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Constraining the time of extinction of the South American fox *Dusicyon avus* (Carnivora, Canidae) during the late Holocene

Francisco J. Prevosti [a,*], Fernando Santiago [b], Luciano Prates [c], Mónica Salemme [b]

[a] *División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina*
[b] *CADIC-CONICET, Ushuaia, Argentina*
[c] *División Arqueología, Museo de La Plata, La Plata, Argentina*

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ABSTRACT

A mass extinction affected South America during the late Pleistocene and early Holocene, when megamammals and large mammals disappeared. Several carnivores became extinct, including the sabretooth (*Smilodon*), the short-faced bear (*Arctotherium*), and some large canids (*i.e., Protocyon*, *Canis dirus*). After this mass event, virtually no carnivores became extinct in South America. The only exception is the fox *Dusicyon avus*, a medium-sized canid (estimated body mass between 10 and 15 kg) with a more carnivorous diet than the living South American foxes (*Lycalopex culpaeus*). The last record of the species comes from middle-late Holocene archaeological sites in the Pampean Region (Argentina) and Patagonia (Argentina and Chile). During the late Pleistocene, *D. avus* had a wide distribution, which covered part of Uruguay, Argentina (Buenos Aires province) and southern Patagonia. Although some remains from late Holocene sites have been published, these remains are still lacking numerical dating to determine the approximate date of extinction of this fox. This paper presents several new records from the Pampean and Patagonia regions, and several taxon dates. The new records indicate that *D. avus* survived in the late Holocene at least until ≈ 3000 BP in the Isla Grande de Tierra del Fuego (Patagonia) and the continent. Since at this time humans were occupying most of the Pampas and Patagonia, a revision of the causes behind the extinction of this fox is needed.

1. Introduction

The Quaternary South American carnivore faunas suffered several extinctions through time. Two events, that correspond to mass extinctions, happened at the middle Pleistocene (the end of the Ensenadan stage/age, ≈ 0.5 Ma) and at the Pleistocene–Holocene transition (latest Lujanian stage/age, ≈ 10–0.8 ka BP) (Prevosti and Soibelzon, in press). The middle Pleistocene event corresponds to a reorganization of the carnivore guild that affected small to large species, when a large ursid (*Arctotherium angustidens*) and large hypercarnivory canids (*e.g., Theriodictis platensis*), but also weasels (*e.g., Stipanicicia*, *Lyncodon bosei*) and a procyonid (*Cyonasua meranii*) disappeared (Prevosti et al., 2009; Prevosti and Soibelzon, in press). The younger event is part of the late Pleistocene megamammal extinction (Cione et al., 2008; Borrero, 2008) and mostly affected larger species, including sabertooth cats (*Smilodon* spp.), short-faced bears (*Arctotherium* spp.), and large canids (*e.g., Protocyon troglodytes*, *Canis dirus*) (Prevosti et al., 2009; Prevosti and Soibelzon, in press).

The only carnivore that became extinct after the late Pleistocene extinction and before the arrival of Spaniards to America is the fox *Dusicyon avus* (Tonni and Politis, 1981; Berman and Tonni, 1987; Berman, 1994). This species was described in the late 19th century from a skull found in Pleistocene levels in Buenos Aires province, Argentina (Burmeister, 1866). This extinct canid is a large fox similar to the living culpeo fox (*Lycalopex culpaeus*, see Sillero Zubiri *et al.*, 2004), but with a more carnivorous dentition and an estimated body mass of 12–15 kg (Kraglievich, 1930; Berman and Tonni, 1987; Prevosti and Vizcaíno, 2006). Since the original description, several specimens were recovered in late Pleistocene and Holocene paleontological and archaeological sites from the Pampean Region and Patagonia (Chile and Argentina) (see Berman, 1994; Caviglia, 1986; Fig. 1). Some of the specimens were collected from late Holocene levels, such as Lobería 1 and Zanjón Seco 2 sites in the Pampean Region (Tonni and Politis, 1981; Tonni, 1985) that are in association with pottery, giving an early age of ≈3 ka BP (see Politis et al., 2001; Fig. 1; Table 1). Other examples are the specimens recovered in three archaeological sites at Punta Bustamante locality (Santa Cruz province, Argentina; Miotti and Berman, 1988; Mansur, 2006, 2007; Fig. 1). Unfortunately, there are few taxon dates of *Dusicyon avus* that refer to the presence of this species in

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* Corresponding author.
E-mail address: protocyon@hotmail.com (F.J. Prevosti).

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Abbreviations

L	length (mesio-distal distance) of dental elements
W	wide (labio-lingual distance) of dental elements
i/I	lower/upper incisor, respectively
c/C	lower/upper canine, respectively
p/P	lower/upper premolar, respectively
m/M	lower/upper molar, respectively
LCB	condilobasal length of the skull
LOO	distance between de occipital condyles and the anterior margin of the orbits
WCP	width of the postorbital constriction
WIM	minimum interorbital width
WPPAR	width across the postorbital processes
WCC	width of the braincase
WP	palatal width
WRC1	width of the rostrum at the canines
LB	length of the bulla
WB	width of the bulla
LM	mandibular length (from condyle to mesial border of the lower canine)
LlaM1	labial length of M1
LliM1	lingual lenth of M1
Ltrm1	trigonid length of m1
Wtalm1	talonid width of m1
Pr1	Perro 1 collection deposited at Centro Austral de Investigaciones Científicas, Ushuaia, Argentina
LM	Loma de los Muertos site collection deposited at the División Arqueología of the Museo de La Plata, La Plata, Argentina
MAR	La Marcelina 1 site collection, deposited at the Centro de Investigación en Antropología, Filosofía y Cultura, Buenos Aires, Argentina

the early Holocene in the Aysén province and in the late Pleistocene of Tierra del Fuego (Chile; Borrero, 2003; Massone, 2004; Velásquez and Mena, 2006) (Fig. 1; Table 1). Thus, the evidence of the presence of this species in the late Holocene is not firmly stated.

