes in bone collagen. *Palaeogeography, Palaeoclimatology, Palaeoecology 499*, 463–474.

Burmeister, G., 1879. *Description physique de la République Argentine d'après des observations personnelles étragères 3 (animaux vertébrés, 1: Mammifères vivants et éteints)*. P.E. Coni, Buenos Aires, 555 pp.

Chimento, N.R. & Agnolin, F.L., 2017. The fossil American lion (*Panthera atrox*) in South America: Palaeobiogeographical implications. *Comptes Rendus Palevol 16*, 850.

Chimento, N., Agnolin, F., Soibelzon, L., Ochoa, J. & Buide, V., 2019. Evidence of intraspecific agonistic interactions in *Smilodon populator* (Carnivora, Felidae). *Comptes Rendus Palevol 18*, 449.

Christiansen, P. & Harris, J., 2005. Body size of *Smilodon* (Mammalia: Felidae). *Journal of Morphology 266*, 369–384.

Churcher, C., 1967. *Smilodon neogaeus* en las barrancas costeras de Mar del Plata, provincia de Buenos Aires. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata* 1, 245–262.

Cope, E.D., 1880. On the extincts cats of America. *The American Naturalist 14*, 833–858.

Cordeiro de Castro, M. & Cardoso Langer, M., 2008. New postcranial remains of *Smilodon populator* Lund, 1842 from South-Central Brazil. *Revista Brasileira de Paleontologia 11*, 199–206.

Corona, A., Perea, D. & Mcdonald, G., 2013. *Catonyx cuvieri* (Xenarthra, Mylodontidae, Scelidotheriinae) from the late Pleistocene of Uruguay, with comments regarding the systematics of the subfamily. *Journal of Vertebrate Paleontology 33*, 1214–1225.

Cuvier, G., 1796. Notice sur le squelette d'une très – grande espèce de quadrupède inconnue jusqu'à présent, trouvé au Paraguay, et déposé au Cabinet d'Histoire naturelle de Madrid. *Magasin Encyclopèdique, ou Journal Des Sciences, Des Lettres et Des Arts 52*, 253–267.

Elissamburu, A., 2012. Estimación de la masa corporal en géneros del Orden Notoungulata. *Estudios Geológicos 68*, 91–111.

Emerson, S.B. & Radinsky, L., 1980. Functional analysis of sabertooth cranial morphology. *Paleobiology 6*, 295–312.

Gervais, H. & Ameghino, F., 1880. *Les Mammiferes Fossiles de lAmérique du Sud*. F. Savy – Igon Hnos., Paris, 225 pp.

Gervais, P., 1855. Recherches sur les mammifères fossiles de l'Amérique méridionale. *Comptes Rendus de L'Academie Des Sciences 40*, 1112–1114.

Ghizzoni, M., 2014. Estimación de la masa corporal de un ejemplar cuaternario del carpincho extinto Neochoerus a través de medidas cráneo-dentales. *Revista Brasileira de Paleontologia 17*, 83–90.

Hammer, O., Harper, D. & Ryan, P.D., 2001. PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica 4*, 1–9.

Hemmer, H., Kahlke, R. & Vekua, A.K., 2011. The cheetah *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l. at the hominin site of Dmanisi (Georgia) – A potential prime meat supplier in Early Pleistocene ecosystems. *Quaternary Science Reviews 30*, 2703–2714.

Kurtén, B. & Werdelin, L., 1990. Relationships between North and South American *Smilodon*. *Journal of Vertebrate Paleontology 10*, 158–169.

Leidy, J., 1853. Description of an extinct species of American lion: *Felis atrox*. *Transactions of the American Philosophical Society 10*, 319–321.

Leidy, J., 1868. Notice of some vertebrate remains from Hardin County, Texas. *Proceedings of the Academy of Natural Sciences of Philadelphia for 1868* 174–176.

Linnaeus, C., 1758. *Systema Naturae per regna tri naturae secundum clasiss, ordines, genera, especies cum characteriebus, differentiis synonymis loci. (Décima edición)*. Laurentii Salvii, Stocolmo, 824 pp.

Losey, R.J., Mclachlin, K., Nomokonova, T., Latham, K. & Harrington, L., 2017. Body mass estimates in Dogs and North American Gray Wolves using limb element dimensions. *International Journal of Osteoarchaeology 27*, 180–191.

Lund, P., 1838. Blik paa Brasiliens Dyreverden för Sidste Jordomvaeltning. Förste Afhandling: Indledning. Det kongelige Danske Vindenskabernes Selskabs naturvidenskabelige og mathematiske. *Afhandliger 8*, 27–60.

