Historical Biology

Large extinct canids from the Pleistocene of Uruguay: systematic, biogeographic and paleoecological remarks

F. J. Prevosti [a]; M. Ubilla [b]; D. Perea [b]

[a] División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" - CONICET, Buenos Aires, Argentina [b] Facultad de Ciencias, Montevideo, Uruguay

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis
Taylor & Francis Group

Large extinct canids from the Pleistocene of Uruguay: systematic, biogeographic and paleoecological remarks

F.J. Prevosti[a]*, M. Ubilla[b1] and D. Perea[b2]

[a]División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" - CONICET, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina; [b]Facultad de Ciencias, Iguá 4225, 1400 Montevideo, Uruguay

The fossil record of Canidae in South America begins in the Late Pliocene. During the Pleistocene large hypercarnivore canids (*Theriodictis*, *Protocyon*, *Canis dirus*) and also large species of Neotropical foxes (*Dusicyon avus*) evolved. Most fossil canids were found in Chile, Ecuador, Bolivia, Brazil, Venezuela and Argentina and are scarce or absent in other countries. From Uruguay only fossils referred to *Dusicyon gymnocercus*, '*Pseudalopex*' and '*Canis*' are currently known. We describe new records that belong to large canids from the Sopas Fm. (Late Pleistocene) of Uruguay and discuss their biogeographic and paleoecologic relevance. These specimens are referred to *Protocyon troglodytes* and *D. avus* by means of descriptive and multivariate analysis and constitute the first records of these taxa for Uruguay, expanding and completing their distribution in the Late Pleistocene of South America. Both species could have been occupied 'niches' not represented by the carnivores previously registered in the Sopas Fm. (*Puma concolor*, *Panthera onca*, *Lontra longicaudis*, etc.) suggesting more complex biotic interactions in the mammalian assemblages than previously assumed. The large hypercarnivorous canid *P. troglodytes* could hunt medium-large sized mammals, pursuing their prey in packs over long distances, while the medium canid *D. avus* could prey on small and middle mammals.

Keywords: Late Pleistocene; South America; large canids

Introduction

The canids of South America show not only a great diversity in the present but also in the past (Kraglievich 1930; Berta 1988; Prevosti 2006), encompassing a large spectrum of sizes and different ecological types. Although this group currently comprises a high number of species (see Berta 1987, 1988), this contrasts with the relatively late immigration from North America (Late Pliocene) of the family into South America (Berta 1988; Berman 1994; Prevosti 2006), and indicates the successful evolution of the group in this new subcontinent. Nevertheless, the large hypercarnivorous forms became extinct at the end of the Pleistocene.

The fossil record of South American Canidae is mainly from the Pampean Region of Argentina, along with few sparse records from other countries such as Bolivia, Peru, Ecuador and Brazil. However, new recent findings are closing geographic gaps and providing several novelties (see Prevosti and Rincón 2007). Nevertheless the canid fossil record of Uruguay remains extremely poor, limited to the Pampean fox (*Dusicyon gymnocercus*) in the Late Pleistocene of the Sopas Formation of northern Uruguay (Ubilla et al. 2004), '*Pseudalopex*' sp. from the southwest of Uruguay (Pampeano superior) (Kraglievich 1927, p. 30) and records of *Canis* sp. (Berro 1929).

In this paper, we describe two fossil canids from the Late Pleistocene of Uruguay (Sopas Formation), a large hypercarnivorous species (*Protocyon trogodytes*) and a large fox (*Dusicyon avus*), and discuss their relevance to our knowledge of this group and to the paleoecology of Late Pleistocene mammalian assemblages at this latitude in South America as well as to the associated fauna.

Geological and paleontological setting

The Sopas Formation is widely exposed in river, stream and creek beds in northern Uruguay in sections up to 12–15 m thick. It includes conglomerates, conglomerate-sandstones, siltstones and sandy siltstones, and was deposited predominantly under fluvial conditions but also shows paleosols in some places (Ubilla 2004). This formation is a rich fossiliferous sedimentary unit as evidenced by the presence of several vertebrate groups (giant terrestrial turtles, lizards, some birds, terrestrial and fresh-water mammals), fresh-water and terrestrial molluscs, wood and continental ichnofossils (Ubilla and Perea 1999; Verde and Ubilla 2002; Ubilla et al. 2004; Verde et al. 2007). Radiocarbon ages range up to >43 ky BP (minimum age), based on wood and fresh-water mollusc shell samples (Ubilla 2001); some TL produced ages

encompass the early Late Pleistocene (Martínez and Ubilla 2004; Ubilla et al. 2004).

Although it includes an important diversity of vertebrates, the mammals from the Sopas Formation are the dominant group that convey biostratigraphic, climatic and environmental information. These rocks are biostrati-graphically correlated to the Lujanian Stage/Age of Buenos Aires province (Late Pleistocene-Early Holocene, see Cione and Tonni 2005) because of the presence of *Equus neogaeus* among other taxa restricted to this unit (Ubilla et al. 2004). Mammals of the Sopas Formation are related to various habitats including fluvial and lacustrine environments, riparian forests and also open woodland to savanna and grassland (Ubilla et al. 2004). Moreover, fresh-water molluscs support the presence of lotic and lentic habitats (Martinez and Rojas 2004) and in some localities, earthworm trace fossils demonstrate the development of paleosols under seasonal climates (Verde et al. 2007). The mammalian fauna includes extinct taxa such as glyptodonts (*Glyptodon clavipes*, *Panochthus tuberculatus*, *Neuryurus*, etc.), armadillos and 'armadillo-like' xenarthrans (*Dasypus*, *Propraopus*, *Pampatherium*), ground-sloths (*Glossotherium robustum*, *Lestodon* cf. *armatus*), and native ungulates such as the notoungulate *Toxodon platensis* and the litopterns *Macrauchenia patachonica* and *Neolicaphrium recens*. Two equids are also recorded from the formation (*Hippidion principale* and *E. neogaeus*) alongside tapirs, artiodactyls such as pecaries, camelids and deer, and rodents of a range of sizes (some sigmodontine rodents, porcupines, caviines, coypus and capybaras). Because of the composition of the Sopas Formation mammal assemblage, including tropical to temperate taxa (*Tapirus*, *Hydrochoerus*, *Myocastor*, *Coendou*, etc.), it has been related to a warm interval of time such as the last interglacial or last interstadial (Ubilla et al. 2004).

Among Carnivora, the two living large predators *Puma concolor* and *Panthera* cf. *Panthera onca* have been recorded as well the extinct sabre-toothed cat *Smilodon populator* and an indeterminated Tremarctinae bear. The living pampean fox *D. gymnocercus* and the living-river-otter *Lontra longicaudis* (see Ubilla and Perea 1999; Ubilla et al. 2004 and references therein) have also been described from this unit.

Material and methods

The measurements reported here were taken with digital calipers accurate to 0.01 mm and are expressed in millimetres (see Tables 1 and 2), following Prevosti (2006). The principal component analyses (PCA) were performed on the covariance matrix of $\log_{10}$ transformed measurements; in the discriminant analyses (DA), all groups have the same probability of classification (see Reyment et al. 1984; Legendre and Legendre 1998). For morphometrics and comparisons, we studied 74 recent

specimens of *Dusicyon culpaeus*, 108 of *D. avus*, and one of *Dusicyon australis* all from different collections (see Acknowledgements). The information of *Protocyon troglodytes* was taken from Prevosti (2006). The systematic scheme for the canids used here is that proposed by Prevosti (2006) and the biostratigraphic-chronostrati-graphic one of Cione and Tonni (2005; see also Woodburne et al. 2006). The geographic distribution data plotted in Figure 1 was taken from Kraglievich (1930), Caviglia (1978, 1986), Berman (1986, 1994), Berman and Tonni (1987), Trejo and Jackson (1998), Hadler Rodríguez et al. (2004), Prevosti (2006) and Amorosi and Prevosti (2008).

