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

Hervé Bocherens [a,b,*], Martin Cotte [a], Ricardo Bonini [c], Daniel Scian [d], Pablo Straccia [d,e], Leopoldo Soibelzon [f], Francisco J. Prevosti [g]

[a] *Department of Geosciences, Biogeology, University of Tübingen, Hölderlinstrasse 12, 72070 Tübingen, Germany*
[b] *Senckenberg Research Center for Human Evolution and Paleoenvironment, University of Tübingene, Hölderlinstrass 12, 72070 Tübingen, Germany*
[c] *División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Buenos Aires, Argentina*
[d] *Museo Municipal de Ciencias Naturales Pachamama, Santa Clara del Mar, Argentina*
[e] *Universidad Nacional de Mar del Plata, Argentina*
[f] *Div. Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque, 1900 La Plata, Argentina*
[g] *Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de Anillaco (CRILAR — CONICET), Entre Ríos y Mendoza s/n, 5301 Anillaco, La Rioja, Argentina*

ABSTRACT

The sabretooth cat *Smilodon populator* was the largest felid in South America. It appears in the fossil record in the Early Pleistocene, as an immigrant from North America, and becomes extinct around the Pleistocene–Holocene boundary. The carbon and nitrogen stable isotopic values of collagen were measured for skeletal remains from *Smilodon* specimens ranging in age from 25 to 10 kyr BP, for the first time in the Pampas region of Argentina. By comparison with similar values obtained on co-eval predators such as *Protocyon* (large canid) and *Panthera onca* (jaguar) and a range of potential prey, such as giant ground sloths, glyptodontids, *Macrauchenia*, *Toxodon*, equids, cervids, and rodents, it could be established that *Smilodon* consumed essentially large prey from open landscape, such as *Macrauchenia* and giant ground sloths during the last 15,000 years of the Late Pleistocene in the Pampa region. It was possibly competing with the large canid *Protocyon* but the jaguar was apparently feeding on smaller size prey. A more humid climate at the beginning of the Holocene might have been unfavorable to this large predator and could have contributed to its extinction. These results also provide an important insight to understand the ecological processes involved in the Great American Biotic Interchange.

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1. Introduction

The sabretooth cat *Smilodon* is an emblematic figure of the Great American Biotic Interchange, during which a number of North American large mammals migrated and settled in South America (e.g. Simpson, 1980; Cione et al., 2015). This genus originated in North America, where two species were recorded: *Smilodon gracilis* in the Late Pliocene — Middle Pleistocene and *Smilodon fatalis* during the Middle — Late Pleistocene (Berta, 1985, 1987; Kurtén and Werdelin, 1990). Based on the fossil record, *Smilodon* migrated to South America at least two times, the first time after the establishment of the Panama land bridge that connected South America with Central America, and the second time in the Late Pleistocene when *S. fatalis* reached the northwest of South America (Berta, 1985; Kurtén and Werdelin, 1990; Rincón et al., 2011; Prevosti and Soibelzon, 2012).

Therefore three species of this genus were recorded in South America: *Smilodon populator* along the continent during the Early — Late Pleistocene, *S. gracilis* in northern South America during the Early — Middle Pleistocene, and *S. fatalis* in the northwest of South America.

Among them, the sabretooth cat *S. populator*, with a weight that could reach up to 400 kg, was the largest felid in South America and one of the largest felids in the world (Christiansen and Harris, 2005; Prevosti and Vizcaíno, 2006; Prevosti and Martin, 2013). It is usually assumed that, when sabretooth cats moved into South America from North America after a land bridge was open between both continents (during the Great American Biotic Interchange, Marshall et al. 1982) after three million years ago, they could have out-competed the metatherian sabretoothed carnivore *Thylacosmilus atrox* (e.g., Simpson, 1980). This endemic South American sparassodont exhibited superficial similarities with *Smilodon*, especially the hypertrophied upper canines. However, *Thylacosmilus* also had significant differences with *Smilodon*, such as a smaller size, differences in the post-cranial skeleton as well as different front teeth morphology and enamel only on the external side of the

* Corresponding author at: Department of Geosciences, Biogeology, University of Tübingen, Hölderlinstrasse 12, 72070 Tübingen, Germany.
E-mail address: herve.bocherens@uni-tuebingen.de (H. Bocherens).

canines (Riggs, 1934; Argot, 2004; Prevosti et al., 2010; Koenigswald, 2011). Moreover, there was a temporal gap of 1.2 to 2 Ma between the last records of *Thylacosmilus* and the first records of *Smilodon*, which argues against a competitive displacement between these carnivorous taxa (see Prevosti et al., 2013). Indeed, *S. populator* appears in the fossil record in the Early Pleistocene (Prevosti and Pomi, 2007; Rincón et al., 2011; Prevosti and Soibelzon, 2012), while the youngest dated specimens are from the very late Pleistocene or even the early Holocene (Barnosky and Lindsey, 2010; Prieto et al., 2010; Prevosti and Martin, 2013; Scanferla et al., 2013; Prado et al., 2015).

If *S. populator* occurred in South America only after the extinction of *Thylacosmilus*, it is conceivable, based on the convergent morphology, that there was an ecological replacement between both successive species if *Smilodon* used the same ecological niche as *Thylacosmilus*. A better understanding of the actual ecology of invasive carnivores in South America, such as *Smilodon*, is needed to test the hypothesis of a competitive displacement or ecological replacement of marsupial carnivores by invasive placental carnivores from North America. After a review of the available evidence on the dietary paleobiology of *Smilodon*, and especially *S. populator*, the results of carbon and nitrogen analyses on bone collagen from this species as well as coeval large mammals will be used to test different hypotheses on the predator behavior and prey choice of this recently extinct predator.

2. Predatory behavior and prey choice of *S. populator*: a short overview

One particular aspect of the paleobiology of the sabretooth cat *Smilodon* has received a high level of attention, i.e. the killing mechanism of this predator without analog in the modern world (e.g. Warren, 1853; Simpson, 1941; Akersten, 1985; Therrien, 2005; McHenry et al., 2007; Andersson et al., 2011; Wheeler, 2011; Wilson et al., 2013; Wroe et al., 2013; Brown, 2014). It must be kept in mind that most of these studies deal with the species *S. fatalis*, not with *S. populator*, the main species in South America, although numerous studies included *S. populator* recently (Christiansen 2008; Slater and Van Valkenburgh 2008; Prevosti and Vizcaíno, 2006; Prevosti et al. 2010; Prevosti and Martin, 2013). In any case, the paleobiology of *Smilodon* is not only about killing mechanism but also includes several other important aspects, such as its habitat(s), the range of prey preferences, its behavior (solitary or social), and to which extent it was competing with other large predators, such as other felids, canids and ursids (e.g., Prevosti and Vizcaíno, 2006; Prevosti and Martin, 2013).

Regarding its habitat, *Smilodon* is typically considered to be an ambush predator, therefore presumably living in wooded landscapes or at least where vegetation was dense enough to offer some cover. Consistent with this hypothesis is the fact that the forearm morphology of *Smilodon* is similar to that of forest felids (Meloro et al., 2013; Schellhorn and Sanmugaraja, 2015), suggesting a closed habitat. Moreover, pectoral and pelvis girdle adaptations indicate enhanced stalking abilities typical for an ambush predator (Naples, 2014).

In terms of prey preference, the specialized character of the very large canines of *Smilodon* has been regularly associated with a specialization for a specific type of prey, such as proboscideans or other very large herbivores (e.g. Meachen-Samuels and Van Valkenburgh, 2010). Most papers consider that *Smilodon* must have hunted large mammals, and they put a lot of emphasis on the techniques of killing (e.g. Andersson et al., 2011), but not much about which prey were hunted, except for some speculations in the nineteenth century about the fact that extraordinary dentition requires extraordinary prey, in this case thick-skinned large prey, such as ground sloth, glyptodonts or proboscideans (e.g. Owen 1846; Cope 1880). Based on taxa frequencies in the Early-Middle Pleistocene of the Pampean Region, Berman (1994) inferred that the "native" ungulate *Mesotherium*, the ground-sloth *Scelidotherium* and the glyptodon *Neosclerocalyptus* were important prey for *S. populator*. Prevosti and Vizcaíno (2006) using estimated

body size of *S. populator* and their potential prey, together with actualistic information about prey–predator body size relationships, inferred that this felid hunted frequently large mammals (e.g. large camelids, equids), as well as mega-mammals (e.g., ground-sloths) and that it was the top predator during the Late Pleistocene in the Pampean Region. Prevosti and Martin (2013), using a similar analysis and stable isotopes, found similar results for the southern Patagonia late Pleistocene fauna. However, paleoecological investigation of other late Pleistocene large felids, such as cave lions, have demonstrated some spatial and chronological variation in the dietary preference of these predators (e.g. Bocherens, 2015; Kirillova et al., 2015), therefore additional investigations on *Smilodon* from other regions are needed.