Lund, P.W., 1842. Blik paa Brasiliens dyreverden för sidste Jordomvaeltning. Fjerde Afhandling: fortsaettelse af pattedyrene. *Det Kongelige Danske Videnskabernes Selskabs Naturnvidenskabelige og Mathematiske Afhandlinger 9*, 137–208.

Manzuetti, A., Perea, D., Ubilla, M. & Rinderknecht, A., 2018a. First record of *Smilodon fatalis* Leidy, 1868 (Felidae, Machairodontinae) in the extra-Andean region of South America (late Pleistocene, Sopas Formation), Uruguay: Taxonomic and paleobiogeographic implications. *Quaternary Science Reviews 180*, 57–62.

Manzuetti, A., Perea, D., Rinderknecht, A. & Ubilla, M., 2018b. New Canid Remains from Dolores Formation, late Pleistocene-early Holocene, Uruguay. *Journal of Mammalian Evolution 25*, 391–396.

Martínez, S. & Ubilla, M., 2004. El Cuaternario en Uruguay. In *Cuencas Sedimentarias de Uruguay. Geología, Paleontología y Recursos Naturales. Cenozoico*. Veroslavsky, G., Ubilla, M. & Martínez, S., eds., Ediciones DI.R.A.C. Universidad de la República Facultad de Ciencias, Montevideo, 195–228.

Méndez-Alzola, R., 1941. El *Smilodon bonaerensis* (Muñiz): estudio osteológico y osteométrico del gran tigre fósil de La Pampa comparado con otros félidos actuales y fósiles. *Anales del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 40*, 135–252.

Merriam, J.C. & Stock, C., 1932. The Felidae of Rancho La Brea. *Carnegie Institution of Washington Publication 422*, 1–231.

Mones, A. & Castiglioni, L.R., 1979. Additions to the knowledge on fossil rodents of Uruguay (Mammalia: Rodentia). *Paläontologische Zeitschrift 53*, 77–87.

Mones, A. & Francis, J., 1973. Lista de los Vertebrados Fósiles del Uruguay: Mammalia. *Comunicaciones Paleontológicas del Museo de Historia Natural de Montevideo 4*, 39–98.

Owen, R., 1837. A description of the cranium of *Toxodon platensis*, a gigantic extinct mammiferous species, referrible by its dentition to the Rodentia, but with affinities to the Pachydermata and the herviborous Cetacea. *Proceedings of the Geological Society of London 2*, 541–542.

Owen, R., 1839. Fossil Mammalia. In *The Zoology of the Voyage of the M.H.S. Beagle*. Darwin, C.R., ed., Smith, Elder & Co., London, 41–64.

Pohlig, H., 1912. Sur une vieille mandibule de "Tetracaulodon ohioticum" Blum., avec défense in situ. *Bulletin de la Société Belge de Géologie 26*, 187–193.

Power, J. & Compion, S., 2009. Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *African Zoology 44*, 36. 36-44.

Prevosti, F. & Forasiepi, A., 2018. *Evolution of South American Mammalian Predators during the Cenozoic: Paleobiogeographic and Paleoenvironmental Contingencies*. Springer Geology, Switzerland, 196 pp.

Prevosti, F. & Martin, F., 2013. Paleoecology of the mammalian predator guild of Southern Patagonia during the latest Pleistocene: ecomorphology, stable isotopes, and taphonomy. *Quaternary International 305*, 74.

Prevosti, F. & Vizcaíno, S., 2006. Paleoecology of the large carnivore guild from the late Pleistocene of Argentina. *Acta Palaeontologica Polonica 51*, 407–422.

Prevosti, F., Ubilla, M. & Perea, D., 2009. Large extinct canids from the Pleistocene of Uruguay: systematic, biogeographic and paleoecological remarks. *Historical Biology 21*, 79–89.

Prieto, A., Labarca, R. & Sierpe, V., 2010. New evidence of the saber-tooth cat *Smilodon* (Carnivora: Machairodontinae) in the late Pleistocene of southern Chilean Patagonia. *Revista Chilena de Historia Natural 83*, 299–307.

Rincón, A., 2006. A first record of the Pleistocene saber-toothed cat *Smilodon populator* Lund, 1842 (Carnivora: Felidae: Machairodontinae) from Venezuela. *Ameghiniana 43*, 499–501.

Rincón, A., Prevosti, F. & Parra, G., 2011. New saber-toothed cats records (Felidae: Machairodontinae) for the Pleistocene of Venezuela, and the Great American Biotic Interchange. *Journal of Vertebrate Paleontology 31*, 468–478.