Anatomical and measurement abbreviations

I/i, upper/lower incisors; P/p, upper/lower premolars; M/m, upper/lower molars; CBL, condilobasal length; LOO, distance between the anterior border of the orbits and the distal limit of the cranial condyle; BICW, width between the lateral borders of the zygomatic archs; BCW, braincase width; WIM, minimum interorbitary width; WP, palatal width, at the M1–P4 contact; WRC1, width of the rostrum at the lateral margin of the C1 alveoli; ZW, zygomatic height; Lmand, length of the mandible, from the anterior border of the c1 to the posterior border of the condyle; HRHm1, mandible height at the distal border of the m1; WRHm1, mandible width at the distal border of the m1; HRHp4, mandible height at the distal border of the p4; WRHp4, mandible width at the distal border of the p4; L, mesiolabial length in canines, premolars, and molars, but labiolingual length in the case of incisors; 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; LLabM1, M1 labial length; LLiM1, M1 lingual length; Ltrm1, length of the m1 trigonid; Wtalm1, width of the m1 talonid.

Institutional abbreviations

AMNH, American Museum of Natural History, Division of Paleontology, New York, USA; MACNU, Museo de Arqueología y Ciencias Naturales, Salto, Uruguay.

Results

Systematic paleontology

Carnivora Bowdich, 1821
Canidae Fischer von Waldheim, 1817
Dusicyon Hamilton Smith, 1839
D. avus (Burmeister, 1866)
(Figure 2, Table 1)

Material referred

MACNU-73: near complete but crushed skull, with right I3, broken left C1, root of right C1, left P2–M2,

Table 1. Craneodental measurements of the MACNU-73 compared to *D. culpaeus*, *D. avus* and *D. australis*.

	MACNU-73	D. culpaeus					D. avus					D. australis (AMNH 13717)
		X	SD	Min	Max	*n*	X	SD	Min	Max	*n*	
CBL	169.35∗	167.69	11.01	137.25	195.20	68	173.63	17.78	161.05	186.20	2	
LOO	103.43	101.46	6.10	85.28	114.83	68	100.53	5.62	96.55	104.50	2	
BICW	97.8	93.04	7.18	74.20	106.80	64	88.60				1	104.97
WIM	32.16	29.76	2.63	24.62	36.60	69	34.67	2.96	31.25	36.40	3	36.73
WBC	56.44	53.07	2.52	46.67	58.53	67	56.97	2.29	54.95	59.45	3	61.07
WP	55.08	48.63	3.15	41.82	57.33	70	56.69	3.13	52.50	59.80	4	61.84
WRC1	32.54∗	28.48	2.71	23.19	35.84	69	32.33	2.53	28.80	35.90	5	36.36
ZW	12.68	9.87	1.13	7.85	12.68	69	10.80				1	15.84
Lmand	138.54	125.93	8.25	100.68	141.98	63	127.67	9.00	113.20	139.02	10	136.19
HRHm1	22.42	18.00	2.05	14.00	23.11	66	19.39	1.80	15.88	23.50	35	23.66
HRHp4	21.74	17.02	1.82	13.31	22.07	66	19.14	1.69	16.30	22.50	20	20.55
LI3	6.32	5.47	1.77	4.62	19.59	69	5.84	0.51	5.20	6.30	4	5.99
WI3	4.9	4.11	0.36	3.33	5.30	68	4.48	0.34	4.12	4.90	4	5.21
LC	9.36	8.81	0.83	7.17	11.35	66	9.00	0.72	7.95	10.02	7	9.24
WC1	6.53	5.69	0.64	4.79	8.27	66	6.23	0.82	4.80	7.20	8	6.1
LP2	10.46	9.23	0.67	7.78	10.89	67	10.52	0.48	9.60	11.30	8	9.79
WP2	4.17	3.47	0.30	2.89	4.27	68	4.03	0.12	3.78	4.20	8	4.24
LP3	11.59	10.62	0.69	8.95	12.50	68	12.08	0.80	10.90	12.95	9	11.55
WP3	4.5	3.82	0.36	3.00	4.70	68	4.63	0.34	4.12	5.05	10	5.04
LP4	18.93	15.99	1.03	13.05	18.89	73	18.99	0.74	17.50	20.44	22	18.84
WP4	9.68	7.69	0.71	6.29	9.78	73	10.06	0.59	9.10	11.10	22	9.61
LLabM1	12.42	10.06	0.79	8.09	12.38	73	12.30	0.71	11.20	13.70	28	12.91
LLiM1	9.19	7.90	0.65	6.45	9.80	73	9.49	0.60	8.40	10.90	30	9.18
WM1	15.3	12.82	0.92	10.74	15.75	73	14.93	0.72	13.74	16.59	28	15.63
LM2	7.43	6.62	0.58	5.41	8.25	73	7.42	0.51	6.52	8.23	19	8.09
WM2	11.43	10.50	1.01	8.66	15.21	73	11.05	0.67	9.97	12.15	17	10.69
Lc1	10.05	9.52	0.88	7.70	12.20	61	9.32	0.91	7.43	11.28	22	8.8
Wc1	6.78	6.22	0.67	4.03	7.66	62	6.27	0.50	5.49	7.19	24	5.8
Lp2	9.63	9.25	0.62	7.66	10.70	69	9.96	0.75	8.60	12.05	33	6.65
Wp2	4.26	3.65	0.34	2.86	4.70	69	4.25	0.32	3.65	4.98	34	4.45
Lp3	11.22	10.16	0.62	8.52	11.50	68	11.40	0.64	10.10	12.91	32	10.1
Wp3	4.46	3.77	0.35	3.03	4.70	68	4.76	0.43	4.06	6.10	34	10.19
Lp4	12.07	10.64	0.65	9.14	12.27	68	12.57	0.67	11.01	14.26	48	9.68
Wp4	5.34	4.47	0.38	3.68	5.49	68	5.66	0.44	4.86	6.90	52	5.66
Lm1	21.42	16.69	0.97	14.06	19.70	69	20.78	1.06	17.73	23.09	68	18.64
Ltrm1	15.64	11.71	0.79	9.92	13.94	69	14.44	0.94	12.55	16.73	69	13.13
Wtalm1	8.19	6.50	0.49	5.47	8.08	69	7.51	0.48	6.13	8.90	68	7.06
Lm2	9.32	8.43	0.57	7.47	9.65	61	9.15	0.60	7.60	10.55	34	9.66
Wm2	6.89	5.98	0.43	5.10	7.00	61	6.59	0.41	5.73	7.65	34	6.78
Lm3	4.28	4.09	0.38	3.39	5.10	51	4.25	0.36	3.76	4.85	12	4.7
Wm3	4.15	3.71	0.34	2.58	4.42	51	3.94	0.37	3.10	4.60	12	3.48

X, mean; SD, standard deviation; Min, minimum; Max, maximum; *n*, sample size; ∗, with error.

right P1, P3–M2, and most of the lower dentition with the exception of the right i1–3, left i1–2 and left p1.