This contribution reviews the available information about the chronological and geographic distribution of *Dusicyon avus*, describes new specimens, and presents new taxon dates that support the presence of the species in the late Holocene. It also explores the possible factors that could be related to its extinction.

2. Background: chronological and geographical distribution of *Dusicyon avus*

The type specimen was collected from Pleistocene levels in the Buenos Aires province (Argentina), but the exact locality is unknown (Burmeister, 1866; Ameghino, 1889). Subsequently, several specimens were collected at different Pleistocene or Late Pleistocene sites from Buenos Aires province and Patagonia (Ameghino, 1889; Roth, 1904; Kraglievich, 1930; Fig. 1; Table 1).

Since the last decades of the 20th century, *D. avus* has been recovered from several Holocene and some Pleistocene sites, mostly archaeological (Caviglia, 1978, 1986; Tonni and Politis, 1981; Berman, 1985, 1986; Berman and Tonni, 1987; Miotti and Berman, 1988; Trejo and Jackson, 1998; Politis and Gutierrez, 1998; Quintana, 2001; Prevosti et al., 2004; Kaufmann and Alvarez, 2007; Bonomo, 2006; Mansur, 2006, 2007; Amorosi and Prevosti, 2008; Fig. 1; Table 1). These records come from the Pampean Region (Buenos Aires Province, Argentina) and southern Patagonia (Chile and Argentina; Fig. 1; Table 1). The published taxon dates are limited to two specimens. One, dated 10575 ± 65 BP (12525 ± 141 cal), came from the Tres Arroyos 1 archaeological site in Isla Grande de Tierra del Fuego (Chile; Borrero, 2003), and the other, dated 7070 ± 25 BP (7860 ± 78 cal), was found in the Baño Nuevo 1 archaeological site (Aysén, Chile; Trejo and Jackson, 1998; Velásquez and Mena, 2006; Fig. 1; Table 1).

The specimens collected at Río Luján coming from late Holocene archaeological levels in the Buenos Aires Province (Pampean Region) were found in a burial (Kriskautzky, 1975) and related to a context where pottery is present, but without evidence of European remains. Prevosti et al. (2004) identified this fossil as *D. avus*. The presence of pottery and the absence of European remains constrain the age of the specimens between ≈ 3 ka BP and ca. 0.5 ka BP (see Politis et al., 2001). Some specimens came from archaeological sites in the Interserrana area of the Pampean Region and have been radiocarbon dated, such as Nutria Mansa 1, with an age between 2705 ± 055 and 3080 ± 110 BP (2792 ± 103 and 3186 ± 265 cal; Bonomo, 2006), Calera, between 1748 ± 42 and 3390 ± 170 BP (1615 ± 99 and 3578 ± 418 cal; Messineo and Politis, 2007), Lobería 1, between 440 ± 60 and 3104 ± 46 BP (425 ± 103 and 3257 ± 118 cal; Tonni, 1985; Mazzanti et al., 2010), and Zanjón Seco 2 between 2270 ± 70 and 3080 ± 40 BP (2195 ± 155 and 3246 ± 110 cal; Politis and Tonni, 1982; Politis et al., 2004). Several remains were collected at the Punta Bustamante area in southern Patagonia (Santa Cruz province, Argentina; Fig. 1) from levels dated between 750 ± 70 and 1060 ± 50 BP (647 ± 98 and 892 ± 97 cal; Miotti and Berman, 1988; Mansur, 2006, 2007), but these specimens have not been fully described or figured.

3. Material and methods

The taxonomic study is based in the revision of most specimens of this species and relatives deposited at paleontological, archaeological, and mammal collections, including several unpublished fossils. Qualitative characters, and quantitative analysis based on cranial and dental measurements (see Kraglievich, 1930; Caviglia, 1986; Berman and Tonni, 1987; Trejo and Jackson, 1998; Amorosi and Prevosti, 2008; Prevosti et al., 2009) were employed, following the sample and methodology utilized in Prevosti et al.(2009). This includes Principal Component Analysis from the Variance-Covariance matrix of the $\log_{10}$ transformed measurements. Table 2 shows the measurements of the new specimens.

The AMS ^{14}C taxon dates were obtained at the NSF-Arizona Accelerator Mass Spectrometry Laboratory (AA), University of Arizona, Tucson, USA. Calibration of ^{14}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 SHCal04 curve for ages younger than 11 cal ka (McCormac et al., 2004), and the InterCal09 curve (Reimer et al., 2009) for older ones (two sigma ranges).

4. Results

4.1. New records, archaeological context, and taxon dates

The most recent findings come from three archaeological sites, two of them located in northern Patagonia (Loma de los Muertos and La Marcelina) and the third one, farther south, in the Isla Grande of Tierra del Fuego. They are briefly described, from north to south.

