



# First taxon date and stable isotopes ( $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ ) for the large hypercarnivorous South American canid *Procyon troglodytes* (Canidae, Carnivora)



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## ABSTRACT

*Procyon troglodytes* was a hypercarnivorous South American canid that died out during the Late Pleistocene-early Holocene extinction, an event that eliminated most large mammals on the continent. The precise timing of these extinctions is poorly understood in South America, primarily due to a lack of radiometric dates on taxa. Of the extinct South American canids, *P. troglodytes* have the most extensive fossil record and widest distribution. However, the age of these specimens is based on relatively coarse association with other dated taxa or sediments. This paper describes an unpublished specimen of *P. troglodytes* and present the first  $^{14}\text{C}$  date and stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) for the species. This is the first taxon date for the genus and species, with an age of  $17,338 \pm 85$  BP, and represents the youngest specimen dated by any means. The isotopes indicate that *P. troglodytes* was a hypercarnivore, in agreement with morphological studies, and that *Equus neogeus*, *Hippidion principale*, *Stegomastodon platensis*, *Toxodon*, and *Megatherium americanum* may have been part of its diet.

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## 1. Introduction

During the Pleistocene, South America had a clade of large hypercarnivorous canids that became nearly extinct by the end of the Pleistocene, leaving the small *Speothos venaticus* as a living hypercarnivore relict (Kraglievich, 1928; Berta, 1989; Prevosti, 2006, 2010; Prevosti and Rincón, 2007; Prevosti et al., 2009a, 2009b). This living species has a body mass of 5–8 kg, whereas the extinct taxa are above 20 kg and probably hunted medium-large mammals in groups (Berta, 1989; Prevosti and Palmqvist, 2001; Prevosti, 2006; Prevosti and Vizcaíno, 2006; Prevosti et al., 2009b). The extinction of these large canids happened at different times, *Theriodictis platensis* and *Procyon scagliorum* became extinct at the end of the Ensenadan (early-middle Pleistocene), while *Procyon tarijensis* and *Procyon troglodytes* became extinct at the end of the Lujanian (Late Pleistocene-early Holocene; Prevosti et al., 2009a).

*P. troglodytes* has the largest distribution and fossil record with several occurrences in South America during the Lujanian (see Cione and Tonni, 2005; Prevosti, 2006; Prevosti et al., 2009a, Fig. 1). However, in the best of cases the age of these specimens are constrained by numeric dates made on other specimens from the same stratigraphic levels or on associated sediments ( $^{14}\text{C}$  and TL dates). As with other South American fossil mammals, the relative lack of taxon dates imposes a strong limitation on understanding the dynamics of Late Pleistocene-early Holocene extinctions (e.g., Borrero, 2009; Barnosky and Lindsey, 2010).

This paper describes a previously unpublished specimen of *P. troglodytes* and presents the first  $^{14}\text{C}$  date and stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) for the taxon. Further, the systematic position of this specimen, the relevance of the date on the youngest record, and the paleoecology of the species, are discussed.

## 2. Material and methods

The measurements reported here were taken with digital callipers accurate to 0.01 mm (see Table 1), following Prevosti (2006). The cusp terminology follows Wang et al. (1999) but has been modified in order to adapt it to the orientation nomenclature

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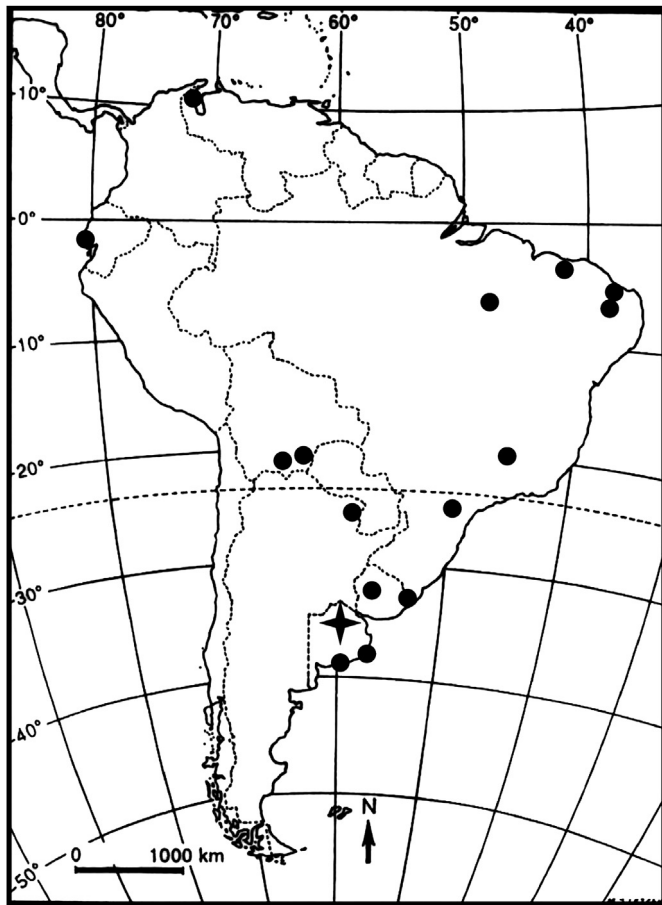