Locality and stratigraphic horizon

Sopas creek, 500 m above Paso Muñoz Bridge (31°15′ S 57°00′; Salto Department, Uruguay; Figure 1).

Description

The skull is almost complete, but not well preserved: the cranial vault is broken and lacks a large portion of the left frontal bone (Figure 2(A)); the left zygomatic arch, and parts of the right parietal and temporal bones; the rostrum is crushed, especially on its left side and the frontals are compressed; the coronoid process is absent in the right mandible and its tip is broken in the left side; the left mandible is broken in the masseteric fossa and at the anterior part of the horizontal ramus (Figure 2(D)).

The frontals are wide and appear to have a slightly rised profile in lateral view (Figure 2(C)). The frontal sinuses invade the postorbitary process and the sagital crest is well-developed but low. Above the postorbital constriction, on the right side of the sagital crest, there is an abnormal ossification (Figure 2(A)). The infraorbital foramen is placed over the mesial portion of the P3, and

Table 2. Eigenvectors and eigenvalues of the PCA performed with the upper carnassials and upper molars (P4–M2) measurements (a) and lower fourth premolar plus first and second lower molar (p4–m2) measurements (b) of MACNU-73, *D. avus*, *D. culpaeus* and *D. australis*.

| Variable	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7
(a)							
LP4	− 0.322368	0.131548	− 0.413143	0.480063	− 0.481569	− 0.475345	0.140590
AP4	− 0.492473	0.472035	− 0.304543	− 0.650272	0.125565	− 0.056838	− 0.007466
LLabM1	− 0.442939	0.099904	0.207397	0.198201	− 0.239943	0.707091	0.392399
LLiM1	− 0.380793	0.107892	0.308841	0.382662	0.712794	− 0.279056	0.124883
AM1	− 0.364850	− 0.110621	− 0.033641	0.196879	− 0.030855	0.217188	− 0.875575
LM2	− 0.328982	− 0.339069	0.627035	− 0.328700	− 0.366930	− 0.375427	0.001728
AM2	− 0.266470	− 0.781698	− 0.451515	− 0.119023	0.226025	0.069648	0.209694
Eigenvalue	0.010629	0.001035	0.000483	0.000413	0.000382	0.000205	0.000102
%	80.22566	7.81388	3.64460	3.12022	2.88365	1.54376	0.76824
(b)							
Lp4	− 0.336964	0.217378	0.045876	0.515677	0.638965	− 0.399804	− 0.055270
Ap4	− 0.498269	0.376705	− 0.691830	− 0.357067	− 0.049999	0.009520	− 0.033244
Lm1	− 0.429627	0.115680	0.398761	− 0.112328	− 0.058821	0.123746	0.782073
Ltr	− 0.444964	0.101831	0.563673	− 0.284506	− 0.196523	− 0.104971	− 0.585940
Atalm1	− 0.360734	− 0.124224	− 0.109277	0.662915	− 0.380043	0.490283	− 0.135022
Lm2	− 0.237796	− 0.581322	− 0.035774	− 0.270739	0.566224	0.448934	− 0.093739
Am2	− 0.262554	− 0.658576	− 0.171194	0.016183	− 0.286532	− 0.609766	0.117724
Eigenvalue	0.012573	0.000812	0.000402	0.000316	0.000225	0.000183	0.000075
%	86.20290	5.56754	2.75391	2.16432	1.54270	1.25170	0.51693

Comp., principal components.
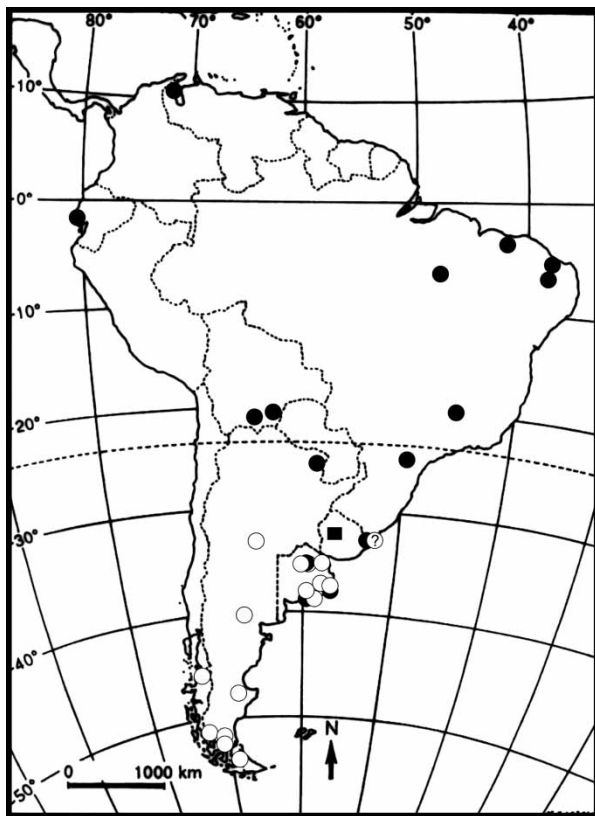
Figure 1.   Map of South America showing the fossil record of *D. avus* (white circles) and *P. troglodytes* (black circles), and the location of the Paso Muñoz bridge (Salto department, Uruguay; black square).

the anterior border of the orbit over the medium of the P4. The skull presents a strong and well dorsally curved zygomatic arch, with a wide scar for the superficial masseteric muscle on its anterolateral extreme. The palate reaches the distal portion of the M2. The bulla is well-inflated and possesses a well-developed external meatus, but an incomplete ventral intrabullar septum. The basioccipital-basisphenoid suture is obliterated. The mastoid process bears a-well-developed tubercle, and the paraoccipital process is ventrally directed, but does not surpass the ventral limit of its suture with the bulla (Figure 2(B)).

The ramus of the mandible is robust, with two mental foramina, one large one below the p1–p2 contact and other small one below the distal portion of the p3. The ramus also has a well-developed subangular lobule, and a deep masseteric fossa that does not reach anteriorly the level of the m3. The symphysis is long and low and caudally expanded to below the mesial border of the p2. The angular process possesses a concave dorsal margin, and a wide scar for the superior ramus of the medial pterigoid muscle. The mandible condyle is at the level of the m1 trigonid (Figure 2(D)).

The dentition is at an advanced stage of wear, especially the carnassials, incisors and molars (Figure 2(B),(D)). The I3 is large and caniniform with a thin mesiolingual cingulum and without accessory cusps. P2 and P3 have long crowns formed only by slender principal cusps; these each have a strong mesiolingual crest and a weaker distal
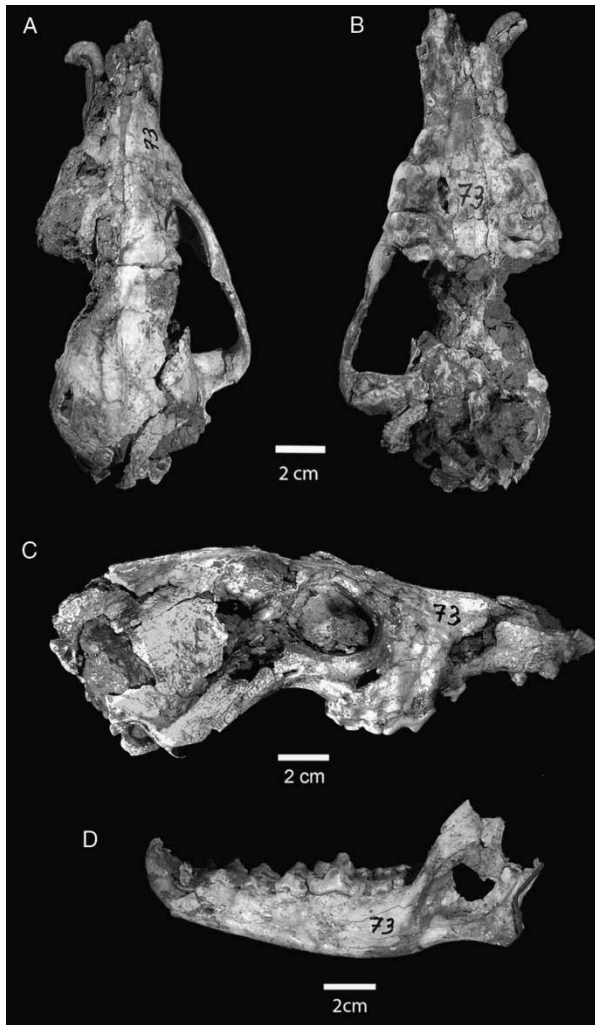
Figure 2.   *D. avus* (MACNU-73): skull: (A) dorsal view, (B) palatal view, (C) lateral view. Mandible: (D) lateral view.