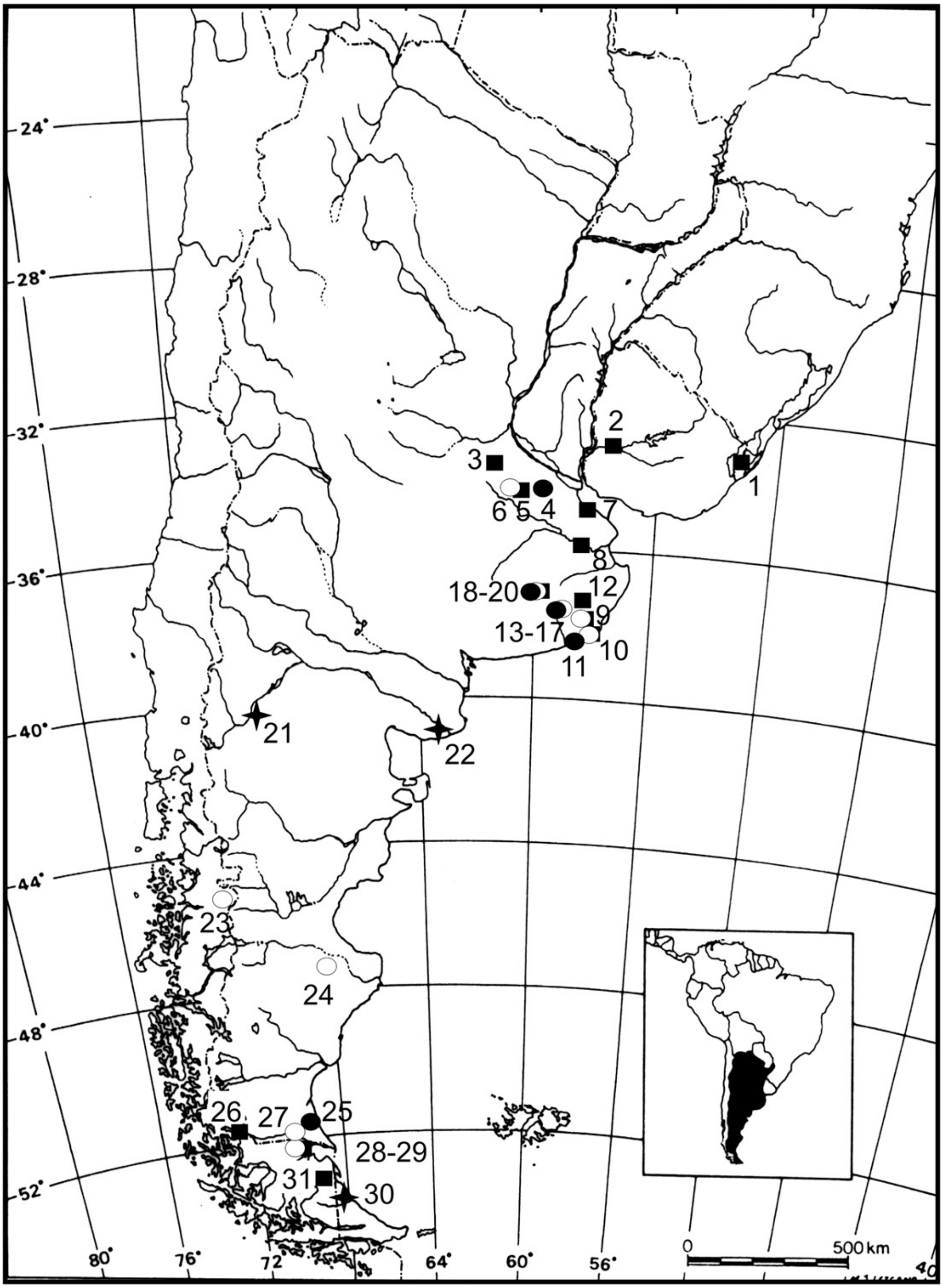

Fig. 1. Map with the localities of *Dusicyon avus* mentioned in the text. See Table 1 for an enumeration of the sites. Black square: late Pleistocene site; white circle: Holocene sites (undifferentiated or middle-early Holocene); black circle: late Holocene; star: new localities.

La Marcelina site is located on the Río Limay basin (northern Patagonia; 40° 37′ S, 70° 20′ W; Fig. 1) in a cave with rock art assigned to "foot prints" style. Several occupations (from ca. 1700 BP to post-Hispanic times) were recorded. The archaeological materials recovered include lithic artifacts (flakes, cores, and tools), faunal remains (*Lama guanicoe*, *Zaedyus pichiy*, and Rheidae), and pottery sherds. It has been suggested that La Marcelina 1 was a campsite where multiple activities were carried out (Sanguinetti de Bórmida et al., 2000). A lower jaw of *D. avus* (MAR 1) was recovered from the level 11 of the La Marcelina site, which was radiocarbon dated to 1700 ± 80 BP (1538 ± 372 cal; Table 1).

The Loma de los Muertos site is located on the left margin of the Río Negro valley (General Conesa District, Río Negro Province, Argentina; 40° 08′ 54″ S, 64° 16′ 22″ W; Fig. 1). At this site, the remains of both human and *Dusicyon avus* burials, and a variety of archaeological material were recorded at the surface. Based on ^{14}C

Table 1
List of Localities of *Dusicyon avus*.

