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ORIGINAL PAPER

New Canid Remains from Dolores Formation, late Pleistocene-early Holocene, Uruguay

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Abstract The fossil record of carnivorous mammals in Uruguay is scarce and fragmentary, but informative. In the present contribution, two new records of canids allocated in sediments of the Dolores Formation (late Pleistocene-early Holocene) are described. These records, based on their anatomical-comparative study and multivariate analysis, correspond to two foxes: one of medium size, *Cerdocyon thous*, conforms to the first record of this taxon in the country, meanwhile the other one, of larger size, is referred to *Dusicyon avus* and is the first fossil record of this animal in the south of the territory and the second record in the whole country. Until now, the only carnivorous mammals registered in this formation were the hunters of large herbivores (*Arctotherium* sp. and *Smilodon populator*). In this way, these discoveries complement and expand the set of placental mammals with a carnivorous diet for this unit, particularly with the capacity to predate over small- and medium-size mammals.

Keywords Dolores Formation · Uruguay · *Dusicyon avus* · *Cerdocyon thous*

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Introduction

The fossil record of placental mammals with a carnivorous diet (Order Carnivora) in Uruguay is formed mostly by fragmentary and relatively scarce, but informative, remains that include skulls and mandibles, isolated teeth, and a diversity of long bones. Particularly, the fossil record of canids includes few taxa, the late Pleistocene *Dusicyon avus* Burmeister, 1866, *Protocyon troglodytes* Lund, 1838, and *Lycalopex gymnocercus* Fischer, 1814, and the Holocene *Canis* Linnaeus, 1758 (Prevosti et al. 2009 and references therein), with variations in body size and level of carnivory.

Most of the canid findings (*Dusicyon*, *Protocyon*, and *Lycalopex*) come from deposits allocated to the late Pleistocene of the northern part of the country (Sopas Formation) (Ubilla 2004; Prevosti et al. 2009; Ubilla and Martínez 2016). However, these findings are rare in deposits of the southern part of the country.

In the present contribution, two canids unearthed from sediments attributable to late Pleistocene-early Holocene (Dolores Formation) from the Department of Colonia (Beach of El Caño Creek) (Fig. 1) are described. This findings belong to two foxes, one of them is the first record of a big-sized fox (*Dusicyon avus*) for this geological unit, while the other corresponded to a medium-size fox (*Cerdocyon thous* Linnaeus, 1766), which is the first record for the country.

Geological Context

The Dolores Formation, mainly located in western and southern Uruguay (Ubilla et al. 2011), is comprised of silty claystones and siltstones, clay deposits, sandstones, and gravel (mudstone). It is generally brownish in color, with gray-green local shades, and a maximum of 10 m thickness. It was

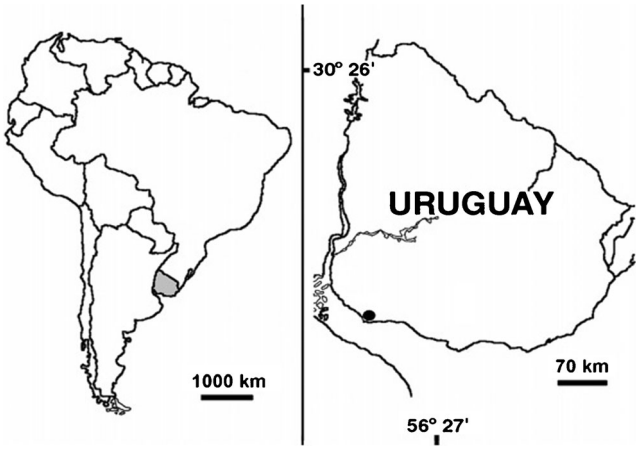

Fig. 1 Map showing the zone of the discoveries (*spot*): Beach of El Caño Creek, Department of Colonia

deposited in semi-arid and cold climatic conditions (Martínez and Ubilla 2004 and references therein; Corona et al. 2013). Several numerical datings based on radiocarbon and OSL/TL methods were obtained for the Dolores Formation, with ages ranging from 30.100–27.000 to 11.150–10.480 years before present (BP) (Ubilla et al. 2011 and references therein). Based on the mammalian assemblage, this unit is correlated with the Lujanian Stage/Age (Ubilla et al. 2011 and references therein). Particularly for the studied area (Beach of El Caño Creek), recent works produced an OSL age of 16.070 +/− 930 years at the base of the outcrop (Corona et al. 2013).

