

# Biostratigraphy, systematics, and paleoecology of *Protocyon* Giebel, 1855 (Carnivora, Canidae) in South America

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## Abstract

*Protocyon* Giebel is a genus of strongly carnivorous canids adapted to open environments that inhabited South America during the Pleistocene. It is represented by four species: *Protocyon orcesi* Hoffstetter from Ecuador; *Protocyon troglodytes* Lund from Bolivia, Ecuador, and Brazil; *Protocyon scagliarum* Kraglievich, the oldest record of the genus (Ensenadan); and a new unpublished species from the Late Pleistocene. These two latter species are exclusive to Argentina. A new record of *P. cf. P. troglodytes* (the first of Argentina) from the Late Pleistocene of Formosa province is reported, and the main records of the genus are listed, with comments on their paleoecological and paleogeographic aspects. The oldest record of the genus is younger than 0.78 Ma BP, whereas the biochron of *P. scagliarum* is between 0.78 and 0.5 Ma BP. The first records of *P. troglodytes* are probably older than 0.5 Ma BP, reaching the late Pleistocene; *P. orcesi* lived between 0.3 Ma and 10 Ka BP and *Protocyon* sp. nov. between 0.5 Ma and 10 Ka BP. This finding in northern Argentina partially fills in the geographic distribution of *P. troglodytes*.

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**Keywords:** Argentina; Biostratigraphy; Canidae; Carnivora; Formosa; Paleoecology; *Protocyon*; Quaternary

## 1. Introduction

The first record of the entrance of canids in South America, as members of the ‘Great American Biotic Interchange’ (Webb, 1991), goes back to the Late Pliocene (Vorohuean). The remains belong to a small fox (*Dusicyon cultridens*; Berman, 1994) found in sediments of the Marplatense stage, Vorohuean substage (2.5–3 Ma BP, sensu Cione and Tonni, 2001). During the Early Pleistocene (Ensenadan), the diversity of this group increased notably; several species of *Dusicyon*, *Chrysocyon brachyurus*, and the genera *Theriodictis*, *Protocyon*, and *Canis* (Berta, 1988; Berman, 1994) are first recorded.

*Protocyon* includes species endemic to South America, middle to large sized (ca. 20 kg), with inferred hypercarnivorous habits (Berta, 1988; Van Valkenburgh, 1991). This genus is known by three species already described and a new, unpublished species. *Protocyon troglodytes* has been found in Brazil (Late Pleistocene; Berta, 1988; Cartelle and Langguth, 1999), Bolivia (‘Middle Pleistocene,’ Hoffstetter, 1963; Berta, 1988), and Ecuador (Late Pleistocene; Berta, 1988; Fig. 1). *Protocyon orcesi* and *Protocyon scagliarum* are restricted to the type localities La Carolina in Ecuador (Late Pleistocene; Hoffstetter, 1952) and Arroyo Santa Elena in the Pampean region (Argentina; late Ensenadan, Early–Middle Pleistocene), respectively (Berta, 1988; Fig. 1). Finally, *Protocyon* sp. nov. is found in the northeast of the Pampean region (Buenos Aires, Argentina; Berman, 1994; Fig. 1).

The objectives of this article are (1) to revise the record of the genus *Protocyon* based on new biostratigraphic patterns, paleomagnetic, and geological studies and new remains; (2) to describe a new specimen for Argentina, assigned to *Protocyon* cf. *P. troglodytes*, and discuss its

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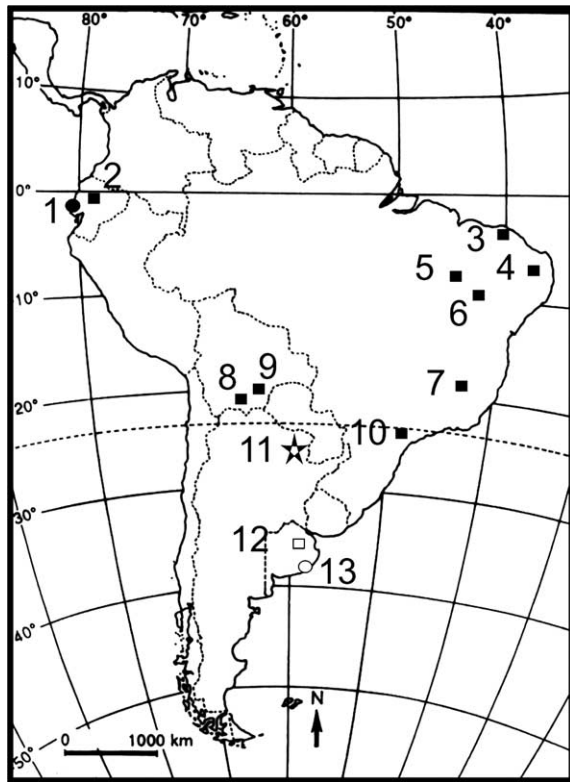