	Localities	Province/Region	Country	Age	References
1	Balneario Hermenegildo	Rio Grande do Sul	Brasil	Pleistocene	Hadler Rodríguez et al., 2004
2	Arroyo Sopas	Salto	Uruguay	late Pleistocene (Lujanian)	Prevosti et al., 2009
3	Fontezuelas	Buenos Aires	Argentina	Pleistocene	Berman, 1986, 1994
4	Sitio Río Luján	Buenos Aires	Argentina	late Holocene (Platan)	Kriskautzky, 1975; Prevosti et al., 2004
5	Mercedes	Buenos Aires	Argentina	late Pleistocene (Lujanian)	Ameghino, 1889
6	Estación J. M. García	Buenos Aires	Argentina	early Holocene (Platan)	Prevosti, unpublished doctoral thesis
7	La Plata	Buenos Aires	Argentina	late Pleistocene (Lujanian)	Berman, 1994
8	Río Salado	Buenos Aires	Argentina	late Pleistocene (Lujanian)	Berman, 1994
9	Cueva Tixi	Buenos Aires	Argentina	late Pleistocene-middle Holocene (Lujanian-Platan)	Quintana, 2001
10	Miramar	Buenos Aires	Argentina	late Pleistocene–Holocene (Platan-Lujanian)	Berman, 1994
11	Sitio Nutria Mansa	Buenos Aires	Argentina	late Holoceno (Platan)	Bonomo, 2006
12	Arroyo Grande	Buenos Aires	Argentina	late Pleistocene (Lujanian)	Berman, 1994
13	Lobería 1	Buenos Aires	Argentina	late Holocene (Platan)	Tonni, 1985; Berman, 1994;
14	Sitio 2 Zanjon Seco	Buenos Aires	Argentina	late Holoceno (Platan)	Politis and Tonni, 1982; Politis et al., 2001
15	Paso Otero	Buenos Aires	Argentina	Holocene (Platan)	Berman and Tonni, 1987
16	Sitio Paso Otero 3	Buenos Aires	Argentina	middle Holocene (Platan)	Martínez, 1999
17	Sitio Paso Otero 4	Buenos Aires	Argentina	early-middle Holocene (Platan)	Gutiérrez et al., 2010
18	Sitio Arqueológico Azul	Buenos Aires	Argentina	Holocene (Platan)	Berman, 1985
19	Tapalqué	Buenos Aires	Argentina	late Pleistocene? (Lujanian?)	Berman, 1994
20	Sitio La Calera	Buenos Aires	Argentina	late Holoceno (Platan)	Kaufmann and Alvarez, 2007
21	La Marcelina	Río Negro	Argentina	late Holocene (Platan)	Sanguinetti de Bórmida et al., 2000
22	Loma de los Muertos	Río Negro	Argentina	late Holocene (Platan)	Prates et al., 2010a
23	Baño Nuevo 1	Aysen	Chile	early Holocene (Platan)	Trejo and Jackson, 1998
24	Los Toldos	Santa Cruz	Argentina	early-middle Holocene (Platan)	Caviglia, 1986; Borrero, 1997
25	Punta Bustamante	Santa Cruz	Argentina	late Holocene (Platan)	Miotti and Berman, 1988; Mansur, 2006, 2007
26	Cueva del Milodón	Ultima Esperanza	Chile	late Pleistocene? (Lujanian?)	Borrero, 1997
27	Las Buitreras	Santa Cruz	Argentina	early-middle Holocene (Platan)	Caviglia, 1986
28	Pali Aike cave	Magallanes	Chile	early Holocene (Platan)	Borrero, 1997
29	Fells cave	Magallanes	Chile	late Pleistocene-middle Holocene (Lujanian-Platan)	Caviglia, 1986; Borrero, 1997
30	Sitio Perro 1	Tierra del Fuego	Argentina	late Holocene (Platan)	Santiago, 2009
31	Tres Arroyos 1	Tierra del Fuego	Chile	late Pleistocene (Lujanian)	Borrero, 2003

dating, four occupations were identified, which cover a time span of 2500 years (between 500 and 3000 BP). The analysis of archaeological materials (human and animal burials, lithic artifacts, pottery sherds), and faunal remains (freshwater molluscs and bones of *Lama guanicoe*, *Ozotoceros bezoarticus*, Rheidae, and fishes) shows that in this site both burials and domestic activities were diachronically carried out (Prates et al., 2010b). The *D. avus* specimen (LM1.E2.2) was dated to 2972 ± 50 BP (AA83516; 3072 ± 151 cal).

Table 2
Cranial and dental measurements (mm) of the new specimens of *Dusicyon avus*.

	MAR 1	LM1.E2.2	Pr1 090	Pr1 089	Pr1 287
LCB			176.3		
LOO			107.83		
WCP		34.11	32.06		
WIM		30.85	35.82		
WPPAR		39.95	47.39		
WCC		56.5	57.31		
WP			58.41		
WRC1			32.87		
LB		23.18	21.86		
WB		15.61	16.34		
LM		121.51			
LC1		9.81	9.53		
WC1		6.81	6.93		
LP4		20.04			
WP4		10.85	9.73		
LlaM1		12.83			
LliM1		10.18			
WM1		15.33			
LM2		7.2			
WM2		10.76			
Lc1	8.49	8.7			
Wc1	6.44	6.67			
Lm1	20.43	19.45		20.67	20.59
Ltrm1	14.78	13.26		14.3	14.04
Wtalm1	7.57	7.03		6.99	6.96
Lm2	10.36	8.95			9.07
Wm2	6.49	5.97			6.77

The Perro 1 archaeological site (53° 30′ 3″ S, 68° 17′ 41″ W) is an open air site located on the eastern bank of an unnamed lake in the middle of the steppe of Tierra del Fuego. The site is located about 30 m above the present shoreline of that lake and about 18 km inland from the Atlantic Ocean coast. Faunal remains (*Lama guanicoe, Ctenomys magellanicus, Lycalopex culpaeus, Dusicyon avus*, and *Ovis aries)* and lithic remains (nodules, cores, flakes, bola stone, scrapers) were deposited at the bottom of a deflation scar. The genesis of this archaeological deposit is the result of multiple processes that have influenced its condition; in the same deflation basin are bones and lithic tools and ecofacts of undoubted human discard, together with natural bone deposition. In this sense, the site is a surface palimpsest. A radiocarbon date obtained on the Pr1 090 specimen, whose skeleton was fully articulated at the bottom of the basin of the deflation scar, yielded an age of 2984 ± 37 BP AA75297; 3085 ± 133 cal) (Santiago, 2009).