Fig. 1. Map with the distribution of *Protocyon troglodytes* in South America. Black star, dated specimen, Mercedes, Buenos Aires, Argentina; black circle, other localities of *P. troglodytes*.

proposed by Smith and Dodson (2003) (e.g., posterior accessory cusp was changed to distal accessory cusp). Other anatomical nomenclature follows Evans (1993). The description is limited to dentaries and teeth because the diagnostic features are on these anatomical elements. The background information for *P. troglodytes* was taken from Prevosti (2006; see also Prevosti et al., 2009a,

**Table 1**  
Measurements (in mm) of the MLP 89-XI-20-1 compared to *P. troglodytes*.

	MLP 89-XI-20-1	<i>Protocyon troglodytes</i>				n	CV*
		Mean	SD	CV	Range		
LM	147.5	158.01	10.12	6.40	149.52–169.20	3	6.30
HRHm1	31.3	30.78	2.51	8.16	26.25–35.00	10	7.75
WRHm1	13.15	13.66	1.70	12.43	11.87–17.70	10	11.89
HRHp4	26.6	26.82	1.98	7.39	23.2–29.35	9	6.98
WRHp4	14.5	13.89	0.92	6.64	12.63–15.25	9	6.38
Lc1	11.1	12.51	0.92	7.34	11.30–14.09	8	7.92
Wc1	8.05	8.52	0.67	7.88	7.70–9.37	8	7.64
Lp2	10.5	11.17	0.86	7.72	10.05–12.49	8	7.54
Wp2	5.9	5.75	0.38	6.54	5.26–6.53	8	6.16
Lp3	11.8	12.62	1.05	8.29	11.42–14.50	9	8.13
Wp3	6.3	6.10	0.36	5.94	5.47–6.60	10	5.70
Lp4	14.3	14.49	0.89	6.14	13.35–15.80	8	5.77
Wp4	6.7	6.91	0.27	3.85	6.50–7.30	9	3.77
Lm1	25.02	26.86	1.38	5.15	25.57–30.20	13	5.30
Ltrm1	18.6	19.81	0.94	4.75	18.32–21.60	13	4.87
Wtalml	8.4	8.95	0.57	6.41	8.12–10.30	14	6.40
Lm2	9.05	9.88	0.89	9.02	8.77–11.45	11	9.00
Wm2	6.95	7.57	0.70	9.20	6.75–8.96	11	9.15

Abbreviations: SD, standard deviation; CV, coefficient of variation; n, sample size; CV\*, coefficient of variation including the MLP 89-XI-20-1.

2009b). The systematic scheme for the canids is that proposed by Prevosti (2006; also see Prevosti et al., 2009a) and the biostratigraphic–chronostratigraphic data are from Cione and Tonni (2005; see also Woodburne et al., 2006). The studied specimen (MLP 89-XI-20-1) was described as the type specimen of a new species of *Protocyon* by Berman (1994; see also Berman, 1989), and a review of this hypothesis is presented here.

The distal portion of the right lower canine root of MLP 89-XI-20-1 was sampled with a dremel tool and shipped to Rafter Radiocarbon, GNS Science, New Zealand for analysis. Microscopic examination revealed cemented dirt that was removed with a scalpel and then the specimen was chemically treated with 0.5 M HCl for acid demineralization. The remainder of the AMS dating and isotope analysis procedures are explained in the methods section of Schubert (2010).

Radiocarbon dates are expressed in years before “present” (BP), and calendar years are noted as cal BP. Calibration of  $^{14}\text{C}$  dates were obtained with the program CALIB 6.0.1 available at <http://intcal.qub.ac.uk/calib/> (Stuiver and Reimer, 1993; Reimer et al., 2009), using the InterCal09 curve (two sigma ranges; Reimer et al., 2009).