Fig. 1. Distribution of *Protocyon* in South America. Black square, *P. troglodytes*; white square, *Protocyon* sp. nov.; black circle, *P. orcesi*; white circle, *P. scagliarum*; star, *Protocyon* cf. *P. troglodytes*. 1, La Carolina; 2, Guamate; 3, Itapipoca; 4, Curimatás; 5, São Raimundo Nonato; 6, Campo Formoso; 7, Lagoa Santa; 8, Tarija; 10, Gruta Clarabela; 9, Ñuapua; 11, Río Bermejo; 12, Mercedes; 13, Arroyo Santa Elena.

paleobiogeographic significance; and (3) to summarize existing information about the paleoecology of the genus.

### 1.1. Abbreviations

I, upper incisor; C, upper canine; P, upper premolar; M, upper molar; and m, lower molar. Measurements: *L*, anteroposterior diameter (length); *W*, transverse diameter (width); RWC1, rostrum width level at the canines; MIW, minimum interorbital width; WCP, postorbital constriction width; PL, palatal length; PW, palatal width; WMESOFT, width of the mesopterygoid fossa; ORBH, orbit height; YH, jugal height; UISW, upper incisor series width; C1–M2L, distance between anterior margin of C1 and posterior margin of the M2; M1LABL, length of the M1 on the labial margin; and M1LINGL, length of the M1 on the lingual margin.

### 1.2. Museum collection abbreviations

Ctes-PZ, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (Corrientes, Argentina); MMP, Museo Municipal de Ciencias Naturales de Mar del Plata ‘Lorenzo

Scaglia’ (Mar del Plata, Argentina); IGC, Instituto de Geociências da Universidade Federal de Minas Gerais (Minas Gerais, Brazil); UZM, Universitets Zoologiske Museum (Copenhagen, Denmark); MNZRJ, Museu Nacional de Rio de Janeiro (Rio de Janeiro, Brazil); and EPN, Escuela Politécnica Nacional (Quito, Ecuador).

## 2. Materials and methods

Measurements of the studied materials were taken with a manual caliper, following Berta (1988), except for WMESOFT, which was measured according to Cartelle and Langguth (1999). WIM, PW, and PCW from Ctes-PZ 7278 were calculated as twice the distance to the sagittal plane, because the left side of the skull is broken. Measurements in mm appear in Table 1.

The biostratigraphy follows Cione and Tonni (1995a,b, 1999, 2001), as well as the chronostratigraphic scheme proposed in their 2001 paper.

## 3. Systematics

Class MAMMALIA Linnaeus, 1758  
Order CARNIVORA Bowdich, 1821  
Family CANIDAE Fischer, 1817  
*Protocyon* Giebel, 1855

### 3.1. Type species

*Protocyon troglodytes* (Lund, 1838).

### 3.2. Diagnosis

Deep zygomata with wide masseteric scar; long palatines extending beyond the toothrow; wide palate; P4 protocone very reduced; M1–2 with very reduced or absent hypocone; coronoid process anteroposteriorly broad and dorsoventrally low; angular process large, usually blunt without dorsal hook, fossa for inferior branch of medial pterygoideus muscle expanded; m1 lacking metaconid and entoconid; M2/m2 small relative to M1/m1; foramen rotundum opening separately from the alisphenoid canal (Berta, 1988; Cartelle and Langguth, 1999).

*Protocyon* cf. *P. troglodytes* (Lund, 1838) (Fig. 2, Table 1).