one. The P2 is implanted parallel to the sagital plane, while the P3 is oblique (the distal border is labially displaced) in line with the P4. In each P4, the protocone is small and lingually directed and the lingual cingulum is moderately developed. M1 and M2 have well-developed metacones and hypocones; the last cusp encircles the protocone and is divided by a transverse notch in the M1. A well-developed metaconule is observed in the first molar, but it is not possible to check the presence of a paraconule because of dental wear. An inflection of the postprotocrista of the M2 makes a small metaconule (Figure 2(B)). In the lower dentition, the i3 presents a shovel like crown, with a small distal accessory cusp. The c1 crown shape is generalised, and the lower premolar series is disposed with diastema between premolars. The lower premolars are similar to the upper ones, but the mesiolingual crest is placed more mesially. The p4 presents a stronger principal cusp, a large distal accessory cusp, a minute secondary distal accessory

cusp and an acute, and transversally compressed distal cingulum. The m1 is proportionally large in relationship to the m2–3, and shows a small metaconid and a much reduced entoconulid. The hipoconulid is a low cingulum placed on the distal portion of the m1 talonid. The entoconid, hipoconid, protoconid, metaconid and mesiolabial cingulum are well-developed in the m2. The small m3 possesses a circular crown in oclussal view that bears a minute central cusp.

Comments

Several morphological characters of this specimen match with the diagnosis of *D. avus*: (1) m1 proportionally large in relationship to p4 and m2, p4 with a laterally compressed distal cingulum and (2) protocone of P4 lingually directed (Kraglievich 1930; Caviglia 1978, 1986; Berman 1986, 1994; Berman and Tonni 1987; Trejo and Jackson 1998). These features clearly separate this specimen from the living species *D. culpaeus*. In addition, *D. australis* possesses a more reduced protocone and metaconid in the P4 and m1, respectively, and the premolars show more acute and erected principal cusps (see Berta 1988; Tedford et al. 1995; F.J. Prevosti, personal observation). The size of the MACNU-73 fall in the range of *D. avus* and in the upper range of *D. culpaeus*, but the size of the carnassials (specially Lm1 and Ltrm1) are larger than in the living species (Table 1). Unfortunately, we can only study one specimen of *D. australis*, which its measurements are a little larger or similar to the specimen of the Sopas Formation, but the premolars are shorter and the Lm1 is conspicuously smaller (see Table 1).

The multivariate analysis of the measurements provided congruent results with the anatomical comparison. The PCA performed using the P4–M2 measurements separates very well *D. avus* from *D. culpaeus*, occupying the first the upper-left quadrant, and the MACNU-73 and *D. australis* fall in the *D. avus* cluster (Figure 3; Table 2). The DA based on these variables separates *D. culpaeus* and *D. avus* (72 and 11 specimens each) nearly perfectly (Wilks' Lambda: 0.33, approx. $F(7.76) = 22.19$, $p < 0.0001$; 98.81% of correct posterior reclassification), and assigns the MACNU-73 to *D. avus* with more than 0.99 posterior probability. *D. avus* has larger P4, larger WM1, LLabM1, and smaller M2 and LLiM1 than *D. culpaeus*.

The multivariate analyses performed using the p4–m1 measurements, and with 61 especimens of *D. culpaeus* and 41 especiments of *D. avus*, give nearly identical results. The PCA separates *D. avus* from *D. culpaeus* along the first component, and places the MACNU-73 with *D. avus*. The DA almost separate both species (Wilks' Lambda: 0.19, approx. $F(5,10) = 84.88$, $p < 0.0001$; 98.15% of correct posterior reclassification) and classified the %
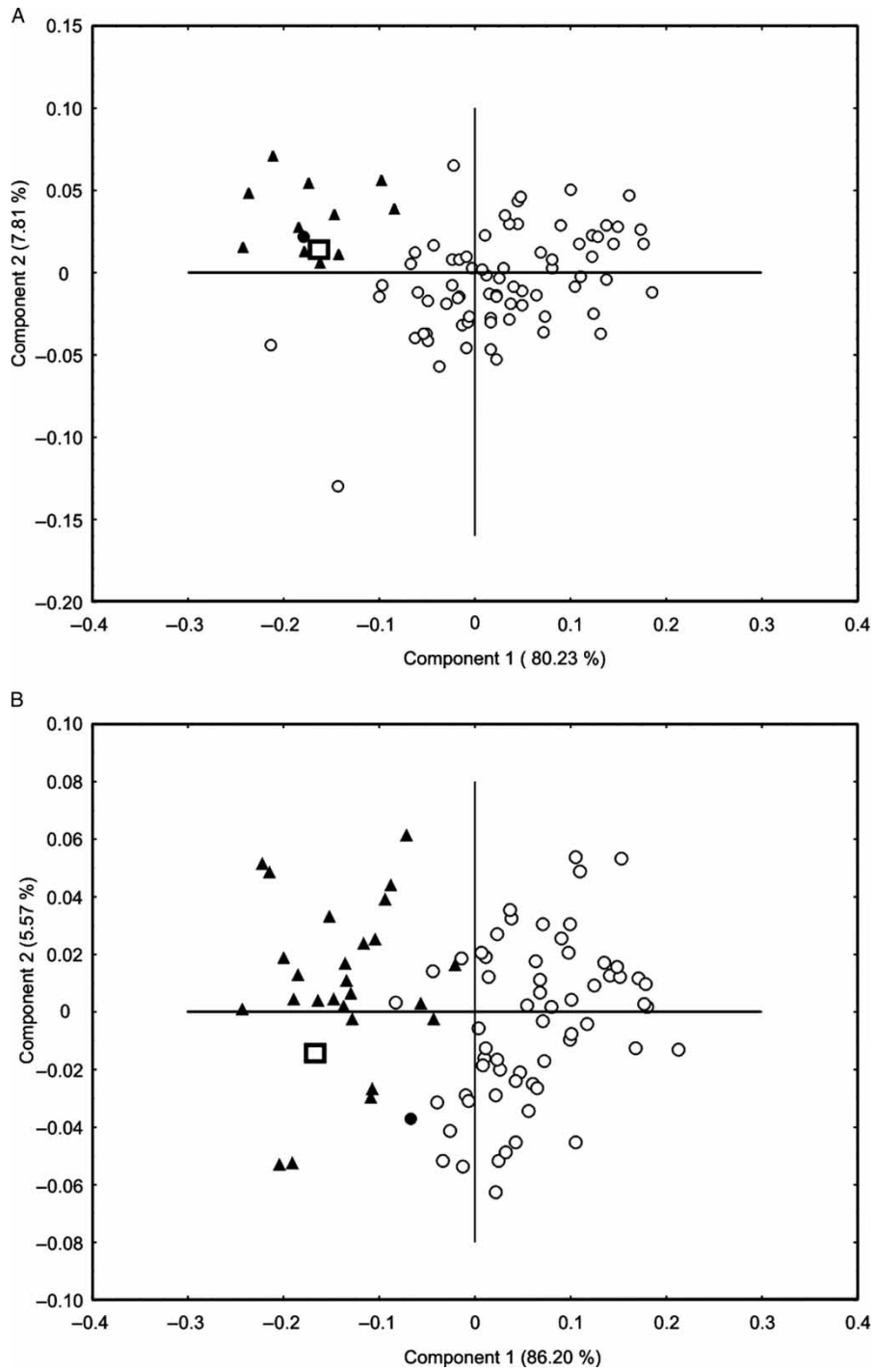
Figure 3.   Biplot of the first and second component of the PCA based on P4–M2 (A) and p4–m2 (B) measurements of MACNU-73, *D. avus*, *D. culpaeus* and *D. australis*. Black triangle: *D. avus*; empty circle: *D. culpaeus*; black dot: *D. australis*; open square: MACNU-73.
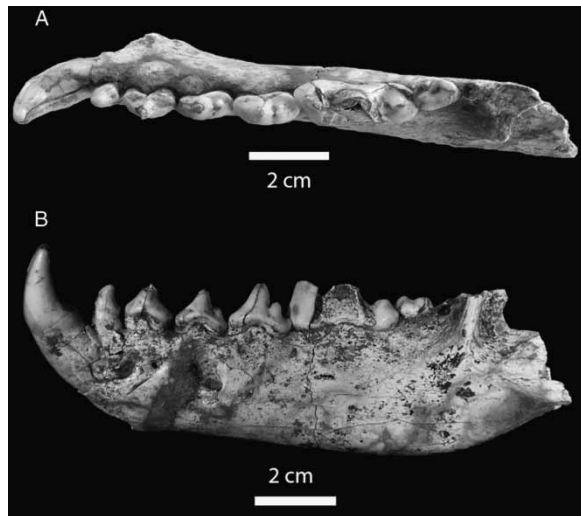
Figure 4. *P. troglodytes* (MACNU-95): left mandible ramus: (A) oclusal view; (B) lateral view.