Stable isotopes are reported as delta values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), together with the %C and %N. Isotopes of *P. troglodytes* were compared with the limited available sample of Late Pleistocene mammals from the Pampean region (e.g., equids, gomphotherids, camelids, and ground sloths; Macfadden et al., 1996; Sánchez et al., 2004; Alberdi et al., 2008; Steele and Politis, 2009). Unfortunately, because the scarcity of good chronologic data for this sample, analysis is limited to Late Pleistocene (mostly between 30 and 10 ka), but clearly it cannot be confirmed that all these taxa coexisted in the same locality. However, this is the only way to compare the isotopic signature of the studied specimen to the signature of potential prey, and these analyses constitute a first, preliminary approach, to explore this issue. This study follows Bocherens (2000) in comparing  $\delta^{13}\text{C}$  obtained from carbonates (apatite) to that obtained from collagen. The only taxon from the Late Pleistocene of the Pampean Region that has some  $\delta^{13}\text{C}$  data based on collagen is *Equus neogaeus*, and this figure ( $-20.8$ ) is in the range of the “corrected”  $\delta^{13}\text{C}$  sample obtained from carbonates (range:  $-21.1/-17.1$ ; see Supplementary data 1). Also explored was the contribution of the herbivores to the *P. troglodytes* diet using an isotopic mixing model with the software Isosource 1.3.1 (Phillips and Gregg, 2003). Runs were performed using the mean, minimum and maximum  $\delta^{13}\text{C}$  value of each potential prey (*Hippidion principale*, *E. neogaeus*, *Stegomastodon platensis*, *Toxodon* sp., *Lama* sp., *Megatherium americanum*), and an enrichment factor from herbivores to predators of 1 and 2  $\delta^{13}\text{C}$ , following actualistic information (see Bocherens and Drucker, 2003; Fox Dobbs et al., 2007), and a tolerance of 0.01, 1 and 2. All these models give very similar results, and thus only the model based on an enrichment factor of 2  $\delta^{13}\text{C}$ , and a tolerance of 1, is presented.

Anatomical and Measurement Abbreviations: C/c, upper/lower canine; HRHp4, dentary height at the distal border of the p4; I/i, upper/lower incisors; L, mesiolabial length of canines, premolars, and molars, but labiolingual length in the case of incisors; LLabM1, M1 labial length; LLiM1, M1 lingual length; LM, length of the dentary, from the anterior border of the c1 to the posterior border of the condyle; Ltrm1, length of the m1 trigonid; M/m, upper/lower molars; P/p, upper/lower premolars; HRHm1, dentary height at the distal border of the m1; W, labiolingual width in canines, premolars and molars, but mesiodistal width in the case of incisors. The width of the P4 was taken including the protocone, and perpendicular to the lateral border in the M1; WRHm1, dentary width at the distal border of the m1; WRHp4, dentary width at the distal border of the p4; Wtalml, width of the m1 talonid.

Institutional Abbreviations: EPN, Collection of the Escuela Politécnica de Quito, Ecuador; MLP, División Paleontología Vertebrados, Museo de La Plata, Argentina; UZM, Lund Collection, Universitets Zoologiske Museum, Copenhagen, Denmark.

### 3. Results

#### 3.1. Systematic Paleontology

Order CARNIVORA Bowdich, 1821

Family CANIDAE Fischer von Waldheim, 1817

*PROTOCYON* Giebel, 1855

*PROTOCYON TROGLODYTES* Lund, 1838

(Fig. 2, Table 1)

Material: MLP 89-XI-20-1, left incomplete dentary with c1, p2–m2; fragment of right dentary with p3–m2; isolated right c1; incomplete right humerus; right tibia; right metacarpal V; right metatarsals III and IV; left metatarsals III and V.

Description: The description herein focuses on dentaries and teeth because the postcranial remains do not add any relevant information about the systematic position of the specimen. Further, a full description of the postcranial remains is part of an ongoing monograph on these canids (Prevosti, in prep; see Prevosti, 2006).

Strong horizontal ramus with very sharp subangular lobule and a deep masseteric fossa that reaches the distal part of the m3. The left ramus presents a large mental foramen below p1, and a smaller one below the p3–p4 contact, but in the left dentary this foramen is placed below the distal half of the p3 (other foramina are not observed in this dentary due to incompleteness). The symphysis is strong, high and extended caudally to the middle of the p2, while the masseteric fossa is deep but does not reach the posterior border of the m3 (Fig. 2). The angular process is very deep and extends distally beyond the position of the mandibular condyle. The inferior and superior scars for the medial branch of the medial pterygoid muscle are clearly observed on the inner side of the angular process, and are dorsoventrally expanded and present a near rectangular shape (Fig. 2).