### 3.3. Referred material

Ctes-PZ 7278, partial skull with most of the rostrum, the right zygomatic arch, part of the braincase, the right petrosal, and almost complete dentition (right I1–3, C, P2–M2 and left I1–P3).

Table 1  
Craneodental measurements (mm) of *Protocyon* cf. *P. troglodytes* (Ctes-PZ 7278) and other *Protocyon* specimens

	cf. <i>P. troglodytes</i> (Ctes-PZ 7278)	<i>P. scagliarum</i> (MMP S 164)	<i>P. troglodytes</i> (IGC 1) <sup>a</sup>	<i>P. troglodytes</i> (UZM L 5697)	<i>P. troglodytes</i> (UZM L 5699) <sup>a</sup>	<i>P. troglodytes</i> (UZM L 187) <sup>a</sup>	<i>P. troglodytes</i> (UZM L 1257) <sup>a</sup>	<i>P. troglodytes</i> (UZM L 251) <sup>a</sup>	<i>P. troglodytes</i> (UZM L 643) <sup>a</sup>	<i>P. troglodytes</i> (UZM L 2145/46) <sup>a</sup>	<i>P. troglodytes</i> (MNZRJ 3231)	<i>P. orcesi</i> (EPN V 2877) <sup>b</sup>
RWC1	50.3		45									
MIW	51.8	44.35	48									
WCP	44.4	44.15	42.5									
PL	97											
PW	88.2	75.15										
WMESOPT	26.1		24.5									
ORBH	29.9	30.15										
YH	18.6	16.3										
UISW	32.95											
C1–M2L	91.6	92.2										
C1L	11.6	11.4		11.75								
C1W	7.7	8.05		8.1								
P1L	8.4			7								
P1W	5.6			5.6								
P2L	11.2	12.2		12.1								
P2W	5.9	6.1		5.7								
P3L	12.8	13.1		13.3								
P3W	6.4	6.2		6.65								
P4L	24.9	25.1	24.6	25.9	26.3			27.6	26	28		
P4W	11.8	11.05	11.6	12.2	12.4	12.5			12.7	13.5		
M1LABL	14.6	14.7	14.4	14.25		16.5					14.56	13.8
M1LINL	9.1	10.2		10.45							10.19	
M1W	18.6	19		18.8		18.6					18.86	19.2
M2L	6.05	6.8	5.2				7.6					
M2W	8.6	9.2	8				9.1					

<sup>a</sup> Cartelle and Langguth (1999).

<sup>b</sup> Hoffstetter (1952).

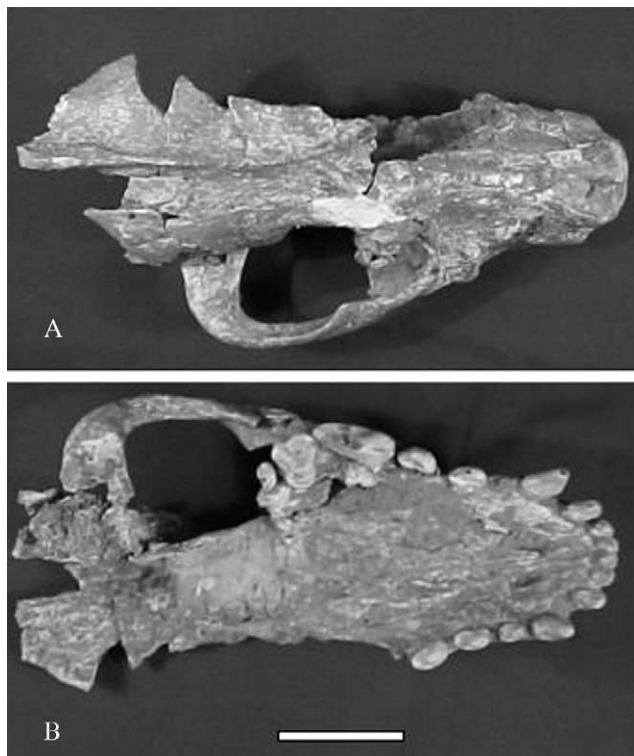


Fig. 2. Skull of *Protocyon* cf. *P. troglodytes* (Ctes-PZ 7278) collected at Bermejo river (Formosa, Argentina). (A) dorsal view; (B) ventral view. Scale, 5 cm.