MACNU-73 as *D. avus* with more than 0.99 posterior probability. *D. avus* is discriminated because has a larger m1 (Lm1) and smaller m2 (Lm2, Wm2).

Protocyon Giebel, 1855
P. troglodytes Lund, 1838
(Figure 4, Table 3)

Material referred

MACNU-95, incomplete right and left ramus of a mandible with c1–m2, and m3 alveolus.

Table 3. Craneodental measurements of the MACNU-95 compared to *P. troglodytes*.

| | MACNU-95 | X | *P. troglodytes* | | | |
			SD	Min	Max	*n*
HRHm1	29.73	31.40	2.88	26.25	35.00	8
WRHm1	11.99	14.00	1.72	12.07	17.70	7
HRHp4	26.84	27.15	2.67	23.20	29.95	6
WRHp4	12.63	14.02	0.81	13.00	14.85	5
Lc1	11.78	12.18	1.01	11.10	13.60	5
Wc1	8.06	8.35	0.50	7.70	8.90	5
Lp2	11.07	11.00	0.85	10.05	12.49	6
Wp2	5.26	5.73	0.19	5.45	5.90	6
Lp3	12.01	13.10	1.15	11.80	14.50	5
Wp3	5.47	6.36	0.18	6.07	6.60	6
Lp4	14.14	14.73	0.91	13.35	15.80	6
Wp4	6.84	6.91	0.31	6.50	7.30	7
Lm1	25.57	26.61	1.24	24.55	28.70	11
Ltrm1	18.32	19.73	0.89	18.60	21.60	11
Wtalm1	8.12	9.13	0.40	8.30	10.65	12
Lm2	8.77	10.03	0.84	9.05	11.45	8
Wm2	6.75	7.47	0.59	6.95	8.45	8

X, mean; SD, standard deviation; Min, minimum; Max, maximum; *n*, sample size.

Locality and stratigraphic horizon

Sopas creek, 500 m above Paso Muñoz Bridge (31°15′ S 57°00′; Salto Department, Uruguay).

Description

A very strong horizontal ramus and a very sharp subangular lobule are observed in the mandible. The right ramus presents a large mental foramen below p1–p2 contact and a small one under the distal part of the p3, but in the left mandible there are a third small foramen near the large one. The symphysis is strong, high and extended caudally to the medium of the p2, while the masseteric fosse is deep but not reaches the posterior border of the m3 (Figure 4).

The c1 is robust, short with a well-developed mesiolingual crest. The premolars are disposed with a very small diastema between them, and form a slightly convex arch (Figure 4). The p1 has one root and a robust cusp that is distally curved. The p2–p4 have two roots, and high and acute principal cusp with strong mesiolingual and distal crests. The distal accessory cusp is only present in p3–p4, and the p4 also has a tiny cusplet on the mesial cingulum, and a more developed and elevated distal one.

The lower carnassial is very large, and shows a long trigonid, short talonid, a cingulum like entoconid, and lacks the metaconid. On the lingual side of the distal face of the protoconid there is a crest that runs to the hypoconid, and another on the lingual side in the place where usually is the metaconid. The m2 has small size in relationship to the m1, wide trigonid and narrow talonid (Figure 3). The metaconid is reduced and adjacent to the protoconid, the entoconid is a cingulum in the lingual border of the talonid, and the mesiolabial cingulum is also extremely reduced (Figure 4).

Comments

The combination of dental morphology, size and robustness of the mandible indicate that this specimen belongs to *Protocyon* (Table 3). This genus is the only South American canid with a m1 without metaconid and entoconid, and premolars with acute and weak principal cusps (Berta 1988; Prevosti 2006; Prevosti and Rincón 2007). In size and morphology, this fossil resembles more the species *P. troglodytes*. *P. scagliarum* is only known from the holotype, and possesses a wider talonid in relationship to trigonid width, and the m2 metaconid is displaced distally with respect to the protoconid (see Prevosti 2006; Prevosti and Rincón 2007). Some measurements (e.g. Lm2, Wm2) are slightly smaller than the comparative sample of *P. troglodytes* (Table 3), that could be interpreted as intraspecific variation.

Protocyon tarijensis is easily distinguishable by the presence of a tiny entoconid in the m1, or a more developed cingulum in its place, than in *P. troglodytes* (Prevosti 2006).

Discussion and conclusion

Taxonomic and biogeographic remarks

The fossil record of canids in Uruguay is scarce and few taxa were reported with reliable taxonomic identification. The set of characters that yield the new fossil material here studied (MACNU-73 and MACNU-95) allows us to confidently determine them as *D. avus* and *P. troglodytes*, respectively. It is the first record of the genus *Protocyon*, the species *P. troglodytes* and *D. avus* for Uruguay, expanding and completing the known Pleistocene distribution of these taxa. They increase the taxonomic information, particularly the canids, available for the Sopas Formation of the Late Pleistocene of Uruguay.