The dentition present wear facets that are more developed in the mesial and distolabial part of the c1, the principal cusps of p3–4, and the trigonid of m1. The c1 is robust and short, with a well-developed mesiolingual crest that is eroded by a wear facet. The premolars are very close together but with a small diastema between p3–4, and an even smaller one between p2–3. The p1 is not preserved, but in the left dentary the bone surface between c1–p2 is abnormal with numerous pits, and a piece of tooth root occurs between them. The p2–4 have two roots, and high and acute principal cusps with strong mesiolingual and distal crests. The distal accessory cusp is only present in p3–4, and it is very small in p3. The distal part of the p4 is placed labially to the mesial part of the paraconid. The m1 is very large, and shows a long trigonid, short talonid, a cingulum like “entoconid”, and lacks the metaconid. A low ridge is on the lingual side of the distal face of the protoconid and runs to the hypoconid, but it is eroded by a wear facet. Another ridge, that is very low, is on the lingual side where the metaconid is typically located. The m2 is reduced in relationship to the m1, and possesses a wide trigonid and narrow talonid (Fig. 2). The metaconid is reduced and adjacent to the protoconid, the entoconid is a cingulum along the lingual border of the talonid, the mesiolabial cingulum is reduced, and the hypoconid is reduced to a cingulum. The m3 and its alveolus are not present in the left dentary, but a small root of the m3 is present in the right dentary.

Locality and Horizon: Mercedes (34° 39' S, 59° 26' W; Buenos Aires, Argentina, Fig. 1). Specimen was found in a 5 m deep excavation associated with the camelid *Lama gracilis* (see Berman, 1994). This is the only available information about the locality and horizon of this specimen.

#### 3.2. AMS date and stable isotopes

The AMS <sup>14</sup>C date is 17,338 ± 85 BP (NZA 29728) and the corrected calendar age is 20,288–21,139 cal BP. The obtained elemental and isotopic values are 24.53 %C, 7.97 %N, –17.4 δ<sup>13</sup>C, and 15.56 δ<sup>15</sup>N. The C:N ratio is 3.6, which indicates well preserved collagen was used in the analyses (DeNiro, 1985). The isotope

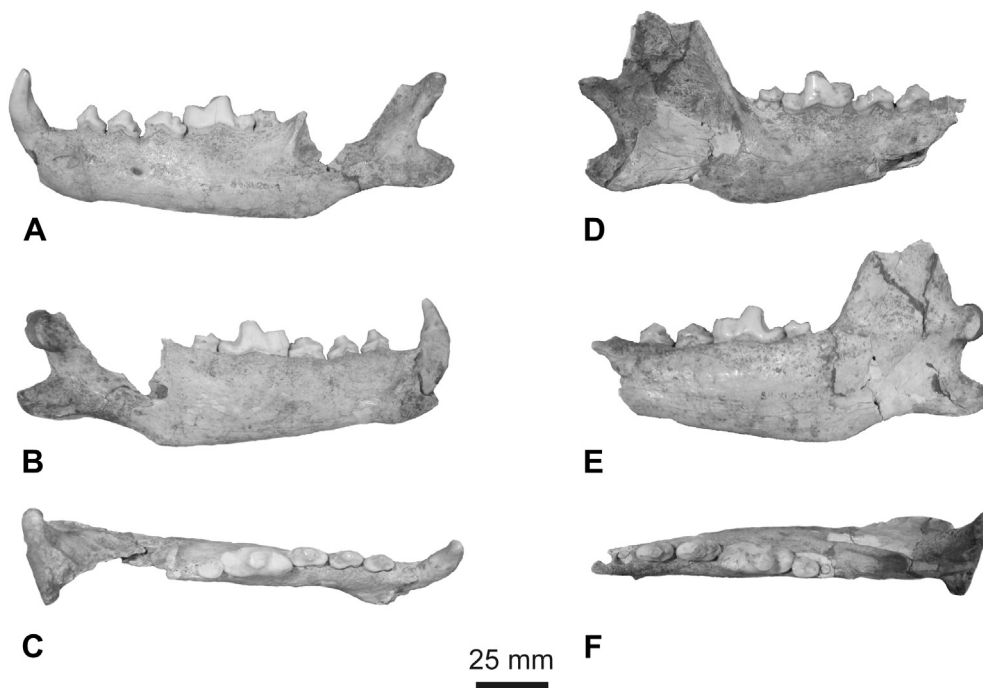


Fig. 2. *Protocyon troglodytes*, MLP 89-XI-20-1. A, left dentary in lateral view; B, left dentary in medial view; C, left dentary in dorsal view; D, right dentary in lateral view; E, right dentary in medial view; F, right dentary in dorsal view.