Materials and Methods

Institutional Abbreviations

FC-DPV, Facultad de Ciencias- Colección de Vertebrados Fósiles, Montevideo, Uruguay; **MNHN**, Museo Nacional de Historia Natural, Montevideo, Uruguay; and **ZVC-M**, Colección de Vertebrados de Facultad de Ciencias, Sección Mamíferos, Montevideo, Uruguay.

For a comparative analysis, materials of *Lycalopex gymnocercus*, *Cerdocyon thous*, and *Chrysocyon brachyurus* housed in the mastozoological collections of the Facultad de Ciencias and the Museo Nacional de Historia Natural (Montevideo) were considered.

All of the measurements were taken by one of us (A. M.) following von den Driesch (1976) and Prevosti et al. (2005, 2015), with digital calipers accurate to 0.01 mm and were expressed in millimeters.

Skull and upper teeth measurements: rostral width (RW, taken from the external edge of the canine alveolus); inter-orbital width (IOW); post-orbital process width (PPW); viscero-cranial length (Prosthion-Nasion); facial length (Prosthion-postorbital process); tooth row length I1-M2 (TRL I1-M2); tooth row length C-M2 (TRL C-M2); tooth row length M1–2 (TRL M1–2); antero-posterior diameter and crown height of the canine (CAP and CCH); antero-posterior and transverse diameter, and crown height of the PM4 (PM4AP, PM4ML, and PM4CH, respectively); and antero-posterior diameter of the M1 (M1AP).

Jaw and lower teeth measurements: antero-posterior diameter and crown height of the canine (cAP and cCH); crown height of the pm2 (pm2CH), antero-posterior diameter of the pm4 (pm4AP); antero-posterior and transverse diameter of the m1, m2, and m3 (m1AP and m1ML; m2AP and m2ML; m3AP and m3 ML, respectively); mandible height at the posterior border of the pm2 (Hpm2), the m1 (Hm1), and the m2 (Hm2); mandible breadth at posterior border of the m1 (Bm1); and tooth row length m1–3 (TRL m1–3).

The multivariate analysis (principal components analysis (PCA) and hierarchical cluster) were performed on the variance-covariance matrix measurements, using the statistical program PAST Version 2.09 (Hammer et al. 2001).

The skull data of *L. griseus*, *L. culpaeus*, and some *L. gymnocercus* and the jaw data of *D. avus*, *D. australis*, and *L. culpaeus* came from the literature (Prevosti et al. 2005, 2015). The information for *C. thous* and most *L. gymnocercus* were collected from specimens housed in the Colección de Vertebrados de Facultad de Ciencias and the Museo Nacional de Historia Natural (Montevideo) (Online Resource 1).

Data availability statement

The described fossil materials are housed in the fossil vertebrate collection of Facultad de Ciencias (FC-DPV), Montevideo, Uruguay. For the comparative analysis, recent materials of *Lycalopex gymnocercus*, *Cerdocyon thous*, and *Chrysocyon brachyurus* housed in the mastozoological collections (ZVC-M and MNHN) of the referred institutions were considered. The dataset of *Cerdocyon thous* and *Lycalopex gymnocercus* generated or analyzed during this study are included in this published article (and its supplementary information files). The other datasets analyzed during the current study are available from the corresponding author on reasonable request.

Results

Carnivora Bowdich, 1821
Canidae Fischer von Waldheim, 1817
Dusicyon Hamilton Smith, 1839

Dusicyon avus (Burmeister, 1866)

Fig. 2 Mandible of *Dusicyon avus* (FC-DPV 2936) in right lateral and occlusal view. Scale 5 cm

Material referred: FC-DPV 2936: fragment of right mandible, with m1, m2, and alveolus of m3 (Fig. 2).

Locality and stratigraphic horizon: Beach of El Caño Creek, near the city of Colonia del Sacramento (Department of Colonia, Uruguay). The material was found in situ in the ravine brownish sediment level that correspond to the late Pleistocene-early Holocene Dolores Formation.