4.2. New specimens of *Dusicyon avus*

The specimen from La Marcelina (MAR 1) is a left mandible with i3-m1 and right mandible with c1-m2 (Fig. 2 A; Table 2). The mandibles are fused along the shymphysis, and the horizontal ramus is strong. The right m3 alveolus is reabsorbed, but the left one is present. The dentition is moderately worn. The lower fourth premolar presents an acute and transversally compressed distal cingulum and a second distal accessory cusp. The m1 is large in

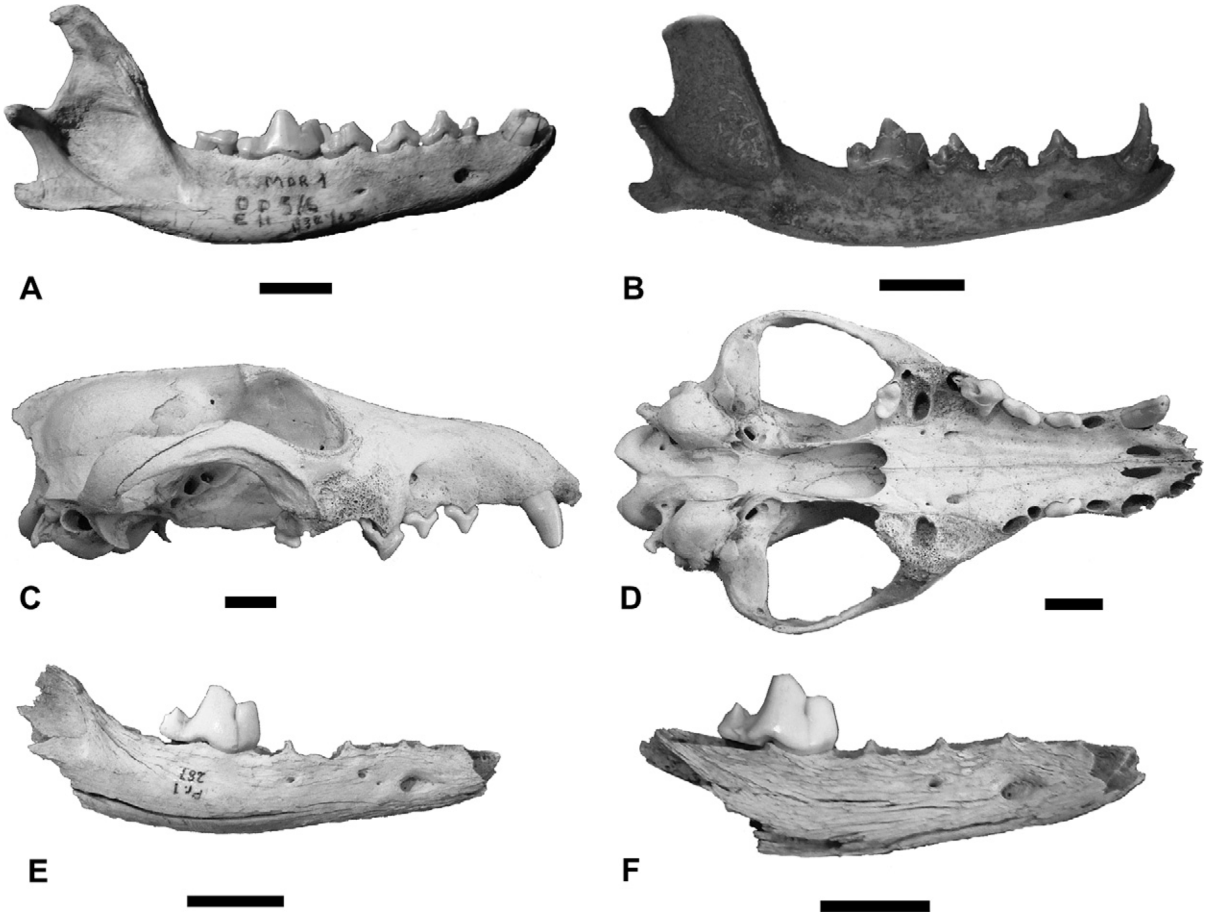

Fig. 2. New specimens of *Dusicyon avus*. A: right mandible in lateral view (MAR 1); B: right mandible in lateral view (LM1.E2.2); C: skull in left lateral view (Pr1 090) (mirrored); D: skull in ventral view (Pr1 090) (reflected); E: incomplete right mandible in lateral view (Pr1 287); F: incomplete left mandible in lateral view (mirrored; Pr1 089). Scale = 20 mm.

relation to other teeth, and bears a well-developed metaconid and, apparently, a large hypoconulid.