mixing model, with the mean  $\delta^{13}\text{C}$  values for herbivores, indicates that *E. neogaeus*, *H. principale*, *Lama* sp., *S. platensis*, *Toxodon* sp., and *M. americanum* may have contributed to the diet of *P. troglodytes* (mean contribution: 18%, 16%, 11%, 21%, and 16, standard deviation: 15%, 14%, 23%, 14%, 17% and 17% respectively; Table 2). Using the minimum value for each taxa *Lama* sp. had the highest percentage of contribution (23%), while the other taxa had values around 15% (Table 2). Analysing the maximum values, *Lama* sp. and *Toxodon* sp. had mean values of ca. 3, *E. neogaeus* and *H. principale* around 15%, *S. platensis* ca. 10% and *M. americanum* had the greatest contribution to the diet of this *P. troglodytes* specimen (ca. 50%; Table 2).

#### 4. Discussion

The dental and dentary morphology, as well as the size, indicate that this specimen belongs to *Protocyon* (Table 1; Fig. 2). *Theriodictis* and *Protocyon* are the only large canids with deep and “rectangular” angular processes and expanded facets for the medial pterygoid muscle (Berta, 1989; Prevosti, 2006, 2010). *Protocyon* is the only large South American canid with an m1 that lacks a metaconid and entoconid, and premolars with acute and weak principal cusps (Berta, 1989; Prevosti, 2006; Prevosti and Rincón, 2007). The specimen differs from *Protocyon scagliarum* because this species has a wider talonid in relationship to trigonid width, with a more developed lingual cingulum (“entoconid”), and the m2 metaconid is displaced distally with respect to the protoconid (see Prevosti, 2006; Prevosti and Rincón, 2007). *Protocyon troglodytes* have a narrow m1 talonid due to a reduction of its lingual cingulum, and an m2 metaconid that is aligned to the protoconid, as in MLP 89-XI-20-1. Specimen differs from *P. tarijensis* because it lacks a tiny entoconid on the m1, or a more developed cingulum in its place (Prevosti, 2006).

Berman (1994; see also 1989) described a new species of *Protocyon* in his unpublished doctoral thesis based on MLP 89-XI-20-1. This diagnosis relied on the following characters: longer angular process than in *P. scagliarum*; closed premolar series (i.e. without diastemas); vestigial p1; p4 without a mesial accessory cusp; principal cusps of premolars mesially placed; long m2 that has a small paracristid, subequal protoconid and metaconid that are joined, and narrow talonid with reduced hypoconid. However, most of these characters are present in different specimens of *P. troglodytes*, and are examples of intraspecific variation. For example, the close lower premolar series and m2s with the described shape are present in several specimens of this species (e.g., UZM L 2157, UZM L 5700, EPN V 2871; see also Cartelle and Langguth, 1999; Prevosti, 2006; Prevosti and Rincón, 2007; Prevosti et al., 2009b; Fig. 2). It is not clear that the p1 is “vestigial”. In fact the porous bone that covers and surrounds the remains of the p1 root suggests a pathological process and that the tooth was lost during the life of this individual. Further, the p1 is occasionally absent in some living canids (Kraglievich, 1930; Young and

Goldman, 1944; Szuma, 1999, 2002, 2003; Prevosti, 2006). The size of the dentition and dentary is within the range of variation of *P. troglodytes*, but some measurements (LM, LC, Lm1) are below its observed range. The size differences were considered insignificant because they are only a few millimetres smaller and the *P. troglodytes* sample is relatively small ( $n < 15$ ). It is important to note that the inclusion of the MLP 89-XI-20-1 in the *P. troglodytes* sample does not increase the coefficient of variation in a significant way, and it actually decreased for some measurements (Table 1).