Anatomical description: The mandible is larger in absolute dimension than *L. gymnocercus* and *C. thous*, but not as much as *C. brachyurus*. The horizontal ramus is high; the masseteric fossa is deep and its anterior border reaches the posterior border of the alveolus of m3; and the inferior border of the ramus is curved downward. The m1 is anteroposteriorly longer than m2 and m3 at the alveolar level. It is broken along its trigonid, which is proportionally large in relationship to the talonid. The paraconid and the protoconid are not well preserved; the metaconid is small. Additionally, and because of tooth wear to the occlusal surface, it is very difficult to distinguish the cusp morphology in the m1 talonid and the m2, and it is deduced that it belonged to an old adult individual.

Measurements, in mm.: H m1, 20.73; H m2, 20; B m1, 9, TRL m1–3, 33.34; m1 AP, 20.63, m1 ML, 7; m2 AP, 8.99, m2 ML, 6.01; and m3 AP, 4 y m3 ML, 3.

Remarks: The PCA performed on m1AP, m1ML, m2AP, m2ML, and Hm1 measurements indicated the presence of five components, and the first two explained more than 95% of the variance of the sample (Online Resource 2). When plotting the values of these components, the fossil material grouped with *D. avus* (Fig. 3). The loadings coefficients of the first component showed that the most influential variables were the Hm1 and m1AP; meanwhile, the others had scarce contributions (Online Resource 2). The cluster analysis concurred with these results and grouped the fossil material with *D. avus* (Online Resource 2).

Cerdocyon Hamilton Smith, 1839

Cerdocyon thous Linnaeus, 1766

Material referred: FC-DPV 1885: almost complete anterior region of skull and jaw, articulated (Fig. 4).

Locality and stratigraphic horizon: Beach of El Caño Creek, near the city of Colonia del Sacramento (Department of Colonia, Uruguay). Although the material was not found in situ, it is possible confidently to assign it to the late Pleistocene-early Holocene Dolores Formation because of the type of fossilization, which is very similar to other fossils collected in that unit from carbonatic levels (Online Resource 3).

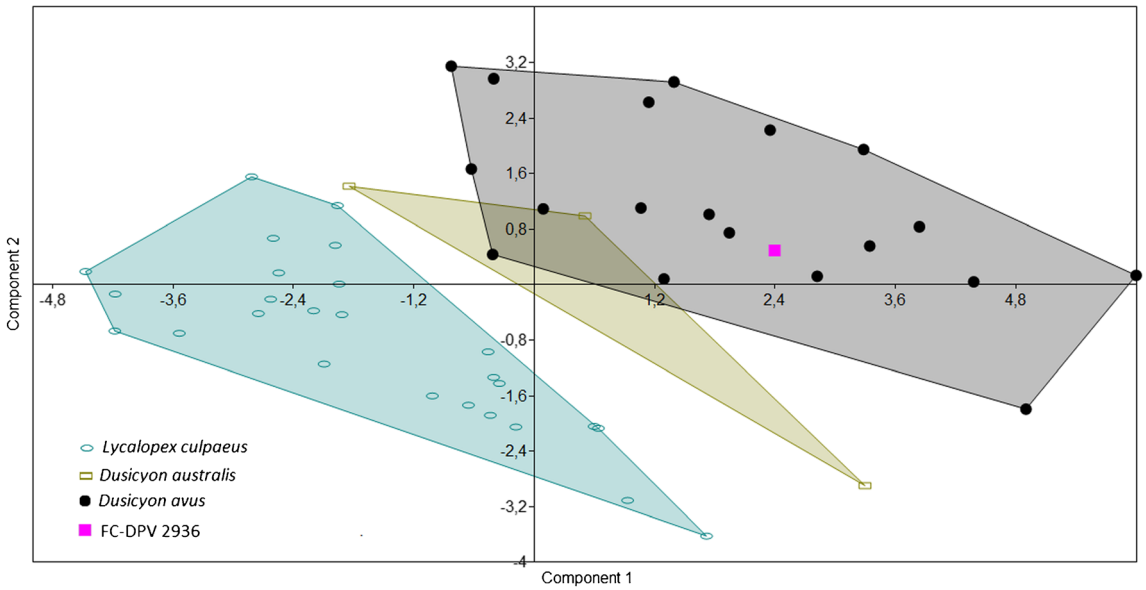

Fig. 3 Biplot of the first two components of the PCA for *D. avus* (FC-DPV 2936). Data of *L. culpaeus*, *D. australis,* and *D. avus* were taken from Prevosti et al. 2015