A partial skull composed by the braincase, a fragment of right maxilla with P4-M2, and left maxillary with P1-2 and the mesial border of the P4, a right mandible with c1-m2 (Fig. 2 B; Table 2), and some limb bones were found at the Loma de los Muertos sites. All these bones belong to only one individual (LM1.E2.2). The frontals are raised and the tympanic bullae are large. The p4 has a second distal accessory cusp and an acute distal cingulum. The m1 is larger and bears a well-developed metaconid and hypoconulid. The P4 protocone is small and lingually directed.

Four specimens were collected at the Perro 1 site: a nearly complete skeleton including the skull with left C1, P2-P4, M2, and right P2 (Pr1 090; Fig. 2 C–D); incomplete right mandible with the m1-m2 (Pr1 287; Fig. 2 E); a fragment of left mandible with lower carnassial (m1; Pr1 089; Fig. 2 F); an edentulous left mandible (Pr1 087) (Fig. 2 C–F; Table 2). The lower carnassials are large, especially in relation to mandible size, and show a well-developed metaconid. A large hypoconulid is present in the Pr1 287 but is apparently absent in the Pr1 089. The m1 alveolus is also large in the Pr1 087. The skull presents wide and slightly raised frontals, short and wide palate, and a wide interorbital constriction. The dentition is much worn and the alveoli of the right P4-M1 (and right M2) are partially reabsorbed indicating that these tooth were lost while living. The protocone of the upper carnassial is small and lingually directed.

The statistical analyses showed a good separation between *Dusicyon avus* and *Lycalopex culpaeus* (Fig. 3). The PCA of cranial measurements indicates that *D. avus* and *D. australis* have wider postorbital process and constriction, and wider tympanic bulla (Fig. 3A–B), and the PCA of lower dentition place the studied specimens in the range of *D. avus* (Fig. 3C–D). In these analyses, the new specimens are contained in a morphometric space occupied by *D. avus*. Finally, a bivariate plot between the length of the m1 and the length of the m2 indicates that *D. avus* has larger m1 in relation to m2, and placed the studied specimens in the range of this extinct species (Fig. 3E).

5. Discussion

In the last twenty years numerous localities for *Dusicyon avus* were reported, expanding the known distribution of this species (see above, Table 1, Fig. 1). Most are archaeological sites, but new paleontological ones extended its distribution to the late Pleistocene in Uruguay (Prevosti et al., 2009), and probably to southern Brazil (Hadler Rodríguez et al., 2004). The record from the archaeological sites located in the Pampean region (Argentina) and in southern Patagonia (Chile and Argentina) left a wide gap in the distribution of this species (Fig. 1). Fortunately, new records analyzed in this paper, Loma de los Muertos and La Marcelina, shorten the gap to some extent, as they are located in northern Patagonia, that is, more or less at the centre of this gap. On the other hand, Perro 1 is the second locality in Isla Grande de Tierra del Fuego with *D. avus* and is located in the steppe area of the northeast part of the island (Fig. 1).

Although there are several records from late Holocene levels, such as Punta Bustamante in Patagonia and Nutria Mansa, Río Luján,