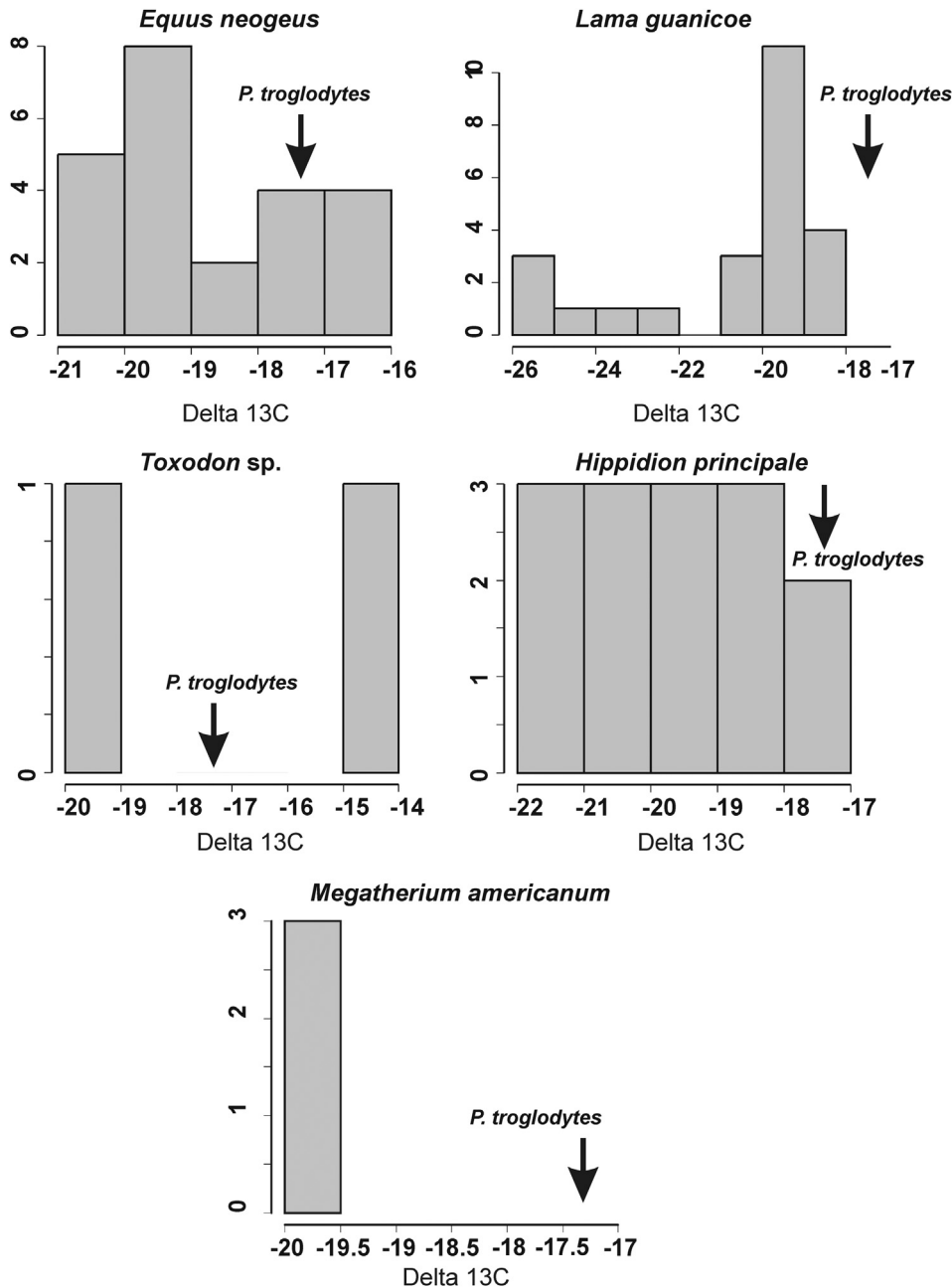
Some previous records of *P. troglodytes* were dated by biostratigraphic and paleomagnetic studies, but most of the specimens lack any associated numeric date (e.g., specimens from La Carolina, Ecuador; Ñuapua, Bolivia; see Prevosti et al., 2009a). Numerous records from Brazilian caves present a special case, because the absence of stratigraphy and the long time span of deposition (between 350 and 9 ka, see Auler et al., 2006) indicate that they could be Bonaerian or Lujanian in age (see Prevosti, 2006; Prevosti et al., 2009a). The only exception from a Brazilian cave is a specimen studied by Cartelle and Langguth (1999) which came from Toca da Boa Vista (Bahia) and was collected above a layer dated  $20,060 \pm 290$  BP (Czaplewski and Cartelle, 1998). New remains from the Inciarte Asphalt Pit in western Venezuela (Prevosti and Rincón, 2007), came from levels dated  $25,500 \pm 600$  BP and  $27,980 \pm 370$  BP (Jull et al., 2004, Fig. 2).

Another specimen came from Lujanian levels of the Bermejo River (Formosa, Argentina; Prevosti et al., 2005, 2009a). Recently an OSL date of  $58,160 \pm 4390$  was reported from the lower section of the Bermejo cliff (Zurita et al., 2009; Soibelzon et al., 2010) but unfortunately this date was taken 100 km south of the Bermejo River (A. Zurita, pers. comm.) and not from the river cliffs. The specimen from the Sopas Formation (Paso Muñoz Bridge, Salto, Uruguay) has a similar situation because it is associated with Lujanian fauna and the formation has a TL date of  $43,500 \pm 3600$  but the dated sample was obtained 600 m away from the canid locality (Ubilla et al., 2004) and the correlation between the layers is not clear. Radiocarbon ages for the formation range up to 43,000 BP, and another TL date of  $58,300 \pm 7400$  (Ubilla et al., 2004) is recorded for another area for the same formation. Younger radiocarbon dates are also known for this formation ( $\sim 12,000$ – $11,000$  BP), but not in association with faunal remains (Ubilla et al., 2004). Thus, it is not possible to relate these numeric dates to these *P. troglodytes* specimens because the correlation between the localities of fossils and dates are not clear.