Fig. 4 Skull and mandible of *Cerdocyon thous* (FC-DPV 1885) in dorsal and left lateral view. Scale 10 cm

Anatomical description: The skull and jaw, cemented by carbonate, are broken in their middle zone, preserving the anterior half. The snout is high, robust, and relatively shorter than *L. gymnocercus* with straight external borders convergent forward and not subparalell like *L. gymnocercus,* as has been mentioned by Kraglievich (1930).

The nasals are broad at the anterior and posterior ends becoming narrow in the middle portion. The suture with the frontal is irregular and located at the anterior border of the orbits. Premaxillae are anteroposteriorly projecting forming a thin wedge between the maxillae and nasals. The skull roof at the postorbital processes is wider and more convex than *L. gymnocercus*, and according to the orientation of the borders posterior to the orbits it can be deduced that the postorbital constriction is less pronounced that in that species (Kraglievich 1930). Overall, the tooth rows are well preserved, although the left tooth row is complete and better preserved than the right one, which lacks the canines. The canines are robust, more than in most *L. gymnocercus* and in the same way as *C. thous*. Because of the occlusal wear of the PM4 and M1, we can conclude that the specimen corresponds to an old adult individual.

Measurements, in mm.: skull: RW, 24; IOW, 28; PPW, 34; prosthion-nasion, 69; prosthion-postorbital process, 83; TRL I-M2, 76.15; TRL C-M2, 63; TRL M1–2, 17; C AP, 6.85 and C CH, 12e; PM4 AP, 13; PM4 ML, 7 and PM4 CH, 7; M1 AP, 10.12; mandible: H pm2, 11; H m1, 16; B m1, 7.5; c AP, 5.49 and c CH, 13e; pm2 CH, 6; pm4 AP, 9; and m1 AP, 14.38.

Remarks: The PCA performed on RW, IOW, TRL C-M2, C AP, PM4AP, PM4ML, and M1AP measurements revealed the presence of seven components, of which the first two explained 95% of the variance of the sample (Online Resource 4). When plotting these values, the fossil material grouped with *C. thous* (Fig. 5). According to our comparative sample and despite having superposition between *C. thous* (smallest specimens) and *L. gymnocercus* (largest specimens), the