Another point of discussion is whether *Smilodon* had a solitary or a collective hunting behavior. If collective hunting was performed, this opens the possibility to kill larger prey, as it is the case for extant large felids (e.g. Hayward and Kerley, 2005; Van Valkenburgh et al., 2016). Some authors consider that *Smilodon* had a social behavior (e.g. Carbone et al., 2009) but others do not agree (e.g. McCall et al., 2003; Kiffner, 2009).

As member of the large predator guild, *Smilodon* would have had to handle competition, especially since other large predators were present in the Late Pleistocene of Argentina, such as other large felids, especially the jaguar *Panthera onca*, as well as large canids, such as *Theriodictis* and *Protocyon*, and the giant ursid *Arctotherium* (e.g. Berman, 1994; Soibelzon and Schubert, 2011; Prevosti and Martin, 2013; Soibelzon et al., 2014). Indeed competition is an important factor in the prey choice and foraging strategies of large predators in modern ecosystems (e.g. Elbroch et al., 2015; Périquet et al., 2015), and similar processes are expected to have also been important in the past (e.g. Domingo et al., 2013; Bocherens, 2015).

The youngest occurring *Smilodon* specimens from South America offer the possibility to use carbon and nitrogen isotopic tracking of bone collagen to refine our knowledge of the paleobiology of this extinct predator. Carbon and nitrogen isotopes in bone collagen are powerful tools to reconstruct prey preference of large predators and to test for potential competition among coeval predators (e.g. Fox-Dobbs et al., 2008; Bocherens et al., 2011; Bocherens et al., 2015a; Yeakel et al., 2013; Bocherens, 2015). Moreover the carbon isotopic values of their prey indirectly track the habitat of the predators. In addition, the range of isotopic variation among individuals of the investigated predator species provides information about flexibility and potentially about collective versus solitary hunting behavior (e.g. Bocherens et al., 2011; Bocherens, 2015). To apply this approach, bones with sufficiently good collagen preservation from different species of herbivores (the potential prey) and the predators (the species being investigated, *Smilodon*, as well as its potential competitors) from the same area and time period are needed. So far, C and N isotopes in *Smilodon* collagen have been published only for specimens of *S. fatalis* in Rancho la Brea (California, USA) (Coltrain et al., 2004; Fuller et al., 2014), and for *S. populator* from southern Chile (Prevosti and Martin, 2013), but none from the Pampean region of the Buenos Aires Province in Argentina.

3. Principles of tracking predator paleoecology with C and N stable isotopes

Carbon stable isotopes have been used as tracers of plant food consumed by herbivores for more than 30 years (e.g. DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Koch et al., 1991). Indeed, the tissues of an animal are formed using the carbon assimilated from the consumed food, and taking into account predictable differences among various fractions, will incorporate the isotopic composition of this plant food. Therefore, the isotopic variations present in the plants will be transferred into the tissues of their consumers. The main source of isotopic variation in terrestrial plants is the type of photosynthesis, namely C_3 or C_4, with C_4 plants having a clearly higher carbon isotopic value ($\delta^{13}C$ value) as their C_3 counterparts (e.g. Smith and Epstein, 1971;

Tieszen et al., 1979). C_4 plants correspond to grass and herbaceous plants adapted to sunlight and warm growing season, while C_3 plants include grass from cooler environments as well as all woody plants, i.e. trees and shrubs. Today, the Argentinean Pampas are located at middle latitudes where C_4 grasses are present together with C_3 grasses (e.g. Jacobo et al., 2000). Climatic as well as local factors, such as soil pH, structure and humidity, as well as topography, determine the relative abundance of C_3 and C_4 grasses in the Pampas (e.g. Perelman et al., 2001). Measurements of $\delta^{13}C$ values on bone collagen from modern and Holocene herbivores in the Pampas region indicate a dominance of C_3 plants, even if some C_4 plants were also consumed in lower proportions by some individuals (e.g. Barberena et al., 2009; Martínez et al., 2009).

Nitrogen isotopic ratios ($\delta^{15}N$) increase significantly between a consumer and its food and therefore this isotopic tracer has been regularly used as an indicator of position in a trophic web for modern and ancient animals (e.g. DeNiro and Epstein, 1981; Bocherens et al., 1994). Since herbivores eat different plants with various $\delta^{13}C$ and $\delta^{15}N$ values, potential prey of a predator differ by their $\delta^{13}C$ and $\delta^{15}N$ values. In such a context, the isotopic values of different predators can be used to evaluate the proportion of the prey consumed by these predators, with possible intra- or inter-specific variations (e.g. Fox-Dobbs et al., 2007, 2008; Bocherens et al., 2011; Bocherens et al., 2015a; Prevosti and Martin, 2013; Yeakel et al., 2013; Bocherens, 2015).

The application of the isotopic approach described above to Pleistocene ecosystems relies on the preservation of collagen in ancient bones, and on the possibility to distinguish reasonably well prey categories with well-defined $\delta^{13}C$ and $\delta^{15}N$ values. Collagen has better chances of preservation at low temperatures and in sheltered deposits such as caves (e.g. Holmes et al., 2005, 2006). These climatic factors are not as favorable in the Argentinean Pampas as at higher latitudes such as in southern Patagonia for instance, since Late Pleistocene sites in the Pampas are open-air sites and the temperatures are not so low. However, local circumstances may allow collagen to be sufficiently well preserved even in globally unfavorable context (e.g. Pestle and Colvard, 2012). Moreover, a number of radiocarbon dates have been obtained on Late Pleistocene bones from the Pampas (e.g. Steele and Politis, 2009; Scanferla et al., 2013; Prado et al., 2015), showing that collagen preservation is nevertheless possible in such sedimentary contexts.

To decipher the proportions of prey consumed by predators such as *Smilodon*, a wide range of species that were coeval with this large felid have to be analyzed, in the same sites as the *Smilodon* specimens or from sites formed under similar environmental conditions. Indeed carbon and nitrogen isotopic composition of plants may vary according to factors such as temperature and aridity (e.g. Tieszen, 1991; Amundson et al., 2003). Mixing fossil remains of prey and predators that lived under different environmental conditions may lead to changes in $\delta^{15}N$ values that could be erroneously attributed to prey change although they just reflect changes in the $\delta^{15}N$ values of a given prey (e.g. Bocherens et al., 2014). In the present study, we limited the chronological range to the Upper Green Sector of the Guerrero member, ranging from around 27,000 yr ^{14}C BP to around 10,000 yr ^{14}C BP, with predominantly dry and cold climatic conditions (Prado and Alberdi, 1999; Tonni et al., 1999). However, due to the poor stratigraphical and chronological resolution, it is not possible to exclude short and abrupt periods of wetter and warmer climatic excursions during this period around the time of the Last Glacial Maximum (Tonni et al., 1999). A temperate humid episode follows this dry and cold episode (Prado and Alberdi, 1999) and such a climatic shift could lead to a decrease of the $\delta^{15}N$ value baseline in the plants. Therefore fossils with radiocarbon ages younger than 12,000 yr BP were not considered in the present study, except for one *Smilodon* dated to around 10,000 yr ^{14}C BP (Prado et al., 2015).

4. Material

Bones from latest Pleistocene sites in the Buenos Aires Province were selected (Fig. 1). We focused on sites where previous studies had

yielded radiocarbon dates on bone collagen with extinct megafauna, namely Rio Salado (e.g. Scanferla et al., 2013), Cascada del Paleolama in Quequén Salado, Paso Otero and Arroyo Tapalqué (e.g., Prado et al. 2015). The site of Camet Norte was also selected due to its rich and diverse large mammal fauna including carnivores such as *Smilodon*, and because organic remains such as fossil plants and herbivore dung were preserved in this site (Pardiñas et al. 1998). Based on previous experience of good collagen preservation under such sedimentary conditions (e.g. Bocherens et al., 1997b; Kuitems et al., 2015), this site was included as well. In addition, a few isolated specimens of Late Pleistocene carnivores from the same area were selected, which would require direct radiocarbon dating if collagen were to be extracted from these bones.