In this chronological context the reported taxon date of  $17,340 \pm 85$  BP is the last known record of *P. troglodytes* and of the genus *Protocyon*. This date is roughly synchronic with the fauna collected in the Guerrero Member of the Luján Formation, dated between 21,000–10,000 BP (Tonni et al., 2003). This fauna has several taxa that indicate a more arid climate, more similar to today's non-Andean Patagonia and central Argentina (Pardiñas et al., 1998; Tonni et al., 1999). The  $\sim 17,000$  BP age

**Table 2**  
Contribution (%) of Late Pleistocene herbivores from the Pampean region to the diet of the specimen *Protocyon troglodytes* studied, estimated with mixed models using the Isosource software. Mean, minimum and maximum refers to the models obtained with the mean, minimum and maximum value of each potential prey, respectively. Min, minimum; Max, maximum; SD, standard deviation.

	Mean				Minimum				Maximum			
	Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
<i>Equus neogaeus</i>	17.7	0	88	15.2	14.9	0	74	12.9	14.5	0	68	12.6
<i>Hippidion principale</i>	16.3	0	82	14	14.4	0	72	12.5	19.7	0	92	16.8
<i>Lama</i>	11.2	0	20	3.9	23.4	18	28	2	3.7	0	20	3.8
<i>Stegomastodon platensis</i>	17.5	0	88	15	14.4	0	72	12.5	10.9	0	52	9.7
<i>Toxodon</i>	21.1	0	82	17.6	16.5	0	82	14.2	2.1	0	12	2.4
<i>Megatherium americanum</i>	16.2	0	80	13.9	16.5	0	82	14.2	49	8	86	13.4



**Fig. 3.**  $\delta^{13}\text{C}$  of potential prey from the Late Pleistocene and Holocene of Buenos Aires province, Argentina. The black arrow indicates the  $\delta^{13}\text{C}$  of *Protocyon troglodytes* (see Supplementary data 1).

(20–21,000 cal BP) also coincides with glacial conditions in Antarctica, Patagonia and the central Andes (Thompson, 2000; Brook et al., 2005; Rabassa, 2008; Smith et al., 2011). The association of *L. gracilis* with this specimen of *P. troglodytes* also suggests the presence of an open and arid environment (Menégaz et al., 1989; Menégaz and Ortiz Jaureguizar, 1995). The presence of this canid in an arid and open environment agrees with its description as a euriotic species that could inhabit different kinds of environments (e.g., grasslands, mosaics of forest and dry deciduous tropical forest; see Prevosti et al., 2005; Prevosti and Rincón, 2007).

The obtained isotope values (specially the  $\delta^{15}\text{N}$ ) point to a hypercarnivore diet, which agrees with the highly specialized skull and dentition (Berta, 1989; Cartelle and Langguth, 1999; Prevosti, 2006, 2010). The  $\delta^{15}\text{N}$  value is higher than most published

values for fossil carnivores (e.g., Bocherens and Drucker, 2007; Koch, 2007). One explanation could be the presence of a diet based on fresh water or marine resources, but this is not in accordance with the behaviour of highly carnivorous living canids (i.e. *Lycaon pictus*, *Cuon alpinus*; MacDonald and Sillero Zubiri, 2004) and the anatomy of *Protocyon* (Berta, 1989; Prevosti, 2006; Prevosti et al., 2009b). Some populations of living *Canis lupus* from islands include in their diets a large proportion of marine resources and have  $\delta^{15}\text{N}$  values (Darimont et al., 2009) that reach the value of *P. troglodytes*. However, Mercedes is more than 100 km from the sea coast, and this distance was greater during the last glacial because the ocean was nearly 120 m below its present level and left an extensive continental platform exposed (Rabassa, 2008). Thus it is unlikely that this individual *P. troglodytes* had access to marine

resources. A probable explanation for the very high values of  $\delta^{15}\text{N}$  is related to the tissue sampled (dentine). There are several studies that indicate dentine has a higher  $\delta^{15}\text{N}$  signal than bone in carnivores, a difference that it is around  $3\ \delta^{15}\text{N}$ . This difference relates to the time of tooth development and lactation in mammals (Bocherens et al., 1997; Bocherens, 2000).