### 3.4. Locality and horizon

Cliffs of the Bermejo river (Formosa province, Argentina; 27°60'S–59°22'W), in front of Presidencia Roca city, approximately 150 km NW of Resistencia (Chaco province) on provincial route 3. These cliffs, 4–5 m high, are characterized by strong sedimentological homogeneity, with no differentiation except for a slight lamination in some levels (Zurita, pers. obs.). Granulometric analysis showed a pink-bearing sediment (5 YR 7/3, Munsell color chart) composed of sand–silt–clay in the following percentages: sand 79.30%, silt 20.03%, and clay 0.58%. Owing to the presence of *Megatherium* aff. *M. americanum* Cuvier (Zurita et al., 2001), it is assigned to the Upper Pleistocene (Bonaerian–Lujanian). However, because the bearing sediments were deposited as an alluvial fan of the Bermejo River, the age of the material studied probably belongs to the Lujanian (<0.13 Ma BP; Cione and Tonni, 1999) (Orfeo, pers. comm.).

### 3.5. Description, comparison, and comments

The rostrum is short and wide, and the zygomatic arch is robust with a large notch at the origin of the surface masseteric muscle. The palate is proportionally wide. The infraorbital foramen is level with the posterior margin of the P3, the jugal contacts the lacrimal, and the temporal ridges join behind the postorbital constriction, forming a relatively

low sagittal crest. The postorbital constriction is relatively wide. The I3 is strongly developed, whereas the C1 is robust but short, and the premolars have small diastemata between each other. The P1 is large, single cuspidate, and single rooted, whereas P2–3 are double rooted with a single main cusp that is robust and slightly backward inclined. The P4 is large with a very reduced protocone that lies on the anterior margin of the paracone and is not separated from the latter by a notch. The labial cingulum of the M1 is scarcely developed. The metacone is small in relation to the paracone. The protocone is low and the metaconule minute. The lingual portion of the M1 is anteroposteriorly compressed, and the posterior margin is straight. The M1 hypocone is very reduced, and the M2 is small and double rooted with only a small paracone and protocone.

The small overall size relative to specimens of *Theriodictis*, short rostrum, wide palate, reduced M2, protocone of the P4, and hypocone of the M1 allow an assignment of this specimen to the genus *Protocyon*. It differs from *P. scagliarum* by its more robust skull, with a wider palate and rostrum, and strong zygomatic arch that is rounded in dorsal view. In *P. scagliarum*, the main cusps of P2–3 are more acute and less inclined posteriorly. In addition, *P. scagliarum* has a well-developed posterior accessory cusp on these premolars, which is absent in Ctes-PZ 7278. The M1 of Ctes-PZ 7278 has a lower and less conic paracone and metacone, and the internal side of the tooth does not incline posteriorly as in *P. scagliarum*. These characters that separate it from *P. scagliarum* are present in *P. troglodytes*, but the lack of an accessory posterior cusp in the P3 differentiates it from the latter (Berta, 1988; Cartelle and Langguth, 1999). Cartelle and Langguth (1999) observe that the presence of an accessory posterior cusp in the P2 of *P. troglodytes* is variable and that this cusp is very reduced in the P3 of some specimens. Thus, the absence of such a cusp in the P3 may reflect intraspecific variability in *P. troglodytes*. *Protocyon orcesi* is known through several mandibular and postcranial remains and one isolated M1 (Hoffstetter, 1952; Berta, 1988). This upper molar is quite similar to that of Ctes-PZ 7278, but the hypocone is more developed and the inner portion of the tooth curves posteriorly. Finally, *Protocyon* sp. nov. (Berman, 1994) was described on the basis of two hemimandibles and several elements of a single specimen and cannot be compared directly with the specimen studied here.

On the basis of the similarities with *P. troglodytes*, the specimen (Ctes-PZ 7278) is assigned tentatively to this species. However, a systematic revision of the genus is needed because the diagnostic characters of the species (i.e. absence of m3, presence or absence of accessory cusps in premolars) are found within the intraspecific variation of some specimens of modern and fossil canids (Kraglievich, 1930; Berta, 1988; Cartelle and Langguth, 1999; Szuma, 1999, 2000, 2001; Prevosti, pers. obs.).