The Rio Salado sites yielded Late Pleistocene fossils found in the floodplain of the Rio Salado River in the vicinity of La Chumbiada, General Belgrano town, and housed at the Museo Historico Municipal "A. E. Múlgura"(General Belgrano, Buenos Aires province, Argentina). Some previously published conventional radiocarbon dates on bone collagen ranged from 13,400 ± 200 to 12,380 ± 190 BP (Scanferla et al., 2013), while AMS radiocarbon dates also on bone collagen ranged from 14,190 ± 60 BP to 11,590 ± 60 BP (Prado et al., 2015; see Mari et al., 2013 and Fucks et al., 2015 for a review of the geology and age of this basin). Some parts of this floodplain could have been swampy and trapped animals, allowing for good preservation conditions (Pomi, 2009). Altogether, 33 specimens from this site were selected, including 7 *Smilodon*, together with bones from giant ground sloths (*Megatherium*, *Scelidotherium*, *Glossotherium*), glyptodontids (*Glyptodon*, *Doedicurus*, *Neosclerocalyptus*), Camelids, Equids, Cervids and rodents (Table S1).

The Camet Norte site is located on the coast of the Atlantic Ocean in the town of Santa Clara del Mar, near Mar del Plata. It yielded about 30 taxa of mainly extinct megamammals and the level, at the basis of the sequence, which yielded most of the mammal fossil remains, has been radiocarbon dated to around 24,500 ^{14}C years BP using herbivore dung as dating material (Pardiñas et al., 1998). The sampled bone material comes for the collection of the Museo Municipal de Ciencias Naturales Pachamama (Santa Clara del Mar, Buenos Aires Province, Argentina). During the life time of the studied fossils, the site was located well inland since the coastline was shifted around 170 km farther east due to the lower sea level at that time (Fig. 1). Twenty-two bones from this site were collected, including 2 *Smilodon*, 2 bears *Arctotherium*, as well as herbivores such as *Macrauchenia*, *Toxodon*, Glyptodontids, Giant ground sloths, Camelids, Cervids, and Equids (Table S1).

Arroyo Tapalqué is a site located in the south of the Buenos Aires Province, which yielded ^{14}C dates covering the last 30,000 years (Figini et al., 1998). Besides *S. populator*, several other large mammal bones have been found in this locality and sabretooth cat, horse and deer from this locality were analyzed in the present study.

Additional interesting specimens were collected from different additional sites in the Buenos Aires Province. Cascada del Paleolama in Quequén Salado is a site located in the southern part of the Buenos Aires Province, containing levels older than 30 ka that were referred to the last interglacial (ca. 120 ka; Pardiñas et al., 1996), but also younger levels, one with a radiocarbon date on bone of 14,020 ± 60 BP (Prado et al., 2012). Moreover, a few additional samples from various localities, including Paso Otero, Cascada del Paleolama in Quequén Grande, Rio Quequén Grande, and Salto Argentina were also included in the present study (Table S1).

Finally, a few bones from fossil carnivores from unknown localities in the Buenos Aires Province, including one mandible of *Lycalopex gymnocercus*, one piece of skull of *Arctotherium*, and one jaguar *P. onca* skull were also sampled since they correspond to carnivorous species that were not present in the main sites studied here and that could be eventually radiocarbon dated if they contained collagen.

Altogether, 70 bones from various species, including twelve pieces belonging to *Smilodon* (9 bones and 3 teeth) were investigated in the
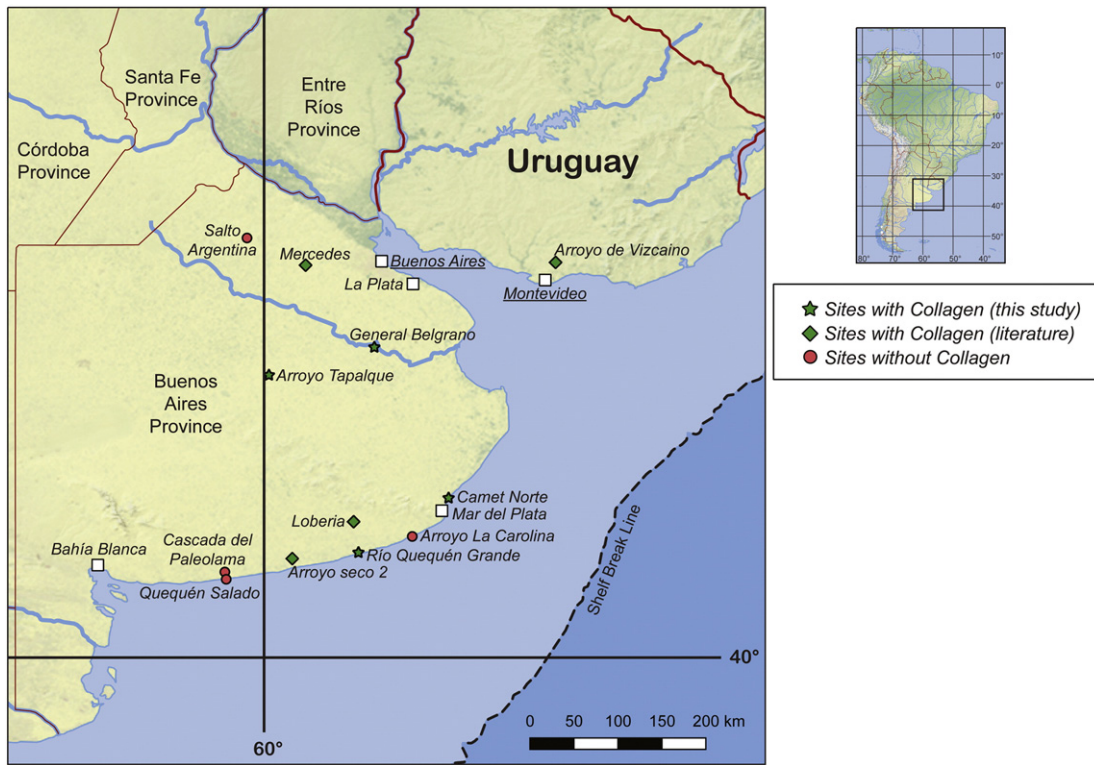
Fig. 1. Map of localities mentioned in the text, with indication of the coast line during the late Pleistocene, at the level of the shelf break line.

present study. All these pieces most likely belong to different individuals. Indeed the material from Rio Salado was collected at very different locations along the Salado River and most of the time years apart. In Camet Norte, the two pieces of *Smilodon* were collected some years apart. Studied material for other carnivores belong to Felidae (jaguar *P. onca*, N = 1), Canidae (*L. gymnocercus*, N = 1; *Dusicyon avus*, N = 1), and Ursidae (*Arctotherium*, N = 3). In addition, skeletal material from herbivores corresponding to the potential prey of *Smilodon* and other carnivores have been sampled, belonging to different groups, such as Proboscidea (*Stegomastodon* N = 2), Perissodactyla (*Hippidion* N = 3; *Equus* N = 3), Artiodactyla (Cervids N = 5, Camelids N = 4), Meriungulata (*Toxodon* N = 3, *Macrauchenia* N = 2), Xenarthrans (four species: of ground sloths: *Megatherium* N = 7, *Lestodon* N = 1, *Glossotherium* N = 3, *Scelidotherium* N = 4, five species of Glyptodonts: *Glyptodon* N = 6, *Panochthus* N = 1, *Doedicurus* N = 3, *Propoapus* N = 1, *Neosclerocalyptus* N = 2), and two Rodentia (*Lagostomus* N = 2).

To complete the isotopic dataset, we searched published data from the existing literature. Although several radiocarbon dates on bone collagen have been published, few of them have been published with their δ13C and δ15N values or have been made on identified specimens (Steele and Politis 2009; Prevosti and Schubert, 2013; Czerwonogora et al., 2011). Nevertheless, we could find nine reported δ13C and δ15N values of interest for the present study (Table 1), including some on one dated specimen of *Glossotherium* from the Buenos Aires Province with δ13C and δ15N values (Czerwonogora et al., 2011), on one *Megatherium* bone from Arroyo Seco 2 (Steele and Politis, 2009) and on three *Lestodon* from southern Uruguay with δ13C and δ15N values (Czerwonogora et al., 2011), these data are considered here since this area is geographically close to the Buenos Aires Province and belong to the same ecological region, today as well as during the Late Pleistocene (Cione et al., 2009; Le Roux, 2012). In addition, some δ15N values have been published by Prado et al. (2015) but without associated δ13C values, for *Hippidion* and *Doedicurus*. These values were considered in combination with the δ13C values measured on other specimens from the same taxa in the present study (Table 2).