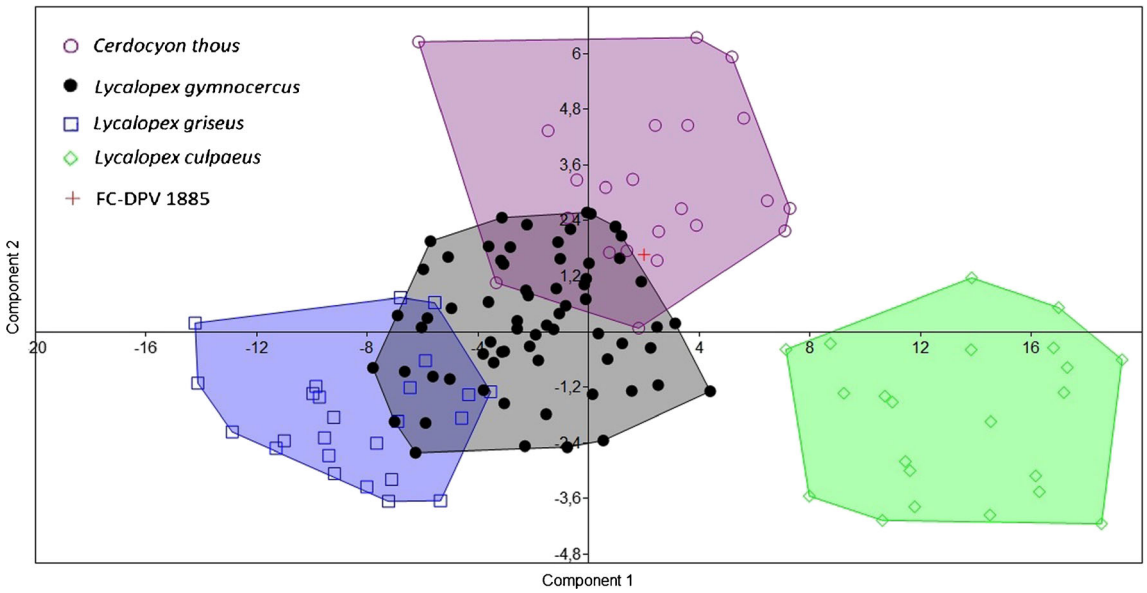

Fig. 5 Biplot of the first two components of the PCA for *C. thous* (FC-DPV 1885). Data of *L. griseus*, *L. culpaeus,* and some *L. gymnocercus* were taken from Prevosti et al. 2005

analysis suggests that our material is not included in the variation of this last species. Concomitantly, the rostral and skull roof morphology is similar to those of *C. thous*. The loading coefficients of the first component showed that the most influential variables were TRL C-M2, RW and the IOW, while the contribution of the other components was low (Online Resource 4). The cluster analysis was consistent with these results and grouped the fossil material with specimens of *C. thous* (Online Resource 4).

Discussion

The fossil record of *D. avus* in South America is abundant and comes from the southern part of the continent (Brazil, Chile, Argentina, and Uruguay), based on several paleontological localities of the late Pleistocene and archaeological sites of the Holocene (Prevosti et al. 2011, 2015; Sillero-Zubiri 2015). Although the main causes of the extinction of this canid remain unclear, this may have occurred in recent times, approximately 324–496 years BP and could be related to a combination of climatic and human causes (Prevosti et al. 2015). On the other hand, the fossil record of *C. thous* is doubtful and scarce. In South America, it is better known from deposits of the late Pleistocene, especially in Brazil (Minas Gerais, Bahía, and Rio Grande do Norte) (Courtenay and Maffei 2004; Oliveira et al. 2005).

Until now, the hunters of large herbivores, the short face bear (*Arctotherium* sp.) and the saber-toothed cat (*Smilodon populator*) (Prevosti and Vizcaíno 2006), were the only records of mammals with carnivorous diets for the Dolores Formation (Ubilla et al. 2011), which meant that the material here analyzed complemented and enlarged the assembly of this type of animal for this unit. Particularly, for the extinct *D. avus*, a 15 kg fox, a more carnivorous diet than the extant foxes was proposed (Prevosti et al. 2011, 2015), with a typical prey size approximately 5 kg and a maximum prey size of approximately 60 kg of weight (Prevosti and Vizcaíno 2006). In this way, not only small- and medium-size rodents would be suitable prey but also medium-size deer, small camelids, and ground sloths could be potential prey (Prevosti et al. 2009, 2011). On the contrary, *C. thous* is a canid of 4 kg to 7–8 kg of weight, and it fed mainly upon small mammals (mostly rodents) and even lizards, frogs, and birds as well as some invertebrates (insects and crabs) and fruits, depending on their availability. It is considered an opportunistic hunter with the capacity to scavenge (Berta 1982; Hover 2003).

It was inferred that *D. avus* could have lived in an arid environment of open areas with shrub-like plants, such as pampean and patagonic regions currently (Sillero-Zubiri 2015). On the contrary, although *C. thous* can be found in a diversity of environments, it is better known for inhabiting dense forested areas (Berta 1982; Lucherini 2015). The Dolores Formation is interpreted as a transition environment between a more arid pampasic context in the south towards more forested and tropical conditions in the north (Corona et al. 2013). This meant that the presence of these two foxes of different ecological requirements was not contradictory at all.

The specimen FC-DPV 2936 of *D. avus* was the first fossil record of this species for the Dolores Formation and the second one in the country after that reported by the Sopas Formation (north of Uruguay) (Prevosti et al. 2009). The specimen FC-DPV 1885 belonged to the extant species *C. thous*, which configured one of the few fossil records for this fox, becoming the first fossil record of this canid for the whole country.

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