The multivariant analysis performed on the basis of cranial, dental and mandibular characters support a confidently identification of the MACNU-73 with *D. avus*, particulary the large carnassials, and relatively small m2/M2, p4 with a laterally compressed distal cingulum, and protocone of P4 lingually directed. *D. avus* has been found in the Late Pleistocene-Holocene of Patagonia, Buenos Aires province (Argentina) and Chile (Caviglia 1986; Berman 1994; Trejo and Jackson 1998; Figure 1). The only record outside these regions is an upper first molar from Balneario Hermenegildo in Rio Grande Do Sul (Brazil), tentatively assigned to *D. avus* (Hadler Rodríguez et al. 2004). Unfortunately, this molar was found out of stratigraphic context and its age could not be established. Then, the presence of *D. avus* in the Sopas Fm of Uruguay confirms that during the Late Pleistocene, this species inhabited the areas located northern and eastern of the de La Plata estuary and the Uruguay River.

According to the current information, *P. troglodytes* had a wider geographic distribution in the Pleistocene than previously thought (see Oliveira et al. 2005; Prevosti et al. 2005; Prevosti 2006; Prevosti and Rincón 2007). It extends from Buenos Aires province in Argentina to Venezuela, through Southern Brazil, Bolivia and Peru (Figure 1). Thus, the record in the Pleistocene of Uruguay of *P. troglodytes* is an expected fact. This distribution encompasses grasslands and/or mosaics of grasslands and some kind of tree biomes developed in the Pleistocene (Prevosti 2006; Prevosti and Rincón 2007; this paper), which suggests that *P. troglodytes* could have been a flexible and euritopic species. This large canid could have inhabited different kinds of habitats, but with a preference of open environments, as occur in the present with some large sized canids as the grey wolf (*Canis lupus*) and the African wild dog (*Lycaon pictus*).

It is worthy of consideration that, it is the first record of *P. troglodytes* in southern South America (i.e. Uruguay, Southern Brasil, Argentina) with an associated dating (see Prevosti 2006). Other remains have been assigned to a Late Pleistocene sensu lato (Lujanian or Bonaerian), or to the Lujanian based on stratigraphic or biostratigraphic information (e.g. Oliveira et al. 2005; Prevosti et al. 2005). This record confirms that *P. troglodytes* was an element of the Lujanian faunas of Uruguay, at least around 43–120 ky BP.

Paleoecological remarks

These two large canids also show that the mammalian predator guild in the Late Pleistocene of northern Uruguay was richer than previously thought. As stated above,

Table 4. Potential preys of *P. troglodytes* according to the fossil record of the Sopas formation (Ubilla et al. 2004).

	Body mass	Habitats	Food habits
Hydrochoerus/Neochoerus	35–90 kg[a]	L/l. Rf.	H
M. patachonica	988 kg[b]	OS	H
Tapirus terrestris	150–250 kg[c]	L/l. Rf.	H
Equus neogeus	379 kg[d]	OS	H
H. principale	460 kg[d]	OS-SOS	H
Hemiauchenia	1000 kg[b,e]	OS	H
Antifer ultra	125 kg[f]	?	H
Morenelaphus spp	50 kg[e]	OS-SOS	H
Paraceros fragilis	50 kg[e]	?	H
G. robustum	1057–1317[f]	OS	H
Nothrotherium cf. *N. maquinense*	60 kg[g]	SF-O (?)	H
Coendou magnus	>4 kg[a]	F-SF (?)	H
N. recens	50 kg (?)	F-SF (?)	H
Lama (Vicugna) sp.	45–55 kg[e]	OH	H
Ozotoceros	40 kg[h]	OH	H
Myocastor coypus	6 kg[g]	L/l, Rf	H
Tayassu/Catagonus	22–43 kg[i]	F/SOS	O

The body mass of *P. fragilis* is considered to be similar to *Morenelaphus*. L, lotic; l, lentic; Rf, riparian forest; H, herbivorous; OS, open savannas; SOS, semiopen savannas; ?, dubios information; SF, semiforested; O, omnivorous; OH, open habitats. [a] Mones and Ojasti (1986) only for the living *Hydrochoerus hydrochaeris*. [b] Fariña et al. (1998). [c] Padilla and Dowler (1994). [d] Alberdi and Prado (1993), Prado and Alberdi (1994). [e] Fariña (1996). [f] Pinder and Grosse (1999) for the living *Blastocerus dichotomus*. [g] Cartelle (1994). [h] Jackson (1987). [i] Mayer and Brandt (1981).

Table 5. Potential preys of *D. avus* according to the fossil record of the Sopas Formation (Ubilla et al. 2004; Perea 2008).

	Body mass	Habitats	Food habits
Nothrotherium cf. *N. maquinense*	60 kg[a]	SF-O (?)	H
C. magnus	>4 kg[b]	F-SF (?)	H
Cavia spp.	800 g[c]	OH	H
Galea spp.	140–560 g[d]	OH	H
Microcavia criolloensis	>380 g[e]	OH	H
N. recens	50 kg (?)	F-SF (?)	H
Lama (Vicugna) sp.	45–55 kg[f]	OH	H
Ozotoceros	40 kg[g]	OH	H
P. fragilis	50 kg	?	H
M. coypus	6 kg[h]	L/l, Rf	H
Tayassu/Catagonus	22–43 kg[i]	F/SOS	O
Morenelaphus spp	50[f]	OS-SOS	H

F, forested; SF, semiforested; OH, open habitats; O, omnivorous; ?, dubios information; H, herbivorous.[a] Cartelle (1994), [b] Walker (1975): larger than the living *Coendou prehensilis*. [c] Rood (1972). [d] Reis et al. (2006). [e] Ubilla (2008) and references therein: larger than *Microcavia australis*. [f] Franklin (1981) according to the living *Vicugna vicugna*. [g] Jackson (1987). [h] Woods et al. (1992). [i] Mayer and Brandt (1981).

five species of Carnivora have been collected from the Sopas Fm.

This is a low number of predators compared to the number of large potential prey (see Tables 4 and 5). The Sopas Formation yields approximately 11 genera of megamammals (*ca*. 1000 kg). Two of the carnivores (i.e. *D. gymnocercus* and *L. longicaudis*) are small (body size <10 kg) neospecies that in the present eat small mammals (rodents, hares), fish, insects and fruits (see Redford and Eisenberg 1992). The other two neospecies are large felids (*Panthera* cf. *P. onca*, *P. concolor*), with body massess between 40 and 130 kg with hypercarnivorous habits that in the present include medium and large mammalian preys up to 300–500 kg (Prevosti and Vizcaíno 2006). The last species is the extinct saberthoothed felid *S. populator*, which could have had a body size around 400–500 kg (Christiansen and Harris 2005). This felid was the top predator during the Pleistocene in South America and hunted larger mammals above 100 kg, and also, less frequently, over megamammals (Prevosti and Vizcaíno 2006). The two living felids are ambush hunters, and perhaps *S. populator* was also, which capture their prey after a short running (Akersten 1985; Anyonge 1996a, 1996b; Biknevicius and Van Valkenburgh 1996; Van Valkenburgh and Hertel 1998; Therrien 2005; Prevosti and Vizcaíno 2006).

P. troglodytes was interpreted as a hypercanivorous large canid (15–30 kg), that could pursue in packs their preys for long distances (Berta 1988; Oliveira et al. 2005; Prevosti 2006). This kind of predator 'niche' is not filled by carnivores previously described from the Sopas Fm. The equids, camelids, medium to large deer and perhaps large rodents recorded in the Sopas Fm. could be considered as potential preys for this canid (see Table 4). Smaller rodents (e.g. *Myocastor*) or juveniles of larger mammals (e.g. *Macrauchenia*, *Glossotherium*) could constitute occasional prey.