5. Methods

For each specimen, a small fragment was carefully sawn with a dremmel rotary tool equipped with a circular diamond-coated blade, then ultrasonicated in acetone and water, rinsed with distilled water, dried and crushed to a powder of 0.7 mm grain size (Bocherens et al., 1997a). Then, for most of the fossil samples, an aliquot of around 5 mg

Table 1
Number of tested specimens per species and number of samples with collagen preserved for δ13C and δ15N values (including those gathered from the literature).

Species	Tested specimens	C and N of collagen		No collagen
		This study	Literature	
Smilodon	12	7	0	5
Panthera onca	1	1	0	0
Protocyon troglodytes	0	0	1	0
Dusicyon avus	1	0	0	1
Pseudalopex	1	0	0	1
Arctotherium	3	0	0	3
Stegomastodon	2	0	0	2
Equus	4	3	0	1
Hippidion	3	1	1	2
Cervidae	4	2	0	2
Camelids	4	0	0	4
Toxodon	3	1	0	2
Macrauchenia	2	2	0	0
Megatherium	7	4	1	3
Lestodon	1	0	3	1
Glossotherium	3	2	1	1
Scelidotherium	4	0	0	4
Glyptodon	6	3	0	3
Panochthus	1	0	0	1
Doedicurus	3	1	2	2
Propoapus	1	0	0	1
Neosclerocalyptus	2	0	0	2
Lagostomus	2	1	0	1
Total	70	28	9	42

Table 2
List of samples for which δ¹³C and δ¹⁵N have been measured in the present study, and those taken from the literature.

Lab #	Museum #	Genus	Sampled	Site	%C	%N	C/N	δ13X	δ15N	14C date	sd	Ref. Date	Reference
ARGC-1	MHM-P85	*S. populator*	Canine	General Belgrano	39.6	14.2	3.3	−17.7	15.4				This study
ARGC-2	MHM-P53	*S. populator*	Femur	General Belgrano	43.8	16.0	3.2	−17.7	14.2	13,400	200	LP-2140	This study and Scanferla et al. 2013
ARGC-19	MHM-P31	*S. populator*	Cranium	General Belgrano	42.9	15.5	3.2	−17.7	14.2				This study
ARGC-20	MHM-P71	*S. populator*	Sinistral radius	General Belgrano	42.1	15.2	3.2	−17.7	13.8				This study
ARGC-44	Santa Clara	*S. populator*	Vertebra	Camet Norte North, level B	45.0	14.9	3.5	−17.4	12.1	24,523	111	ETH-57,488	This study
ARGC-45	Santa Clara	*S. populator*	Tibia	Camet Norte North, level B	42.7	14.8	3.4	−17.6	11.2				This study
ARGC-66	MLP 98-II-20-1	*S. populator*	Canine	Arroyo Tapalque	41.9	14.8	3.3	−17.2	13.4	10,140	60	GrA-49,131	This study and Prado et al. 2015
ARGC-36	MLP 82-IV-7-1	*Panthera onca*	Skull (zygomatic arch)	"post-pampaneo"	42.7	15.3	3.2	−17.3	10.1	12,116	40	ETH-57,487	This study
NZA 29728	MLP 89-xi-20-1	*Protocyon troglodytes*	Canine root	Mercedes	24.5	8.0	3.6	−17.4	15.6	17,338	85	NZA 29728	Prevosti and Schubert, 2013
ARGC-6	MHM-P57	Hippidion	Distal tibia	General Belgrano	35.9	12.7	3.3	−21.2	11.2				This study
GrA-49,323	MLP-no number	Hippidion	Skull	General Belgrano		15.0		−21.2	9.9	14,190	60	GrA-49,323	Prado et al. 2015
ARGC-73	MLP-80-VIII-13-95	*Equus neogeus*	Metapodium	Paso Otero (Rio Quequén Grande)	41.2	14.5	3.3	−19.8	3.7	13,930	60	GrA-47,132	This study and Prado et al. 2015
ARGC-74	MLP-86-III-25-17	*Equus neogeus*	Phalange 2	Arroyo Tapalque	42.2	14.8	3.3	−21.0	7.1				This study
ARGC-80	MHM-P 73	Equidae	Bone	General Belgrano	41.0	14.5	3.3	−17.9	7.5				This study
ARGC-71	MLP 86-III-25-24	Cervidae	Humerus	Arroyo Tapalque	42.5	14.9	3.3	−20.3	6.1				This study
ARGC-72	MLP 86-III-25-25	Cervidae	Tibia	Arroyo Tapalque	44.6	15.7	3.3	−21.2	6.7				This study
ARGC-48	Santa Clara	Macrauchenia	Fibula (+tibia)	Camet Norte North, level B	41.3	14.4	3.3	−17.1	10.3	24,732	112	ETH-57,489	This study
ARGC-62	Santa Clara	Macrauchenia	Fibula (+tibia)	Camet Norte North, no context	31.9	11.0	3.4	−17.0	10.2				This study
ARGC-61	Santa Clara	Toxodon	Humerus	Camet Norte North, level B	38.9	13.5	3.4	−20.8	10.3	23,691	103	ETH-57,490	This study
ARGC-24	MHM-P74	Lagostomus	Sinistral femur	General Belgrano	16.0	5.6	3.4	−20.8	5.9				This study
ARGC-3	MHM-P52	Megatherium	Molar	General Belgrano	27.1	9.7	3.3	−18.7	14.0				This study
ARGC-4	MHM-P52	Megatherium	Mandibula, dextral	General Belgrano	37.2	13.5	3.2	−19.7	12.4				This study
ARGC-46	Santa Clara	Megatherium	Mandible	Camet Norte North, level B	35.5	12.4	3.4	−17.3	9.5				This study
ARGC-64	Santa Clara	Megatherium	Molariform dentine	Camet Norte North, level B	38.8	13.2	3.4	−17.8	10.7				This study
OxA10387		Megatherium	Tibia.	Arroyo Seco 2, Argentina				−19.7	5.2	12,155	70	OxA10387	Steele and Politis, 2009
ARGC-58	Santa Clara	Glossotherium	Maxilla	Camet Norte North, level B	34.1	11.8	3.4	−19.4	10.4				This study
A5	MLP.83.XI.5.1	Glossotherium		Loberia	40.1	13.8	3.4	−20.6	10.4				Czerwonogora et al. 2011
ARGC-76	MLP 80-VIII-13-92	Glossotherium	Humerus R	Rio Quequén Grande	39.5	14.0	3.3	−20.3	8.8	14,160	60	GrA-47,131	This study and Prado et al. 2015
A1P	CAV unnumbered	*Lestodon armatus*	Rib	Arroyo de Vizcaíno	34.0	12.0	3.3	−18.7	9.6				Czerwonogora et al. 2011
A12P	CAV 121	*Lestodon armatus*	Humerus	Arroyo de Vizcaíno	32.1	11.5	3.3	−18.8	9.4				Czerwonogora et al. 2011
A14P	CAV unnumbered	*Lestodon armatus*	Rib	Arroyo de Vizcaíno	34.9	9.4	3.3	−18.2	9.4				Czerwonogora et al. 2011
ARGC-52	Santa Clara	Glyptodon	Skull	Camet Norte North, level B	20.0	6.8	3.4	−21.6	9.7				This study
ARGC-63	Santa Clara	Glyptodon	Pelvis	Camet Norte North, level B	41.7	14.5	3.4	−19.4	7.7	24,405	110	ETH-57,491	This study
ARGC-65	Santa Clara	Glyptodon	Tooth dentine	Camet Norte North, level B	14.9	5.0	3.5	−20.0	9.4				This study
ARGC-60	Santa Clara	Doedicurus	Osteoderm plates	Camet Norte North, level B	35.9	12.2	3.4	−20.9	10.4				This study
GrA-48,480	MACN-2821	Doedicurus		General Belgrano		15.0		−20.9	8.4	14,140	60	GrA-48,480	Prado et al. 2015
GrA-48,961	MACN-6764	Doedicurus		General Belgrano		15.0		−20.9	8.1	12,860	50	GrA-48,961	Prado et al. 2015

was used to measure the nitrogen content (%N) of the whole bone, in order to screen out samples with excessive collagen loss (Bocherens et al., 2005). For instance, fresh bones contain 4% nitrogen while ancient bones with less than 0.4% nitrogen usually fail to yield good collagen (Bocherens et al., 2005). The measurements were performed using a Vario EL III elemental analyzer using Sulfanilic acid from Merck as internal standard. The mean standard errors were better than 0.05% for %N.