The scanty  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data for Late Pleistocene mammals in the Pampean Region precludes a detailed comparison. However, based on the information available, the  $\delta^{13}\text{C}$  value of the *P. troglodytes* ( $-17.40\ \delta^{13}\text{C}$ ) was compared with some relatively contemporaneous regional taxa, such as equids (*H. principale* minimum–maximum:  $-21.1/-17.10\ \delta^{13}\text{C}$ , *Equus neogaeus* minimum–maximum:  $-20.70/-16.20\ \delta^{13}\text{C}$ ), gomphotherids (*S. platensis* minimum–maximum:  $-21.11/-15.09\ \delta^{13}\text{C}$ ), toxodonts (*Toxodon* sp. minimum–maximum:  $-19.50/-14.00\ \delta^{13}\text{C}$ ), ground sloth (*M. americanum* minimum–maximum:  $-19.8/-19.5\ \delta^{13}\text{C}$ ) and a camelid (*Lama* sp.:  $-7.8\ \delta^{13}\text{C}$ ; Macfadden and Shockey, 1997; Sánchez et al., 2004, 2006; Alberdi et al., 2008; Steele and Politis, 2009; Prado et al., 2011). Using the values of the Late Pleistocene herbivores and the reported enrichment from prey to predator observed in living communities ( $0-2\ \delta^{13}\text{C}$ , see Bocherens and Drucker, 2003; Fox Dobbs et al., 2007), it is possible that *S. platensis*, *H. principale*, *E. neogaeus*, *M. americanum* may have contributed to the diet of *P. troglodytes* (Fig. 3). *Lama guanicoe* may have also contributed if the isotopic signal of the specimens from the Late Pleistocene specimens of the Pampean Region is similar to the recorded in Holocene specimens. Further, using the  $\delta^{13}\text{C}$  range of *Toxodon* sp. it is also possible that they were in the diet of *P. troglodytes* (Fig. 3). On the other hand, the only  $\delta^{13}\text{C}$  data for *Lama* sp. from the Late Pleistocene is too high to be a significant part of the *P. troglodytes* diet using the value obtained from the studied specimen ( $-17.40\ \delta^{13}\text{C}$ ). It is clear that additional isotope samples on *P. troglodytes* and Pleistocene herbivores are needed to better understand the dietary relationships of these taxa. Unfortunately these samples are not available at this time. The isotope mixing model agrees with this interpretation, indicating that *S. platensis*, *H. principale*, *E. neogaeus*, *M. americanum* and *Toxodon* sp. produced values that are consistent with the dietary values for the *P. troglodytes* specimen and therefore could have contributed to the diet of the species. *Lama* sp. has the lower contribution to the isotopic signal of the studied *P. troglodytes* specimen, and only in the model based in minimum values get a greater contribution than other taxa (mean = 23%) and the model based on maximum values indicates that *M. americanum* could have the greatest contribution followed by equids and then by *M. americanum*. These results only provide a preliminary glimpse at dietary relationships, and a basis for future comparison.

Some previous reconstructions based on body mass and prey size estimations interpreted that *Procyon* and other extinct large South American canids could prey on equids and camelids (Prevosti and Palmqvist, 2001; Prevosti, 2006; Prevosti and Vizcaíno, 2006), in accordance with these findings. However, it is unlikely that *P. troglodytes* hunted adult specimens of *S. platensis*, *M. americanum* and *Toxodon* based on the large body size of these herbivores, however, it is likely that the remains of these herbivores were eaten as carrion by canids (Prevosti, 2006).

## 5. Conclusion

This work demonstrated that the specimen MLP 89-XI-20-1 belongs to the extinct hypercarnivore canid *P. troglodytes*, and not to a new species. The morphology and size of this specimen falls in the range of variation of *P. troglodytes*, and the reduction of the first lower premolar was a mistaken observation made by Berman (1994) because the tooth was lost during the life of this

individual. The first taxon date of a South American large hypercarnivore canid indicates that *P. troglodytes* was present at least until ca. 17 ka BP.

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes corroborated the hypercarnivorous diet of *P. troglodytes*, as was previously established using morphological approaches. The scant information about the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signal of other Late Pleistocene mammals in the Pampean Region suggests that *E. neogaeus*, *H. principale*, *S. platensis*, *Toxodon*, and *M. americanum* could have been an important contribution to the diet of the specimen of *P. troglodytes* analysed here, but the only analyzed specimen of *Lama* sp. made a limited contribution.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.quaint.2012.07.003>.

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