Rinderknecht, A., 1998. Nuevos microvertebrados fósiles para el Pleistoceno superior del Uruguay (Amphibia, Reptilia, Aves). *Comunicaciones Paleontológicas del Museo de Historia Natural de Montevideo 2*, 133–144.

Roth, S., 1899. El mamífero misterioso de la Patagonia *Grypotherium domesticum*. II. Descripción de los restos encontrados en la Caverna de Última Esperanza. *Revista del Museo de La Plata 9*, 421–453.

Schaller, G.B., 1972. *The Serengeti lion – A Study of Predator-Prey Relations. Wildlife Behavior and Ecology Series*. University of Chicago Press, Chicago, 504 pp.

Shockey, B., & 10 others, 2009. New Pleistocene Cave Faunas of the Andes of Central Perú: Radiocarbon Ages and the Survival of Low Latitude, Pleistocene DNA. *Palaeontologia Electronica 12*, 1–15.

Soibelzon, L. & Prevosti, F., 2007. Los carnívoros (Carnivora, Mammalia) terrestres del Cuaternario de América del Sur. *Monografies de la Societat D'Historia Natural de Les Balears 14*, 49–68.

Soibelzon, L. & Prevosti, F., 2013. Fossil of South American land carnivores (Carnivora, Mammalia). *In Molecular Population Genetics, Evolutionary Biology and Biological Conservation of Neotropical Carnivores*. Ruíz-García, M. & Shostell, J.M., eds, Nova Science Publishers Inc., New York, 509–527.

Soibelzon, L. & Schubert, B., 2011. The Largest Known Bear, *Arctotherium angustidens*, from the Early Pleistocene Pampean Region of Argentina: With a Discussion of Size and Diet Trends in Bears. *Journal of Paleontology 85*, 69–75.

Soibelzon, L. & Tarantini, V., 2009. Estimación de la masa corporal de las especies de osos fósiles y actuales (Ursidae, Tremarctinae) de América del Sur. *Revista del Museo Argentino de Ciencias Naturales 11*, 243–254.

Sunquist, M.E. & Sunquist, F.C., 2009. Felidae (Cats). In *Handbook of the Mammals of the World: vol. 1. Carnivores*. Wilson, D.E. & Mittermeier, R.A., eds, Lynx Ediciones, Barcelona, 54–169.

Temminck, C.J., 1844. Apercu géneral et spécifique sur les Mammiféres qui habitent le Japon et les Iles qui en dépendent. In *Fauna Japonica (Mammiféres)*. Lugduni Batavorum, 60.

Turner, A. & Antón, M., 1997. *The Big Cats and Their Fossil Relatives: An Illustrated Guide to Their Evolution and Natural History*. Columbia University Press, New York, 234 pp.

Ubilla, M. & Martínez, S., 2016. *Geology and Paleontology of the Quaternary of Uruguay*. SpringerBriefs in Earth System Sciences, Switzerland, 77 pp.

Ubilla, M., Perea, D., Lorenzo, N., Gutiérrez, M. & Rinderknecht, A., 2011. Fauna Cuaternaria Continental. In *Fósiles de Uruguay*. Perea, D., ed, Edición DI.R.A.C- Facultad de Ciencias, Montevideo, 283–314.

Ubilla, M., Rinderknecht, A., Corona, A. & Perea, D., 2018. Mammals in last 30 to 7 ka interval (late Pleistocene-early Holocene) in southern Uruguay (Santa Lucía River Basin): last occurrences, climate and biogeography. *Journal of Mammalian Evolution 25*, 291–300.

Van Den Hoek Ostende, L.W., Morlo, M. & Nagel, D., 2006. Majestic killers: the sabre-toothed cats. *Geology Today 22*, 150–157.

Van Valkenburgh, B., 1990. Skeletal and dental predictors of body mass in carnivores. In *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Damuth, J. & Macfadden, B.J., eds, Cambridge University Press, Cambridge, 181–205.

Van Valkenburgh, B. & Jenkins, I., 2002. Evolutionary patterns in the history of Permo-Triassic and Cenozoic synapsid predators. *The Paleontological Society Papers 8*, 267–288.

Von Den Driesch, A., 1976. *A Guide to the Measurement of Animal Bones from Archaeological Sites*. Harvard University Press, Cambridge, 136 pp.

Werdelin, L., Mcdonald, H.G. & Shaw, C.A., 2018. *Smilodon: The Iconic Sabertooth*. Johns Hopkins University Press, Baltimore, 241 pp.

Wied-Neuwied, M.A.P., 1824. Verzeichnis der Amphibienwelche in zweiten Bande der Naturgeschichte Brasiliens von Prinz Max von Neuwied werdenbeschreiben Werden. *Isis von Oken 14*, 661–673.