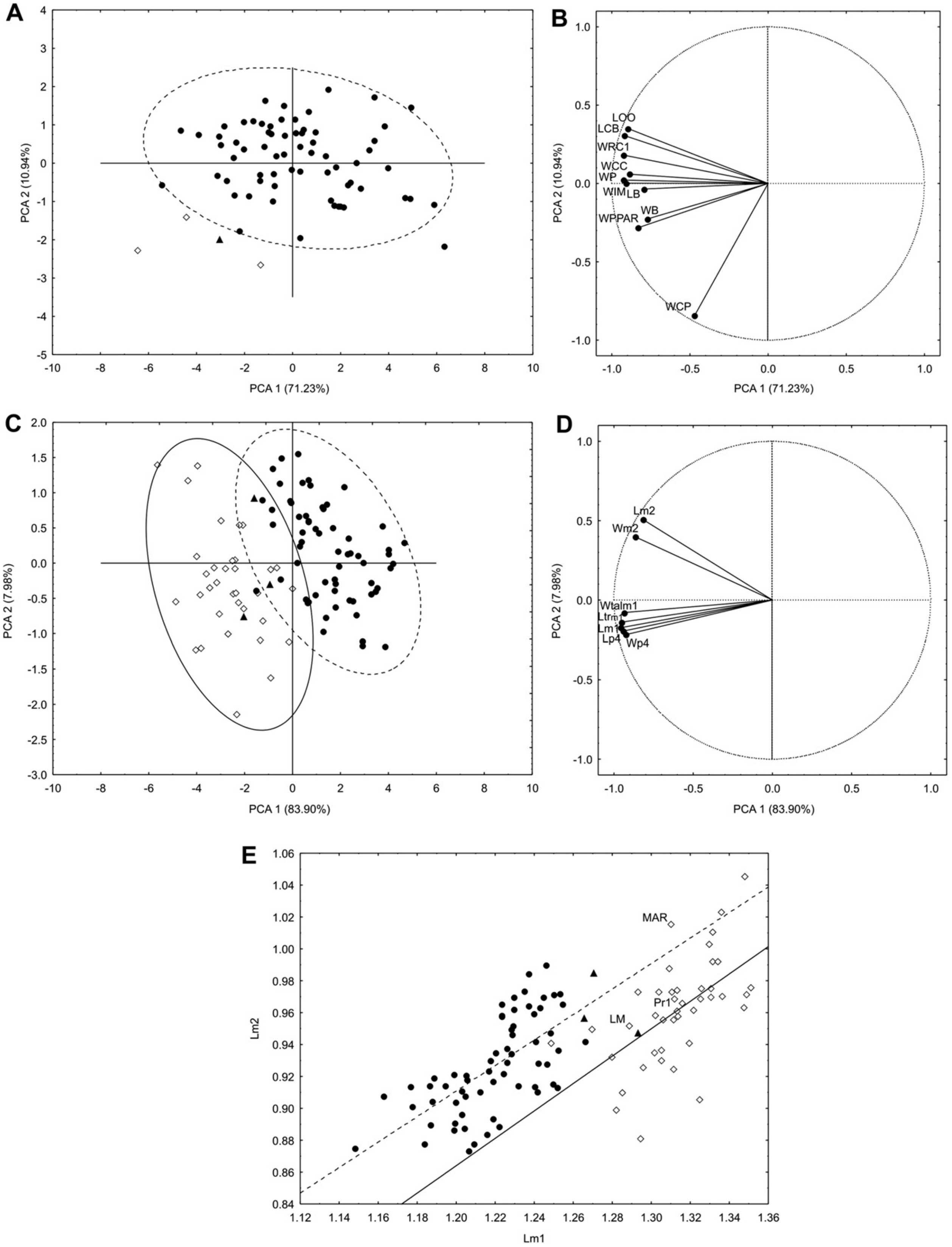

Fig. 3. Principal component analyses and bivariate graph of dental and cranial measurements. A: principal component axis (PCA) 1 versus 2 of cranial measurements. The percentage of explained variance is between brackets; B: graphical representation of the eigenvectors of the first two PCA based on cranial measurements; C: principal component axis (PCA) 1 versus 2 of lower dental measurements. The percentage of explained variance is between brackets; D: graphical representation of the eigenvectors of the first two PCA based on lower dental measurements; E: bivariated graph between the length of the first lower molar (Lm1) against the length of the second lower molar (Lm2). Black dot: *Lycalopex culpaeus*; white rhombus: *Dusicyon avus*; black triangle: *D. australis*; MAR: La Marcelina 1 site specimen; LM: Loma de los Muertos site specimen; Pr1: Perro 1 site specimen; Broken line ellipse: 0.95 confidence ellipse of *L. culpaeus*; Solid line ellipse: 0.95 confidence ellipse of *D. avus*; broken line: least square adjusted line of *L. culpaeus* ($y = -0.1669 + 0.859$ x); broken line: least square adjusted line of *D. avus* ($y = -0.049 + 0.7998$ x).

and Zanjón Seco in the Pampean region (Table 1), there are no published taxon dates that validate the age of these specimens. As was stated by Borrero (2003), with a supposed Holocene *Dusicyon avus* from Tres Arroyos 1 archaeological site that was dated at more than 10 ka BP (see above), taphonomic bias could mix older specimens in younger levels. The taphonomic complexity and the absence of taxon dates makes problematic the chronological assignation of other specimens of *D. avus* collected in some classical sites (*e.g.*, Cueva del Milodón; Fell's cave, Pali Aike cave; see Martín, 2007). Thus, it is very important to get taxon dates to constrain the time of extinction of this fox. The results obtained in this paper clearly corroborate the presence of *D. avus* in the late Holocene (around 3 ka BP, see above) in northern and southern Patagonia. The age of the other specimens found in the late Holocene must be dated, especially the Punta Bustamante ones that came from the earliest levels of those sites. Radiocarbon dating of the La Marcelina specimen is currently underway, which is expected to be younger (ca. 1700 years based on the available dates of the bearing level) than the 3 ka here obtained. On the other hand, work in progress by F. Martin's team produced slightly younger dates (F. Martin, personal communication). Increasing the number of radiocarbon dating surely could bring more light to the time of extinction of this canid.

The new specimens have a set of characters that are diagnostic of *Dusicyon avus*: the presence of a well-developed hypoconulid in the m1, a second accessory cusp and a narrowed distal cingulum in the p4, and a protocone placed lingually in the P4 (see above and Fig. 2). Other similarities are clearly shown by the PCA and the biplot graph (Fig. 3), like the presence of wider postorbital constriction and processes, larger m1 in relation to m2, and wider bulla. *Lycalopex culpaeus* has a similar general size, but lacks a second accessory cusp in the p4, and the distal cingulum is wide in this tooth, the m1 hypoconulid is smaller, the protocone of the p4 is placed mesially or linguo-mesially, and the frontal region and tympanic bulla are narrower (Fig. 3). *Dusicyon australis* shares some characters with *D. avus* (*e.g.*, wide frontal region and tympanic bulla; large m1), but possess a more reduced protocone in the P4 and and smaller metaconid in the m1. The principal cusps of the premolars are taller and more acute in *D. australis*, and the distal cingulum of the p4 is also narrow and acute in *D. australis*; it is raised and in some specimens is cusp-like, but a true second accessory distal cusp is not present in this species. Summing up, the cranial and dental anatomy and the morphometric analyses allow identifying the specimens of the Perro 1, La Marcelina 1, and Loma de los Muertos sites as *D. avus*.

Two hypotheses about the extinction of *Dusicyon avus* were given (Berman, 1986; Berman and Tonni, 1987). The first one is that the change from an arid or semiarid to a more humid climate in the Pampean region during the late Holocene caused the declination and extinction of this species. The second one involves hybridization between *D. avus* and the domestic dog (*Canis familiaris*; Berman, 1986; Berman and Tonni, 1987).