The collagen was purified according to a well-established protocol (Bocherens et al., 1997a). The elemental and isotopic measurements were performed at the Isotopic Geochemistry unit of the Department of Geosciences at the University of Tübingen (Germany), using an

elemental analyzer NC 2500 connected to a Thermo Quest Delta + XL mass spectrometer. The elemental ratios C/N were calculated as atomic ratios. The isotopic ratios are expressed using the "δ" (delta) value as follows:

$$\delta^{13}C = \left[\left({}^{13}C/{}^{12}C \right)_{sample} \Big/ \left({}^{13}C/{}^{12}C \right)_{reference} - 1 \right] \times 1000\permil$$

$$\delta^{15}N = \left[\left({}^{15}N/{}^{14}N \right)_{sample} \Big/ \left({}^{15}N/{}^{14}N \right)_{reference} - 1 \right] \times 1000\permil.$$

The international references are V-PDB for δ¹³C values and atmospheric nitrogen (AIR) for δ¹⁵N values. Measurements were normalized to δ¹³C values of USGS24 (δ¹³C = −16.00‰) and to δ¹⁵N values of IAEA 305 A (δ¹⁵N = 39.80‰). The reproducibility was ±0.1‰ for δ¹³C measurements and ±0.2‰ for δ¹⁵N measurements, based on multiple analyses of purified collagen from modern bones.

The reliability of the isotopic signatures of the extracted collagen was addressed using their chemical composition (%C, %N, and C/N ratio). These values must be similar to those of collagen extracted from fresh bone to be considered reliable for isotopic measurements and radiocarbon dating. Several studies have shown that collagen with atomic C/N ratios lower than 2.9 or higher than 3.6 is altered or contaminated, and should be discarded, as well as extracts with %N < 5% (e.g., DeNiro, 1985; Ambrose, 1990).

Radiocarbon dating was performed on some of the collagen extracted from the megafauna samples in the Labor für Ionenstrahlphysik at ETH in Zurich (Switzerland). The obtained radiocarbon ages were calibrated using the software Calib 7.1 with the calibration curve IntCal13 (Reimer et al., 2013).

6. Results

6.1. Collagen preservation

In terms of collagen preservation, only 22 specimens of the 61 tested bones had nitrogen content higher than 0.4% among the 61 tested samples (Table 1). This means that 39 tested specimens had lost more than 90% of their original collagen and could not be investigated further. In addition, 10 bones could not be tested for nitrogen content but 7 of them yielded good collagen, the 3 others yielded extracts that had chemical composition unlike that of collagen and had to be discarded as well (Table S1). The proportion of samples without collagen was higher in Rio Salado than in Camet Norte, with proportions of bones without collagen being 70% and 45% in Rio Salado and Camet Norte, respectively. Unfortunately, due to this high rate of collagen degradation, none of the specimens that belonged to taxonomic groups such as bears, canids, proboscideans, camelids, and the Xenarthrans Lestodon, Panochthus and Neosclerocalyptus could not be used to derive isotopic data from them. The remaining 32 bones yielded an extract that could be analyzed for carbon and nitrogen isotopic values. Among these samples, in addition to the 3 samples already discarded, one bone from Rio Salado (ARG-5), belonging to a glyptodontid Doedicurus, yielded an extract with a C/N ratio higher than 3.6 and therefore is outside the acceptable range for reliable collagen. This sample will not be discussed in palaeobiological terms. All other extracts exhibited C/N ratios ranging from 3.2 to 3.5 and had %N ≥ 5, therefore they can be considered as not significantly different from the biogenic values. We can notice nevertheless that the collagen from bones with less than 1% nitrogen yielded lower %N and %C indicating some degradation of the collagen.

6.2. Carbon and nitrogen stable isotopes

The δ¹³C values of the sufficiently well preserved collagen ranged from −21.6 to −17.0‰ (Table 2). The Smilodon bones and teeth exhibited a narrow range of δ¹³C values from −17.7 to −17.2‰, while the

jaguar specimen was in the same range (−17.3‰). Among the herbivores, Macrauchenia had the less negative δ¹³C values (−17.1 and −17.0‰), while Hippidion, most glyptodontids, Toxodon and the rodent Lagostomus had among the lowest δ¹³C values. The giant ground-sloths had intermediate δ¹³C values.

Smilodon exhibited the highest δ¹⁵N values of all of analyzed specimens, ranging from 11.2 to 15.4‰, this highest values being measured on a canine tooth. From studies on modern carnivores, it is known that tooth collagen exhibits δ¹⁵N values on average around 1.4‰ higher than bone collagen (Bocherens, 2015). The highest δ¹⁵N values for Smilodon bone collagen are 14.2‰ (Table 2). The jaguar exhibited a lower δ¹⁵N value (10.1‰) than Smilodon. Among the herbivores, most measured specimens had rather high δ¹⁵N values, with Megatherium having two specimens in the same range of δ¹⁵N values than Smilodon. Hippidion and Macrauchenia also had δ¹⁵N values approaching the lowest ones of Smilodon and only one Glyptodon, one horse and the rodent Lagostomus had significantly lower δ¹⁵N values.

6.3. Radiocarbon dates

Four collagen from Camet Norte bones were AMS radiocarbon dated. They yielded rather similar ages, ranging from 23,691 ± 103 BP to 24,732 ± 112 BP (Table 2). Once calibrated with two standard-deviations, the ages ranged from 27,589–27,969 cal BP to 28,478–29,036 cal BP. The isolated jaguar skull that yielded collagen was dated to 12,116 ± 40 BP (Table 2), giving a calibrated age with two standard-deviations of 13,816–14,127 cal BP.

7. Discussion

7.1. Dating and environmental context

This study yielded the first AMS radiocarbon dates on bone collagen from Camet Norte. The four radiocarbon dates obtained for the bone collagen belonging to four different species, Smilodon, Macrauchenia, Toxodon and Glyptodon, are in a narrow range of dates that is very close to the radiocarbon date already obtained on herbivore dung from the same site and the same level B (Pardiñas et al., 1998). This chronological attribution, as well as the composition of its fauna (Pardiñas et al., 1998; Prevosti and Pardiñas, 2001), corresponds to the dry and cold climatic episode represented by the Upper Green Zone in the Guerrero member, as defined by Prado and Alberdi (1999). Based on the narrow range of dates for the level B in Camet Norte, we assume that all other bones from this level have a similar age and a similar palaeoenvironmental context.

The radiocarbon date obtained on the jaguar skull (12,116 ± 40 BP) is also consistent with a chronological attribution to the same chronological phase and to similar palaeoenvironmental context. During this palaeoclimatic phase, the conditions were predominantly colder and clearly dryer than today, even if short wetter events cannot be totally ruled out (Tonni et al., 1999). The sea level was several dozen meters lower than today, leading to a shift of the coast line almost 200–300 km eastwards (Tonni and Cione, 1997; Guilderson et al., 2000; Cione et al., 2015). This larger distance from the coast would have led to more continental and less humid climatic conditions in the study area (Tonni et al., 1999).

7.2. Ecology of the potential prey of large predators

Even if collagen purification was not successful for all tested bones and some mammalian taxa could not be included, this study provides the first δ¹³C and δ¹⁵N values for many species in this context (Fig. 2). In addition to allow the definition of the isotopic landscape of potential prey for Smilodon and other predators, the isotopic values obtained on herbivorous taxa provide invaluable information about the ecology of these species, since not many collagen isotopic data have been gathered
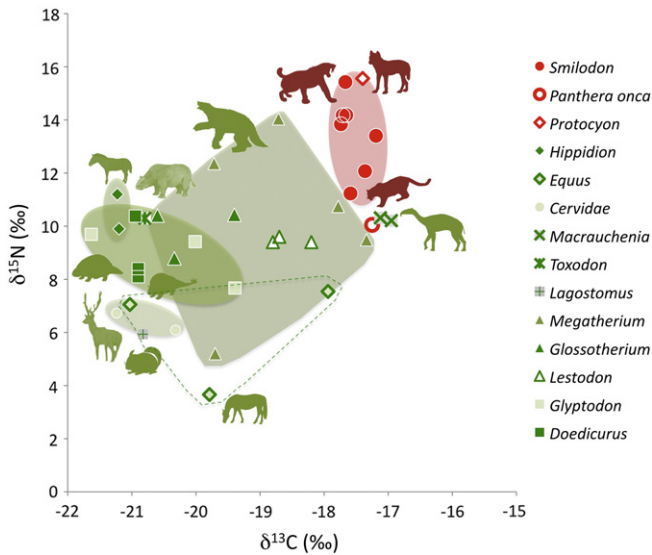
Fig. 2. Scatter-plot of $\delta^{13}C$ and $\delta^{15}N$ values for the specimens of different species from the late Pleistocene of the Pampas.

for South American extinct megamammals. It also provides some insights about the structuration of the herbivore community in this context.