#### 4. Geographic and stratigraphic distribution

The first record of the genus is the holotype of *P. scagliarum*, which was found at the base of coastal cliffs near the mouth of Santa Elena Creek (Buenos Aires, Argentina; 37°51'S–57°30'W; Fig. 1) (Kraglievich, 1952). Several authors (Kraglievich, 1952; Berta, 1988; Van Valkenburgh, 1991) believed it was found in 'Uquian' levels (=Marplatan, Upper Pliocene; Cione and Tonni, 1995a). However, recent biostratigraphic and paleomagnetic studies in this area (Tonni et al., 1992, 1998; Berman, 1994; Vucetich et al., 1997; Bidegain et al., 1998; Verzi et al., 2002) demonstrate that the age of the oldest stratigraphic levels is actually upper Ensenadan (Lower–Middle Pleistocene). In addition, the correlation of the bearing level with the normal polarity sector (Bruhnes Chron) of the paleomagnetic profile of Bidegain et al. (1998), 10 km SW, indicates that this specimen is likely to have come from the uppermost Ensenadan (0.78–0.5 Ma BP).

However, the first records of *P. troglodytes* are from San Pedro (Tarija, Bolivia; 21°30'S–64°41'W; Berta, 1988; Fig. 1). They were found in levels 2 and 10 of MacFadden and Wolff's (1981) (Fig. 4; R. Hulbert, pers. comm.) profile, which represent the upper levels of the Tolomosa Formation, assigned to the Brunhes Chron due to their normal polarity (MacFadden and Wolff, 1981; MacFadden, 2000). Based on the <sup>13</sup>C of remains of *Equus* and *Cuvieronius*, these authors suggest that the section was deposited during a warm period that may correspond to Isotopic Stage 15 or 17. The correlation of these isotopic stages results from the assignment of this fauna to the Ensenadan and the supposition that the limit Ensenadan–'Lujanian' (sensu Marshall et al., 1984) would not be younger than 0.5 Ma BP. Because most collections lack precise stratigraphic data (e.g. Werdelin, 1991) and isotopic data are scarce, the age of the upper levels of the Tolomosa Formation is not known with certainty. Marshall et al. (1984) propose that it might correspond to the Upper Pleistocene. In summary, the age of these materials is younger than 0.78 Ma BP, but there are no criteria to restrict the minimum age, so it may correspond to the Late Pleistocene (<0.13 Ma BP).

Another specimen determined as *Protocyon* cf. *P. troglodytes* by Berta (1988) was found in Tarija but without precise stratigraphic provenance. This species was recorded in the Bolivian locality of Ñuapua (Chuquisaca; 20°52'S–63°04'W; Fig. 1) in sediments with normal polarity from the Bruhnes Chron (<0.78 Ma BP, 'Ñuapua 1,' see Hoffstetter, 1968; MacFadden and Wolff, 1981). This stratigraphic level may correspond to the Upper Pleistocene ('late Bruhnes epoch,' MacFadden and Wolff, 1981), or it may be somewhat older ('late Ensenadan,' Marshall et al., 1984). Berta (1988) also cites a specimen of *P. troglodytes*, found in a locality from the 'Late Pleistocene' in Ecuador (Guamote, Chimborazo; 1°55'S–78°42'W; Fig. 1), together with remains of *Glossotherium*, *Equus*, and *Paleolama*.

Hoffstetter (1986) assigns this fauna to the 'Puninian' and refers it to the Late Pleistocene ('from late interstadial until the end of the Pleistocene').