Several facts argue against the climate change hypothesis. First, the assumption that *Dusicyon avus* was adapted to arid environments is not consistent with the distribution of the species. A large portion of its geographic range (*i.e.*, most of Patagonia) continued to be an open and arid area from late Pleistocene until present times. The strong climatic variability detected during the middle-late Holocene in the Pampean and Patagonian regions using different proxies (*e.g.*, palynology, dendroclimatology, paleosols, sea level changes, mammal distribution) were not stronger or sharper than the ones registered in the late Pleistocene-early Holocene (*e.g.*, Clapperton, 1993; Markgraf, 1993; Prieto and Stutz, 1996; Tonni et al., 1999, 2001; Mancini, 2003; Schäbitz, 2003; Grill et al., 2007; Mancini et al., 2008; Borromei et al., 2010). This lapse contains neoglacial advances, the Little Ice Age, but also warm events, comprising the Medieval Warm Period (Tonni et al., 1999, 2001; Favier-Dubois, 2007; Borromei and Quattrocchio, 2008; Ponce, 2008; Waldmann, 2008; Ponce et al., 2011). The environmental changes recorded in the large region were *D. avus* lived were not uniform, and different areas experienced dissimilar conditions (*e.g.*, Mancini et al., 2008).

Other points to be considered are based on its wide geographic distribution, and its cranio-dental anatomy, which suggest a generalist diet slightly more carnivorous than the living *Lycalopex culpaeus* (see Prevosti and Vizcaíno, 2006). It is clear that *Dusicyon avus* was an eurioic species similar to living jackals (*e.g.*, *Canis aureus*), coyote (*Canis latrans*), or other South American foxes (*e.g.*, *L. culpaeus*). In this context, it is difficult to relate those environmental changes to the disappearance of *D. avus,* and there is no clear link between the environmental changes and the extinction of this generalist canid.

There is no evidence of hybridization in the osteological remains of late Holocene *Dusicyon avus*. The dental, cranial, and postcranial anatomy has several similarities with South American foxes, and it has none of the characters typical of *Canis familiaris* (*e.g.* Caviglia, 1986; Prevosti, unpublished doctoral thesis, 2010). Ancient DNA also failed to find any trace of *C. familiaris* in *D. avus* samples (A. Cooper and J. Austin, personal communication). Moreover, there is a gap of at least 2 ka between the oldest *C. familiaris* (≈1 ka BP) record in the Pampean region and Patagonia and the latest record of *D. avus* (≈3 ka BP; Prates et al., 2010a).

Some remarkable aspects of the record of this fox are that it is commonly found in archaeological sites (vide supra), and it is abundant in some of them (*e.g.*, Baño Nuevo, Fell's Cave, Pali Aike cave; Trejo and Jackson, 1998; Amorosi and Prevosti, 2008). In most cases, the samples are dental and cranial elements, and evidence of human consumption is not common, except in Tres Arroyos 1 where the mandible displays a cutmark (Mengoni Goñalons, 1987). At least in two sites (Loma de los Muertos and Río Luján) this species was associated with mortuary contexts; moreover, in Loma de los Muertos it has been suggested that the animal was intentionally buried, as a human would have been (Prates et al., 2010b). Another place where this canid is present is the Calera site, which has been interpreted as a ritual site (Messineo and Politis, 2007). In Arroyo Seco 2, several human burials contained necklaces or wrist bracelets made of hundreds of canine teeth (canids; Fidalgo et al., 1986; Salemme, in press). Some of these canines could belong to *Dusicyon avus* but the taxonomic identification is uncertain. All these facts and the "supernatural" connotations of carnivores in hunter-gatherer societies (Bonomo, 2006) suggest that *D. avus* had probably a high symbolic value among the humans that inhabited the Pampas during the late Holocene. This could have implied a more intensive hunting of *D. avus*, mainly since the late Holocene (ca. 3 ka BP), when human population in Tierra del Fuego, Patagonia, and the Pampean Region increased strongly (Borrero, 1990; Béguelin et al., 2006; Martínez and Gutiérrez, 2008; Salemme and Miotti, 2008; Morales et al., 2009). Perhaps this human factor would have generated an additional pressure for the extinction of *D. avus* towards the late Holocene.

There are some ethnographic references of two fox species in Tierra del Fuego, forty years before the introduction of the gray fox on the island (Gallardo, 1910:71). Lothrop (1928:28) says: "For the Ona, the second important place among the terrestrial animals belonged to foxes, in two varieties, one of which grows to unusual size". If this "large fox" corresponded to *Dusicyon avus*, then this animal had not become extinct until many years after the European presence (they arrived 200 years ago), at least in the Isla Grande de Tierra del Fuego. But it cannot be ruled out that the two foxes could be only intraspecific variations of *Lycalopex culpaeus* (some specimens from Tierra del Fuego reached a very large size; see

Kraglievich, 1930). This and the absence of archaeological remains younger than 3 ka do not support this hypothesis.

6. Conclusions

New remains of *Dusicyon avus* were found in three archaeological sites (Loma de los Muertos, La Marcelina 1, and Perro 1) from the late Holocene of Patagonia. Two archaeological sites are located in northern Patagonia, and they close the geographic gap of previous records that were restricted only to the Pampean region and southern Patagonia. Two ^{14}C taxon dates confirmed the presence of this fox in the late Holocene, and constrained its last records to ≈ 3 ka BP.

At the present moment is not clear why *Dusicyon avus* became extinct, but there is no evidence in support of the hypotheses of environmental change or hybridization with domestic dog. As proposed in other cases of mass extinction in South America (*e.g.*, Cione et al., 2008) and considering the symbolic connotation of carnivores in hunter-gatherer societies, probably humans had some influence in the extinction process. Even though the direct evidence of this situation is still scarce, it should be considered in future research.

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