The range of $\delta^{13}C$ values measured on herbivores, from -21.6 to -17.0 ‰, is higher than the threshold value of -22.0 ‰ that would indicate foraging in a closed canopy forest (Drucker et al., 2008), which is consistent with the reconstruction of an open landscape for the Pampas in the late Pleistocene (e.g. Tonni et al., 1999). Some herbivorous species are restricted to the lowest $\delta^{13}C$ values within this range, such as *Hippidion*, the cervids, *Toxodon*, *Lagostomus* and the glyptodonts, while others, such as *Equus* and the giant ground sloths, exhibit a large range of $\delta^{13}C$ values including values higher than $-19‰$, which corresponds to feeding in open arid landscapes, where C3-plants exhibit higher $\delta^{13}C$ values and/or some C_4 plants with much higher $\delta^{13}C$ are consumed together with C_3 plants by herbivores. Consistently high $\delta^{13}C$ values were measured for *Macrauchenia*.

The $\delta^{15}N$ values of the herbivorous taxa cover a very wide range of around 10‰. The lowest values were essentially measured on cervids, *Equus* and *Lagostomus*, while $\delta^{15}N$ values higher than 10‰ were essentially measured for *Hippidion*, *Toxodon*, and giant ground sloths especially *Megatherium*. These nitrogen isotopic differences are difficult to link with food preferences of herbivores. In northern middle and high latitudes, woody plants usually have low $\delta^{15}N$ values compared to grasses, allowing to decipher browsing versus grazing in ancient herbivores (e.g. Bocherens et al. 2015b; Kuitems et al., 2015). In some tropical regions, such as northern Australia, a similar pattern among plants was documented (Schmidt and Stewart, 2003), but in other tropical regions, these nitrogen isotopic differences were not present. For instance, $\delta^{15}N$ values were similar in C_3 and C_4 plants in southern African arid contexts (Heaton, 1987), and in trees, forbs and grasses from South African savannas (Codron et al., 2005). This makes it difficult to use nitrogen isotopic values to decipher between browsing and grazing in arid open contexts. In the context of the Late Pleistocene Pampas, spatial and chronological variations of aridity played probably a more important role and are probably responsible for the large range of $\delta^{15}N$ values. In some taxa that will be discussed below, the incorporation of some animal food resources might also be involved.

For some individual extinct taxa of herbivores, the obtained isotopic values can provide some hints about their palaeoecology. The extinct equid *Hippidion* yielded a comparatively low $\delta^{13}C$ value of $-21.2‰$, indicative of a pure C_3 diet, which is consistent with the browsing feeding specialization reconstructed from the skull morphology of this genus

(Bernardes et al., 2013). Based on previous palaeoecological studies of *Hippidion*, it seems that this equid was flexible enough to incorporate some grass in its diet (García et al., 2008; Prado et al., 2011). In the present case, the low $\delta^{13}C$ values indicate a diet of leaves with the possible addition of C_3-grass. In contrast to *Hippidion*, *Equus* exhibited more variable $\delta^{13}C$ values, ranging from -21.0 to $-17.9‰$ (Table 2). The $\delta^{15}N$ values were lower than those of *Hippidion*, ranging from 3.7 to 7.5‰ (Table 2). Such carbon isotopic values indicate a more open habitat than *Hippidion*.

The two specimens from the litoptern *Macrauchenia* had very similar $\delta^{13}C$ and $\delta^{15}N$ values although they belonged to two different individuals. The $\delta^{13}C$ values are the highest measured in this study and indicate a diet with some arid C_3 plants or even some C_4 plants, therefore clearly an open environment. This conclusion is consistent with the high $\delta^{15}N$ values for this herbivore, also indicative of aridity. These first collagen isotopic values for *Macrauchenia* indicate a rather open landscape for this species, consistent with its presence in the steppes of southern Patagonia (Bond, 1999). These isotopic results are also compatible with the paleoecology of this extinct species reconstructed as a possible high-browsing ecomorph, ecologically equivalent to moose and giraffe (Bond, 1999; Varela and Fariña, 2015), but including grass in addition to high foliage in a mixed diet, based on molar hypsodonty (Bond, 1999). However, these isotopic results are in contradiction with the aquatic adaptation suggested by some authors (e.g. Hoffstetter and Paskoff 1966; Guérin and Faure 2004).

Toxodon exhibits $\delta^{13}C$ values indicative of exclusively C_3 diet and high $\delta^{15}N$ values more in accordance with a grazing strategy in a rather humid environment. This fits well the picture of a rather flexible large herbivore, as described by MacFadden (2005). In the studied context, it would be more in an open C_3 environment than in a steppic one.

The diet and ecology of the giant ground sloth *Megatherium* is still debated. The skull morphology, especially the narrow muzzle, as well as the limited tooth wear, suggests selective feeding on a non-abrasive diet (Bargo 2001; Bargo et al. 2006), and browsing tree leaves would correspond to this picture. However, a more omnivorous diet has also been suggested (Bargo and Vizcaíno 2008) and even claims for a carnivorous predatory or scavenging behavior have been made (Fariña and Blanco 1996). The $\delta^{13}C$ and $\delta^{15}N$ values obtained in the present study were very variable, ranging from -19.7 to $-17.3‰$ and from 9.5 to 14.0‰, respectively. The $\delta^{15}N$ value of a *Megatherium* from Arroyo Seco 2 was even lower, at 5.2‰ (Steele and Politis, 2009). The highest $\delta^{15}N$ values for this species are among the highest in the studied fauna, in the same range as *Smilodon*, and may indicate the consumption of animal proteins. However, high $\delta^{15}N$ values were also found in undoubtedly herbivorous species such as *Hippidion*, *Toxodon* and *Macrauchenia*, showing that the consumption of some plants in some environmental conditions may lead to high $\delta^{15}N$ values as well. It is still unclear why the giant ground sloth has so variable isotopic values. One could speculate that, in a similar way as the surviving tree sloth house symbiotic algae and moths in their fur, from which they complement their nitrogen-depleted food with precious nutrients (e.g. Pauli et al., 2014), giant sloth such as *Megatherium* could have eaten symbiotic invertebrates growing on their fur. Interestingly, one $\delta^{15}N$ measurement of a modern tree sloth *Bradypus* yielded a $\delta^{15}N$ value of 10.4‰, significantly higher than those of coeval herbivores (Nardoto et al., 2006). The other ground sloth *Glossotherium* had $\delta^{13}C$ and $\delta^{15}N$ values in the range of those for *Megatherium*, but in the higher part of the range. One specimen from Río Quequén Grande also had a rather high $\delta^{15}N$ value. The prediction that the broad muzzle *Glossotherium* pictured as a bulk feeder would have a diet from more open environment than the narrow muzzled *Megatherium* (Bargo and Vizcaíno, 2008) is not confirmed by the $\delta^{13}C$ values of both taxa, since *Glossotherium* has lower $\delta^{13}C$ values than *Megatherium*. The three specimens of *Lestodon*, another broad muzzle ground sloth considered to be a grazer (Bargo and Vizcaíno, 2008), also exhibited high $\delta^{15}N$ values and $\delta^{13}C$ values indicative of C3 plant diet, but slightly more enriched than the $\delta^{13}C$ values

of *Glossotherium* (Czerwonogora et al., 2011). Altogether, the specimens of the three different genera of ground sloth cover a broad isotopic range, which is not directly related to the niche partitioning expected from the skull morphology. It is worth noting that the other herbivores, except some glyptodontids, have isotopic values outside the range of the ground sloth, possibly reflecting some niche partitioning between ground sloth and the rest of the herbivore guild.