Most specimens of *P. troglodytes* were found by Lund in Lagoa Santa caves (Minas Gerais, Brazil; 19°39'S–43°53'W; Berta, 1988; Cartelle and Langguth, 1999). Other remains were found in Itapipoca caves (Ceará, Brazil; 3°29'S–39°35'W; Gomide, 1989), Campo Formoso (Bahia, Brazil; 40°51'S–10°09'W; Cartelle and Langguth, 1999), Curimatãs (Paraíba, Brazil; ~7°03'S–36°21'W; Bergqvist, 1993), São Raimundo Nonato (Piauí, Brazil; 8°59'S–42°41'W; Guérin, 1991), and Gruta Clarabela (Paraná, Brazil; 24°38'S–49°32'W; Born and Sedor, 2001) (Fig. 1). Cartelle (1999) refers the age of these specimens and the faunas from the Brazilian caves to the latest Pleistocene and considers them relatively synchronous. Unfortunately, there is only a single radiocarbon date associated with the specimens of *P. troglodytes* found in Campo Formoso, ~20 Ka BP (Cartelle and Langguth, 1999). Cartelle's (1999) hypothesis about the synchrony of these faunas must be tested; some materials are likely to be older than the latest Pleistocene because of the distance between the sites and the particular deposition environment. Holocene fossils found in the same caves (Cartelle, 1999) also suggest a longer time span of deposition.

The record of *Protocyon* cf. *P. troglodytes* (Ctes-PZ 7278) in northern Argentina agrees with the wide geographic distribution of *P. troglodytes* and partially fills the gap between the Andean and Brazilian records.

Specimens of *P. orcesi* were found in La Carolina (Santa Elena; 2°12'S–80°58'W; Fig. 1) in Ecuador and are associated with 'Lujanian' fauna (Carolinian of Hoffstetter, 1952) from the Late Pleistocene. However, the precise age of this and other sites in Ecuador is not known (i.e. Guamote, vide supra) because of the lack of absolute dating or accurate biostratigraphic schemes for the region.

Berman (1994) describes a new species on the basis of remains in the NE of the Pampean region (Mercedes, Buenos Aires, Argentina; 34°39'S–59°26'W; Fig. 1), 5 m deep and associated with *Lama gracilis*. The latter species restricts the age of the deposit to the Bonaerian and Lujanian (Middle Pleistocene–Early Holocene, 0.5 Ma–8.5 Ka BP) because it is an exclusive taxon of these ages (Cione et al., 1999). Berta (1988) describes a mandibular fragment with p3 and part of p4 as *Protocyon* sp., from the SE of the Pampean region; however, this remain belongs to a felid—*Puma* sp.—not a canid (Berman, 1994).

In summary, the lack of isotopic dating and paleomagnetic, geologic, and biostratigraphic studies makes it difficult to determine the age of several specimens of *Protocyon* and its associated fauna with precision. Dating taxa would be extremely useful, especially in those karstic deposits of Brazil in which low sedimentation rates and reworking may produce considerable time averaging within some vertebrate associations (Cartelle, 1999). The recent thermoluminescence dating of the lower layers of the Toca

do Boqueirão da Pedra Furada (Piauí, Brazil) that extends the deposition of this sequence to 100 Ka AP (Valladas et al., 2003) supports the last hypothesis.

## 5. Paleoecology

The craniodental morphology of *Protocyon* is typical of hypercarnivorous species and has been recognized since the nineteenth century by several paleontologists (e.g. Winge, 1895; Kraglievich, 1928; Kraglievich, 1952), who show the similarity with modern species of hypercarnivorous canids (e.g. *Cuon alpinus*, *Speothos venaticus*). More recently, Berta (1981, 1987, 1988) includes this genus within the adaptive zone of moderate- to large-sized carnivores, together with *Panthera onca*, *Puma concolor*, *Smilodon populator*, and *Theriodictis*. *Protocyon* would likely have pursued its prey and probably also scavenged opportunistically.

In a study of the iterative evolution of the hypercarnivory in canids, Van Valkenburgh (1991) used three morphological indices: PS, the shape of lower largest premolar, estimated by dividing the labiolingual width by the anteroposterior length of the tooth; RPS, the relative size of lowermost developed premolar, calculated by dividing its length by the estimated body mass; and RGA, the relative grinding area of lower molars, estimated by dividing the occlusal surface of the talonid in m1 and that of the other molars by the length of the trigonid of the lower carnassial molar. Using these indices, she defined a region of three-dimensional morphospace in which the species of hypercarnivorous canids can be placed. Likewise, she scored the morphology of the talonid of m1 (fully trenchant, with no entoconid; moderately trenchant, with reduced entoconid; not trenchant, bicuspid talonid, hypoconid, and entoconid similar in size) as a key character to infer feeding habits in extinct species. According to the results of this study, *Protocyon* would be hypercarnivorous (meat from vertebrate prey represents more than 70% of its diet), because it lies within the region of the morphospace occupied by modern canids with hypercarnivorous habits and has a moderately trenchant talonid on the m1. The specimen of *Protocyon* cf. *P. troglodytes* here studied shows several characters suggesting it had a hypercarnivorous diet (e.g. P4 proportionally large, M2 reduced, short and wide palate, robust canines, protocone of P4 and hypocone of M1 very reduced) that are present in other specimens of the genus.