On the other hand, *D. avus* was a large fox (10–14 kg) that could have had a more carnivorous diet that the living culpeo fox (*D. culpaeus*; Prevosti and Vizcaíno 2006). Medium deer, small camelids and perhaps small ground-sloths (*Nothrotherium* cf. *N. maquinense*) could be potential preys for this extinct fox (Table 5), but certainly most likely small and medium rodents (e.g. *Cavia*, *Microcavia*, *Coendou*, *Myocastor*) as occurs with the living species (*D. culpaeus*).

Verde and Ubilla (2002) described carnivore mammal coprolites from the Sopas Formation, that show biotic interactions involving predation on small rodents. These coprolites have inclusions of bones and teeth of a caviine rodent (certainly not the genus *Cavia*, most likely *Galea* or *Microcavia*). Having less available information about the diversity of carnivores mammals from the Sopas Formation, Verde and Ubilla (2002), interpreted the large felids recorded in this unit as a possible makers of these coprolites. Taking into account the size ranges of the coprolites and the body size estimated for *D. avus*, in fact, these large canids here described could be considered as the potential coprolite-maker.

The presence of these two canids in the Sopas Fm, increase the diversity and disparity of the carnivore guild to levels similar to the present and yet described for Late Pleistocene sites (Prevosti 2006; Prevosti and Vizcaíno 2006).

With the new record, the carnivore guild of the Sopas Fm. contains seven species, with three (*D. gymnocercus*, *D. avus*, *L. longicaudis*) specialised to predate on small mammals, one (*D. gymnocercus*) occasionally could hunt medium sized mammals, and four of them (*P. concolor*, *Panthera* cf. *P. onca*, *S. populator*, *P. troglodytes*) that actively predate on medium and large mammal. But only *S. populator* could occasional hunt over megamammals. Still with the new carnivores, this guild appears to be

unable to cope with the large diversity of megammals (11 genera), but different factors could explain this issue.

Firstly, most of the megamammals are xenarthrans that lack good live analogues and probable had very different life characteristics than living megamammals, with lower metabolic rates and population densities (see Prevosti and Vizcaíno 2006; Vizcaíno et al. 2006). Furthermore is the taphonomic analysis performed by Ubilla and Lorenzo (2001) in one locality of the Sopas Formation (Malo creek, Tacuarembo Department), shows a low number of megamammals in the total number of taxa and bones and the predominance of deer and camelids instead.

Secondly, megamammals could be outside the hunting range of these fossil carnivores (cf. Hummel and Clauss 2008), something that is apparently the case for most of these predators (except *Smilodon*), and only could be consumed as carrion, or by predation of juvenile/sub adult individuals (Prevosti and Vizcaíno 2006).

Lastly, if this diversity of megammamals are available as food resources, it could sustain and increase population densities of one or more carnivore species (Prevosti and Vizcaíno 2006). Probably a combination of these 'mechanisms' could have regulated the mammalian communities of the Late Pleistocene in southern South America.

Acknowledgements

Notes

1. Email: ubilla@fcien.edu.uy
2. Email: perea@fcien.edu.uy

References

Akersten WA. 1985. Canine function in Smilodon (Mammalia: Felidae: Machairodentinae). Contrib Sci Los Angeles Mus. 356:1–22.

Alberdi M, Prado J. 1993. Review of the genus *Hippidion* Owen, 1869 (Mammalia, Perissodactyla) from the Pleistocene of South America. Zool J Linn Soc. 108:1–22.

Amorosi T, Prevosti FJ. 2008. A preliminary review of the canid remains from Junius Birds excavations at Fell's and Pali Aike caves, Magallanes, Chile. C Res Pleist. 25:25–27.

Anyonge W. 1996a. Locomotor behaviour in Plio-Pleistocene sabre-tooth cats: a biomechanical analysis. J Zool London 238:395–413.

Anyonge W. 1996b. Microwear on canines and killing behavior in large carnivores: saber function in *Smilodon fatalis*. J Mamm. 77(4):1059–1067.

Berman WD. 1986. Revisión sistemática de *Canis platensis* Mercerat, 1891 (Carnivora, Canidae) del Pleistoceno tardío (Lujanense) de la provincia de Buenos Aires. Ameghiniana. 23(3–4):225–227.

Berman WD. 1994. Los carnívoros continentales (Mammalia, Carnivora) del Cenozoico en la provincia de Buenos Aires. Unpublished Doctoral Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Berman WD, Tonni EP. 1987. *Canis* (*Dusicyon*) *avus* Burmeister, 1864 (Carnivora, Canidae) en el Pleistoceno tardío y Holoceno de la provincial de Buenos Aires. Aspectos sistemáticos y bioestratigráficos relacionados. Ameghiniana. 24(3–4):245–250.

Berro AC. 1929. Catálogo de cuatro pequeñas colecciones paleontológicas del Uruguay (Formación Pampeana). 1ª edición. Mercedes, Uruguay: Marzoa & Cia. p. 1–12.

Berta A. 1987. Origin, diversification, and zoogeography of the South American Canidae. Field Zool (n.s.). 39:455–471.

Berta A. 1988. Quaternary Evolution and Biogeography of the Large South American Canidae (Mammalia: Carnivora). Univ Calif Publ Geol Sci. 132:1–149.

Biknevicius AR, Van Valkenburgh B. 1996. Carnivore behavior, ecology, and evolution. In: Chapter 12, Design for killing: craniodental adaptations of predators. Vol. 2, 1st ed. Ithaca, NY: Cornell University Press. p. 393–428.

Bowdich TE. 1821. An analysis of the natural classifications of mammalia for the use of students and travelers. Paris: J Smith. p. 1–115.

Burmeister G. 1866. Lista de los mamíferos fósiles del terreno Diluviano. An Mus Nac Bs As. 1(3):121–232.

Cartelle C. 1994. Tempo Passado. Mamíferos do Pleistoceno em Minas Gerais. 1erst ed. Sao Paulo: Editora Palco. p. 1–131.

Caviglia SE. 1978. La presencia de *Dusicyon avus* (Burmeister), 1864 en la Capa VIII de la Cueva las Buitreras (Patagonia, Argentina): su relación con otros hallazgos en Patagonia Meridional. Paper presented at: VI Congreso Nacional de Arqueología del Uruguay, Proceedings: Salto.

Caviglia SE. 1986. Nuevos restos de cánidos tempranos en sitios arqueológicos de Fuego-Patagonia. An Inst Patagonia Ser Cienc Soc. 16(1):85–93.

Christiansen P, Harris JM. 2005. Body size of *Smilodon* (Mammalia: Felidae). J Morphol. 266(2):369–384.

Cione AL, Tonni EP. 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina. Paper presented at: Geología y Recursos Minerales de la Provincia de Buenos Aires. Proceedings of the XVI Congreso GeológicoArgentino, La Plata, Argentina.

Fariña RA. 1996. Trophic relationship among Lujanian mammals. Evol Theory. 11(2):125–134.

Fariña RA, Vizcaíno SF, Bargo MS. 1998. Body mass estimations in Lujanian (late Pleistocene-early Holocene of South America) mammal megafauna. Mastozool Neotrop. 5(2):87–108.

Fischer von Waldheim G. 1817. Adversaria Zoologica. Mém Soc Imp Natu. 5:368–428.