7.3. Predatory ecology of Smilodon

Isotopic values of *S. populator* are well grouped, in stark contrast with the scattering of isotopic values from the large herbivores that would represent its potential prey (Fig. 2). Especially the range of $\delta^{13}C$ values is very narrow, suggesting that the prey consumed were originating for open arid environment (Fig. 3). This tight clustering of isotopic values may indicate some specialization on one type of prey with a specific isotopic signature, in the same way as cave lions feeding essentially on reindeer in Late Pleistocene Europe (Bocherens et al., 2011; Bocherens, 2015), or may indicate an averaging of different types of prey in a similar way for all individuals, as it was observed for cave hyenas in Europe (Bocherens et al. 2011; Bocherens, 2015). In any case, the high $\delta^{15}N$ values suggest a position as top predator as already suggested in other studies (Prevosti and Vizcaíno, 2006; Prevosti and Martin, 2013). If the second hypothesis is correct, it would support a collective behavior, with an access to more or less any prey present in the landscape. Based on C and N isotopes in bone collagen, a similar situation has been described for *S. fatalis* in Rancho la Brea (Coltrain et al. 2004). In contrast, the isotopic results obtained on another sabretooth felid from the Late Pleistocene, *Homotherium* from Alaska and Yukon, were scattered and may indicate an individualistic prey preference and a different prey choice among the individuals of the Late Pleistocene (Fox-Dobbs et al., 2008; Bocherens, 2015).

The high carbon isotopic values indicate the consumption of prey from open landscape in a dry, essentially C_3 environment, and not in a forested landscape as suggested by some morphological features of *Smilodon* (Meloro et al. 2013; Schellhorn and Sanmugaraja 2015). This suggests that, at least in the Late Pleistocene open Pampas ecosystem, an ambush predator such as *Smilodon* could successfully hunt large herbivores, possibly in a similar manner as lions in African savannas today (e.g. Loarie et al., 2013). Interestingly, the $\delta^{13}C$ values of *Smilodon* did not change significantly with the age of the dated specimen in this study, ranging from 24,000 to 10,000 ^{14}C years BP (Table 2), suggesting
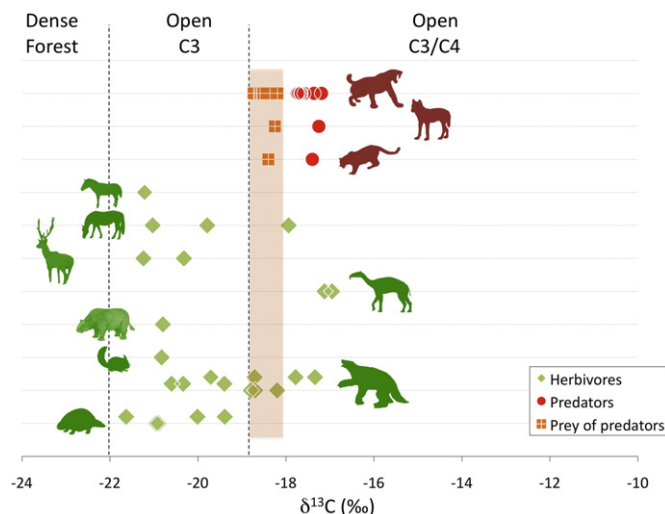
Fig. 3. Range of $\delta^{13}C$ values per species in relationship with type of habitat. The habitats were delineated following Bocherens (2015, Fig. S2), with the threshold value for open landscape with C_3/C_4 set at the maximum $\delta^{13}C$ value of herbivore collagen in pure C_3 landscapes (Bocherens, 2015).

a similar prey choice and habitat during the last 15,000 years before the extinction of the species.

We tried to obtain a more precise determination of prey preference among the analyzed herbivores from Buenos Aires Province using more quantitative approaches. The first approach is based on the range of $\delta^{13}C$ and $\delta^{15}N$ values of the consumed prey, obtained by applying the range of differences measured in modern predator–prey pairs (Bocherens and Drucker, 2003). By subtracting 0.8 to 1.3‰ to the average $\delta^{13}C$ value of *Smilodon* (−17.6‰), we obtain a range of value from −18.9 to −18.4‰, and by subtracting 3 to 5 ‰ to the average bone $\delta^{15}N$ value (13.1‰), we obtain a range from 8.1 to 10.1‰. This matches the isotopic values measured for *Lestodon*, but could also be obtained by mixing prey with lower or higher $\delta^{13}C$ values, such as *Hippidion* (low $\delta^{13}C$ values) and *Macrauchenia* (high $\delta^{13}C$ values). A second approach yielded a statistical evaluation of the different prey contribution in the diet of *Smilodon*, but also for *P. onca* (jaguar) and a canid, *Protocyon*, based on $\delta^{13}C$ and $\delta^{15}N$ values measured on a tooth of *Protocyon troglodytes* from the Late Pleistocene of Buenos Aires Province (Prevosti and Schubert, 2013). We used a Bayesian mixing model approach performed in the SIAR package (Parnell et al., 2010), using the R software, version 3.0.2 (R Core Team 2013), with the same parameters as Bocherens et al. (2015a) for the isotopic fractionation factors between prey and predators. This approach yields 50%, 75% and 95% credibility intervals for the proportion of different prey in the diet of the three predators considered here. The obtained prey proportions show some overlap among the three tested predators, but also some interesting differences (Fig. 4). For *Smilodon* and *Protocyon*, *Macrauchenia* appears to be the most consumed prey, while the giant ground-sloths *Megatherium* and *Lestodon* are also consumed in significant amounts. The other prey species are in very small quantities, with the highest probability being lower than 5% in the diet (Fig. 4). In contrast, the jaguar would have consumed less *Macrauchenia* than *Smilodon* and *Protocyon*, but more herbivorous species with lower $\delta^{15}N$ values, such as horse and vizcacha. However, the obtained proportions should not be taken as absolute values since some other potential prey, such as camelids and proboscideans, could not be included in the isotopic survey of potential prey due to the lack of preserved collagen in the studied specimens. In Patagonia, camelids exhibited relatively high $\delta^{13}C$ and $\delta^{15}N$ values compared to coeval herbivores (Prevosti and Martin, 2013). Moreover, some isotopic data of the carbonate fraction from tooth enamel have been published for camelids and proboscideans in the Late Pleistocene Pampa region, and they indicate an open habitat with relatively dry conditions for both types of herbivores (Domingo et al., 2012). Especially the $\delta^{13}C$ values indicate a mixture of C_3 and C_4 plants in their diet, and therefore it does not exclude these herbivores from the possible prey spectrum selected by *Smilodon*, in a similar way than *Macrauchenia*. At this stage, despite these limitations, it is possible to state that *Smilodon* was not specialized on prey from the most densely vegetated part of the prey spectrum, such as *Hippidion* or *Toxodon*, despite its morphological features indicative of ambush predation, and that it was more focused on prey from the most open part of the prey spectrum, such as *Macrauchenia*. Hunting giant ground sloths such as *Lestodon* and *Megatherium* is very likely and therefore, the large burrows made by these animals in the study region could well be an anti-predator behavior, as suggested by Vizcaíno et al. (2001). Consistent with this hypothesis, Soibelzon et al. (2009) observed that before the Early Pleistocene, records of large burrows are scarce in the Pampean Region, although putative burrow excavators were present and therefore suggested that this behavior would have been acquired or generalized after the arrival of large carnivores.