The body mass estimated for *P. troglodytes*, *P. orcesi*, and *P. scagliarum*, based on simple regressions proposed by Van Valkenburgh (1990), would be 16, 25, and 11 kg, respectively (Van Valkenburgh, 1991). The masses estimated for *P. scagliarum* and *P. troglodytes* are too low if the relative size of the known skeletal elements are taken into account (Table 1). Other methods (e.g. multiple regression)

would provide a more accurate estimation of the mass of these canids (e.g. Palmqvist et al., 1999; Prevosti and Palmqvist, 2001), but unfortunately, we do not have enough data to so currently.

The postcranial remains of *P. troglodytes*, *P. orcesi*, and *P. sp. nov.* show that they were canids with generalized limbs, typical of cursorial species of open environments (e.g. *Dusicyon culpaeus*) (Cartelle and Langguth, 1999; Prevosti, pers. obs.).

Cartelle and Langguth (1999) supposed that *P. troglodytes* fed on medium-sized mammals such as cervids, camelids, equids, and tayassuids but not on large edentates or other megamammals. The postcranial morphology (vide supra) suggests that they actively pursued their prey in environments with open vegetation, probably forming packs, as do the modern species of *Canis lupus*, *Lycaon pictus*, and *Cuon alpinus*. This trait may exist in all species of the genus.

According to Van Valkenburgh (1991), the abundance of herbivores and scarcity of other hypercarnivorous forms would have allowed the coexistence of several species of hypercarnivorous canids (e.g. *Protocyon* spp., *Theriodictis platensis*, *Canis dirus*). However, among these canids, there likely would have been interspecific competition, with *Protocyon* being displaced by the larger *Theriodictis* and *Canis*, as occurs between the living species *Canis lupus* and *Canis latrans* (Johnson et al., 1996).

However, the wide temporal, geographic, and altitudinal distribution of *P. troglodytes* suggests that it was an eurytopic species adapted to different environments (e.g. mosaic of ‘cerrado’ and ‘mata atlántica’ in Brazil, grassland in the Andes of Bolivia and Ecuador; MacFadden and Shockey, 1997; Cartelle and Langguth, 1999) that probably chose different prey across its geographic and temporal distribution according to availability. Notably, it has not been found south of 26°S latitude, and the specimens of Tarija lived during a warm climatic stage (MacFadden, 2000). In addition, the association of *Protocyon* sp. nov. and *L. gracilis*, a camelid adapted to relatively xeric grasslands (Menéaz and Ortiz Jaureguizar, 1995), suggests that this canid may have inhabited open and semiarid environments (Berman, 1994).

## 6. Conclusions

The oldest records of *Protocyon* are younger than 0.78 Ma BP. *Protocyon scagliarum* existed between 0.78 and 0.5 Ma BP, and the first records of *P. troglodytes* are probably older than 0.5 Ma BP, thus reaching the latest Pleistocene. *Protocyon orcesi* lived in the ‘late Pleistocene’ (0.3 Ma–10 Ka BP), and *Protocyon* sp. nov. lived in the Middle–Late Pleistocene (0.5 Ma–10 Ka BP).

The specimen studied here, assigned to *Protocyon* cf. *P. troglodytes*, was found in Upper Pleistocene sediments. This

record, from northern Argentina, partially fills a large gap in the geographic distribution of *P. troglodytes*, an eurytopic species with a wide geographic and temporal distribution adapted to a large variety of environments.

*Protocyon* includes species of hypercarnivorous canids of middle to large size (~20–25 kg) that were adapted to hunt medium-sized mammals (e.g. camelids, equids, cervids) in environments with relatively open vegetation.

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