Franklin WL. 1981. Mammalian Biology in South America. In: Special Publication Pymatuning Laboratory of Ecology, University of Pittsburgh, PA. Biology, ecology and relationships to man of the South American camelids. p. 457–489.

Hadler Rodríguez P, Prevosti FJ, Ferigolo J, Ribeiro AM. 2004. Novos materiais de Carnivora para o Pleistoceno do Estado do Rio Grande do Sul, Brasil. Rev Bras Paleont. 7(1):77–86.

Hamilton Smith C. 1839. Dogs. Canidae or genus Canis of authors. Jardine's Nat Lib. 9:1–267.

Hummel J, Clauss M. 2008. Megaherbivores as pacemakers of carnivore diversity and biomass: distributing or sinking trophic energy? Evol Ecol Res. 10:925–930.

Jackson E. 1987. *Ozotoceros bezoarticus*. Mamm Species. 295:1–5.

Kraglievich L. 1927. Catálogo N° 1 in Berro A.C. Contribución al conocimiento de los fósiles de la República Oriental del Uruguay. Rev Soc Amigos Arqueol. 1(1):74–103.

Kraglievich L. 1930. Craneometría y clasificación de los cánidos sudamericanos, especialmente los argentinos actuales y fósiles. Physis. 10:35–73.

Legendre P, Legendre L. 1998. Numerical ecology. 1st ed. Amsterdam: Elsevier. p. 1–853.

Martinez S, Rojas A. 2004. Quaternary continental mollusks from northern Uruguay: distribution and paleoecology. Quat Int. 114: 123–128.

Martínez S, Ubilla M. 2004. Cuencas sedimentarias de Uruguay: El Cenozoico. Facultad de Ciencias, DIRAC, El Cuaternario en Uruguay. p. 195–227.

Mayer J, Brandt P. 1981. Mammalian Biology in South America. Special Publication Pymatuning Laboratory of Ecology, University of Pittsburgh, PA. Identity, distribution and natural history of the peccaries, Tayassuidae. p. 433–455.

Mones A, Ojasti J. 1986. *Hydrochoerus hydrochaeris*. Mamm Species. 264:1–7.

Oliveira EV, Prevosti FJ, Pereira JC. 2005. *Protocyon troglodytes* (Lund) (Mammalia, Carnivora) in the late Pleistocene of Rio Grande Do Sul, and their palaecological significance. Rev Bras Paleontol. 8(3): 215–220.

Padilla M, Dowler RC. 1994. *Tapirus terrestris*. Mamm Species. 481: 1–8.

Perea D. 2008. *Nothrotherium* cf. *N. maquinense* (Xenarthra, Tardigrada) en la Formación Sopas (Pleistoceno Tardío de Uruguay). Rev Soc Urug Geol. 14(1):2–6.

Pinder L, Grosse AP. 1999. *Blastocerus dichotomus*. Mamm Species. 380:1–4.

Prado J, Alberdi M. 1994. A quantitative review of the horse *Equus* from South America. Palaeontology. 37(4):459–481.

Prevosti FJ. 2006. Grandes cánidos (Carnivora, Canidae) del Cuaternario de la República Argentina: Sistemática, Filogenia, Bioestratigrafía y Paleoecología. Unpublished Doctoral Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Prevosti FJ, Rincón AD. 2007. A new fossil canid assemblage from the Late Pleistocene of northern South America: the canids of the Inciarte tar pit (Zulia, Venezuela), fossil record and biogeography. J Paleontol. 81(5):1053–1065.

Prevosti FJ, Vizcaíno S. 2006. The carnivore guild of the late Pleistocene of Argentina: Paleoecology and carnivore richness. Acta Paleontol Polonica. 51(3):407–422.

Prevosti FJ, Zurita AE, Carlini AA. 1855. Biostratigraphy, systematics and palaeoecology of the species of Protocyon Giebel, 1855 (Carnivora, Canidae) in South America. J S Am Earth Sci. 20(1): 5–12.

Redford KH, Eisenberg JF. 1992. Mammals of the Neotropics 2. The Southern Cone. Chicago, IL: University of Chicago Press. p. 1–430.

Reis NA, Perachi PW, Lima I. 2006. Mamíferos do Brasil. Londrina, Brazil: Universidade Estadual Londrina. p. 1–437.

Reyment RA, Blackith RE, Campbell NA. 1984. Multivariate morphometrics. London: Academic Press. p. 1–233.

Rood J. 1972. Animal Behaviour Monographs. Part 1. Ecological and behavioural comparisons of three genera of argentine cavies. London: Bailliere Tindall. p. 1–83.

Tedford R, Taylor BE, Wang X. 1995. Phylogeny of the Caninae (Carnivore: Canidae): the living taxa. Am Mus Novitates. 3146: 1–37.

Therrien F. 2005. Feeding behaviour and bite force of sabretoothed predators. Zool J Linn Soc. 145(3):393–426.

Trejo V, Jackson D. 1998. Cánidos patagónicos: identificación taxonómica de mandíbulas y molares del sitio arqueológico Cueva Baño Nuevo 1. An Inst Patagonia Ser Cienc Hum. 26(1):181–194.

Ubilla M. 2001. Comment on "The continental Uruguayan Cenozoic: an overview" by Panario, D.Gutiérrez, O. (Quaternary International 62:75–84). Quat Int. 76–77(2):259–260.

Ubilla M. 2004. Mammalian biostratigraphy of Pleistocene fluvial deposits in northern Uruguay, South America. Proc Geol Assoc Lond. 115(3):347–357.

Ubilla M. 2008. Postcranial morphology of the extinct caviine rodent *Microcavia criolloensis* (late Pleistocene, South America). Zool J Linn Soc. 154:795–806.

Ubilla M, Lorenzo N. 2001. Tafonomía de mamíferos en depósitos fluviales de la formación tardío (A° Malo, Dpto. Tacuarembó), Uruguay. Actas XI Congreso Latinamericano de Geología, III Congreso Uruguayo de Geología: 1–8.

Ubilla M, Perea D. 1999. Quaternary vertebrates of Uruguay: biostratigraphic, biogeographic and climatic overview. Quat SA Antarct Pen. 12(1):75–90.

Ubilla M, Perea D, Goso C, Lorenzo N. 2004. Late Pleistocene vertebrates from northern Uruguay: tools for biostratigraphic, climatic and environmental reconstruction. Quat Int. 114(2): 129–142.

Van Valkenburgh B, Hertel F. 1998. The decline of North American predators during the late Pleistocene. Ill State Mus Sci Pap. 27(3): 357–374.

Verde M, Ubilla M. 2002. Carnivore mammal coprolites from the Sopas Formation (Upper Pleistocene, Lujanian Stage) of Uruguay. Ichnos. 9(1):77–80.

Verde M, Ubilla M, Jiménez JJ, Genise JF. 2007. A new earthworm trace fossil from paleosols: aestivation chambers from the Late Pleistocene Sopas Formation of Uruguay. Palaeogeogr Palaeoclimatol Palaeoecol. 243(3):339–347.

Vizcaíno SF, Bargo MS, Cassini GH. 2006. Dental occlusal surface area in relation to body mass, food habits and other biological features in fossil xenarthrans. Ameghiniana. 43(1):11–26.

Walker E. 1975. Mammals of the World. Baltimore II: The John Hopkins University Press. p. 647–1500.

Woods Ch, Contreras L, Willner Chapmann G, Whidden H. 1992. *Myocastor coypus*. Mamm Species. 398:1–8.