The obtained isotopic results on three large predators of the Late Pleistocene Pampas allow an evaluation of the dietary competition between these carnivores, although preliminary since only one specimen of each predator other than *Smilodon*, i.e. jaguar and *Protocyon*, could be analyzed so far. Interestingly, none of the analyzed carnivores seems to have consumed high proportions of prey from the most closed
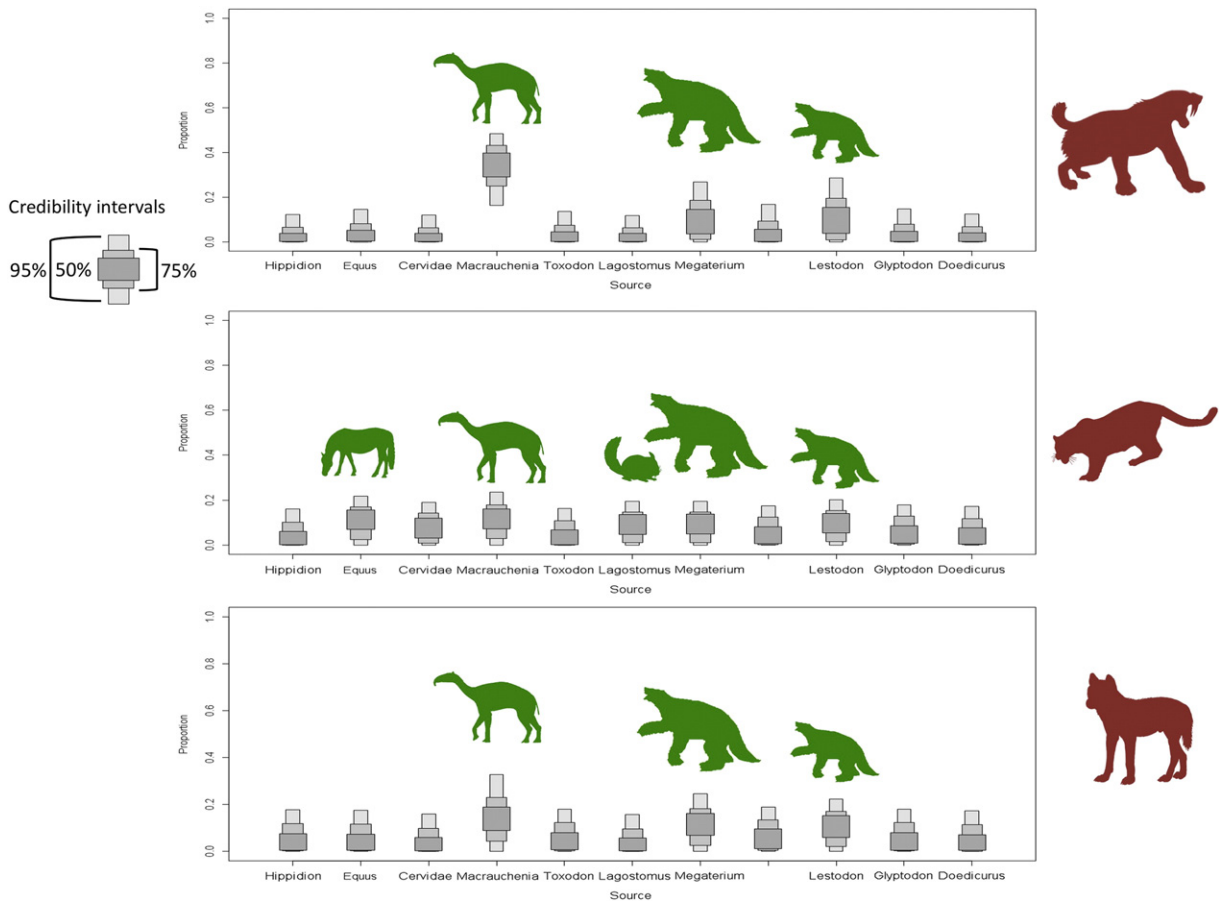
Fig. 4. Proportion of prey species as calculated using SIAR for *Smilodon* (top), *Panthera onca* (middle) and *Protocyon* (bottom).

habitats. The isotopic results obtained in the present study suggest limited competition between both large felids, *Smilodon* and jaguar, the latter exhibits clearly lower δ^{15}N values than *Smilodon*, indicating a diet composed of more prey with lower δ^{15}N values, possibly horse. This preliminary conclusion is consistent with the observation of a similar pattern of isotopic difference in southern Patagonia between *Smilodon* and jaguar, this time based on several individuals (Prevosti and Martin, 2013). The tooth of *P. troglodytes* from the Late Pleistocene of Buenos Aires Province yielded almost the same δ^{13}C and δ^{15}N values as the canine of *Smilodon* from Rio Salado (Prevosti and Schubert, 2013). Not surprisingly, the prey proportions yielded by SIAR are very similar between *Smilodon* and *Protocyon* (Fig. 4), suggesting that some competition may have occurred between these two carnivores. Since the canid was much smaller than the felid, it is conceivable that the former was scavenging the prey killed by the largest predator. However, the morphology of *P. troglodytes* suggests similarities with the African wild dog *Lycaon pictus*, an active social predator (Prevosti et al., 2005), therefore more direct competition cannot be ruled out. More isotopic data will be needed to confirm this pattern. In Rancho La Brea, a Late Pleistocene site in California where the sabretooth cat *S. fatalis* coexist with the American lion American lion *Panthera atrox* and a large canid, the dire wolf *Canis dirus*, the δ^{13}C and δ^{15}N values of all three large predators are very similar, suggesting some competition between the three large predators of this context (Coltrain et al., 2004).

Unfortunately, the possibility of dietary competition between *Smilodon* and the South American short-faced bear *Arctotherium* could not be tested in the present study since the three bear bones that were analyzed yielded no collagen. In Southern Patagonia, similar δ^{13}C and δ^{15}N values measured for these two large carnivores indicate a possible dietary competition between *Smilodon* and this giant bear that may have been acting as a scavenger on carcasses of prey killed by

Smilodon (Prevosti and Martin, 2013). Further isotopic research will be needed to test if this situation also existed in the Pampas.

We can compare the reconstruction of predatory behavior of *Smilodon* from the Late Pleistocene Pampas with previous isotopic studies for this taxon. In southern Patagonia there was a possibility to suggest which herbivore was preferentially consumed when combining isotopic results on the whole of Patagonia, and the results indicate that *Smilodon* could have eaten all the analyzed potential prey in more or less the same proportions, including equids, ground sloth, the flightless bird ñandú, and camelids, all of them from open environments (Prevosti and Martin, 2013). In the Californian site of Rancho la Brea, a preference for the prey species with high δ^{13}C and δ^{15}N values was noted, corresponding to the ruminants in this case (Coltrain et al., 2004). In the present study, the *Smilodon* from the Late Pleistocene Pampas were also consuming a large spectrum of prey, but with a clear preference for prey inhabiting open and dry landscape rather than prey from humid and well vegetated areas, and most probably including giant ground sloth. So far, a preference for open habitats seems to be observed in the three studied *Smilodon* occurrences, in North and South America at different latitudes and under different climatic conditions.

In all its distribution area, the sabretooth cat *Smilodon* coexisted with another large felid lacking enlarged canines, *P. onca*, the jaguar, in South America and *P. atrox*, the American lion, in North America. Based on the available carbon and nitrogen isotopic data, it seems that *Smilodon* and the American lion may have competed for preys with similar isotopic values in the Californian site of Rancho la Brea (Coltrain et al., 2004), while dietary competition seem to have been limited between *Smilodon* and the jaguar in the Pampas and southern Patagonia (Prevosti and Martin, 2013; this study). These differences in competition between two large felids might be linked to the much larger size difference

between *S. populator* (220–400 kg) and *P. onca* (95–138 kg) (range of weights according to Prevosti and Vizcaíno, 2006) than between *S. fatalis* (140–280 kg, according to Christiansen and Harris, 2005) and *P. atrox* (200–350 kg, according to Christiansen and Harris, 2009). The differences in the available prey species in North and South America could also have played a role in this different dietary behavior of large felids (Prevosti and Vizcaíno, 2006; Prevosti and Martin, 2013).

8. Conclusion

The present isotopic paleobiological investigation suggests that the sabretooth cat *S. populator* was hunting predominantly prey from very open environments, and possibly behaved as a social predator. Although the exact type of prey consumed is not clearly defined, it does not seem to include high proportions of extinct megaherbivores from more humid habitats, such as glyptodontids, toxodonts, and equids. In contrast, giant ground sloths seem to belong to the spectrum of consumed prey. It is possible that camelids and proboscideans were also consumed but additional data are needed to test this possibility. During the last 15,000 years of the Late Pleistocene in the Pampa region, *Smilodon* seems to have been hunting prey from very open habitats, possibly taking advantage of its unusual pectoral girdle morphology for stalking even in relatively open landscape. A more tentative outcome of this study is that, despite their differences in size, *Smilodon* and *Protocyon* seem to have preferred the same types of prey in this context, while the jaguar was more focused on smaller prey species, as was suggested using body size estimations (Prevosti and Vizcaíno, 2006; Prevosti and Martin, 2013). If the preference for prey from open habitat was a feature of the fundamental niche of *Smilodon*, the climate change of the early Holocene towards more humid conditions (e.g. Prado and Alberdi, 1999; Tonni et al., 1999) might have been unfavorable to this large predator and could have been a factor in its extinction. These new inferences on the ecological preferences of *Smilodon* will also help to elucidate the possible ecological replacement of marsupial predators such as *Thylacosmilus* by invasive large felids such as *Smilodon*.

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Acknowledgments

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