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CANIDS (CANINAE) FROM THE PAST OF VENEZUELA

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PLEASE SCROLL DOWN FOR ARTICLE

REVISITING *RINGOSAURUS CAUDAMIRUS* FROM THE UPPER CRETACEOUS OF PATAGONIA

Detailed description of the axial skeleton and a revised diagnosis for this taxon establishes firmly its validity.

MACROEVOLUTIONARY HISTORY OF BODY SIZE IN ARCHOSAUROMORPHS

Analysis of more than 400 species indicate increasing size after the Permian/Triassic boundary.

STEM PLATYRRHINE FROM THE MIOCENE OF PATAGONIA

A well-preserved humerus of *Homunculus patagonicus* from the Santa Cruz Formation points to a robustly built arboreal quadruped that weighed between 2.2 and 2.6 kg.

CANIDS (CANINAE) FROM THE PAST OF VENEZUELA

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Abstract. There are three extant species of wild canids in Venezuela: *Urocyon cinereoargenteus*, *Cerdocyon thous*, and *Speothos venaticus*, excluding the feral domestic dog (*Canis familiaris*). However, a review of paleontological material that was published previously, along with newly reported ancient specimens, reveals a distinct historical diversity for the same region. The gray fox, *U. cinereoargenteus*, is the only small-sized taxon and the only Vulpini (true fox) identified to date in the fossil record of Venezuela; its presence is limited to the late Pleistocene of the Mene de Inciarte site, Zulia State. In contrast, large canids are more abundant. *Aenocyon dirus* (subtribe Canina), the dire wolf from the late Pleistocene, was reported from the sites El Mene de Inciarte, Muaco in Falcón State, and for the first time in El Breal de Orocuál (ORS20) in Monagas State. The genus *Protocyon*, a native South American canid (subtribe Cerdocyonina), is recognized in the country from late Pleistocene Inciarte (*Protocyon troglodytes sensu lato*), and late Pliocene–early Pleistocene Orocuál (ORS16) (*Protocyon orocuálensis* sp. nov.). Finally, we report a possible genus *Theriodictis* from the late Pleistocene Orocuál; this is a Cerdocyonina not previously mentioned for the northern region of South America. These records present broader diversity and suggest a more complex evolutionary history than previously thought for South American canids.

Key words. *Aenocyon dirus*. *Protocyon*. South America. *Theriodictis*. *Urocyon cinereoargenteus*.

Resumen. CÁNIDOS (CANINAE) DEL PASADO DE VENEZUELA. En Venezuela existen tres especies vivientes de cánidos: *Urocyon cinereoargenteus*, *Cerdocyon thous* y *Speothos venaticus*. Sin considerar al perro doméstico asilvestrado (*Canis familiaris*), estos cánidos corresponden a formas de pequeño tamaño. La revisión del material paleontológico hasta ahora reportado para el país, más nuevos elementos fósiles, muestran una diversidad distinta para el pasado de la región. El zorro gris, *U. cinereoargenteus* es la única especie de tamaño pequeño y el único Vulpini (zorro real) identificado en el registro fósil de Venezuela; su presencia se limita al Pleistoceno tardío del sitio Mene de Inciarte, Estado Zulia. Por su lado, los grandes cánidos son más abundantes. *Aenocyon dirus* (subtribu Canina), el lobo terrible del Pleistoceno tardío, fue reportado en los sitios El Mene de Inciarte, Muaco en el Estado Falcón y por primera vez en El Breal de Orocuál (ORS20) en el Estado Monagas. El género *Protocyon*, que pertenece a los cánidos nativos suramericanos (subtribu Cerdocyonina), está reconocido en el país para el Pleistoceno tardío de Inciarte, con la especie *P. troglodytes (sensu lato)* y para el Plioceno tardío–Pleistoceno temprano de Orocuál (ORS16), por *P. orocuálensis* sp. nov. Finalmente, se reporta la presencia del género *Theriodictis* en el Pleistoceno tardío de Orocuál, un Cerdocyonina no antes mencionado para la región norte del continente. Estos registros muestran una amplia diversidad y una evolución más compleja de lo que se pensaba para los cánidos suramericanos.

Palabras clave. *Aenocyon dirus*. *Protocyon*. América del Sur. *Theriodictis*. *Urocyon cinereoargenteus*.

AS IN SOUTH AMERICA (SA), the presence of canids in Venezuela is an outcome of a biogeographic event named the Great American Biotic Interchange (GABI). The GABI was a pivotal event in SA that marked the end of the isolation of the Paleogene–early Neogene South American mammalian faunas (xenarthrans, metatherians, meridiungulates, caviomorphs, and platyrrhines) and the enrichment of North and South America with taxa coming from both American continents (Simpson, 1950; Reig, 1981; Marshall, 1988; Woodburne, 2010; Cione *et al.*, 2015; among others).

Three lineages of canids occupied SA as a consequence

of the diversification process and migratory pulses of the GABI: Cerdocyonina, Vulpini, and Canini (Wang & Tedford, 2008). Tedford *et al.* (2009) proposed the clade Cerdocyonina for the extant native foxes *Cerdocyon thous*, *Atelocynus microtis*, *Lycalopex* spp. (approximately six species); the recently-extinct *Dusicyon australis*; and the extinct *D. avus* and “*L. cultridens*”.

Other non-fox species within cerdocyonine canids include the bush dog *Speothos venaticus* and its extinct relative *S. pacivorus*; the maned wolf *Chrysocyon brachyurus*; and the extinct large-sized canids *Protocyon troglodytes*, *P.*

tarijensis, *P. scagliorum*, *Theriodictis platensis*, and “*Canis*” *gezi*. The Vulpini or “true foxes” are represented in SA only by the gray fox, *Urocyon cinereoargenteus* (Eisenberg, 1989; Prevosti, 2006; Prevosti & Forasiepi, 2018).

The lineage of Canini is represented prominently in SA by the emblematic dire wolf, *Aenocyon dirus* (Berta, 1988; Dundas, 1999; Prevosti & Forasiepi, 2018). Although the domestic dog, *Canis familiaris*, also is present from pre-Hispanic times (Linares, 1987; Prates *et al.*, 2010), its occurrence is not necessarily related to the GABI. In recent years, the coyote, *C. latrans*, has been seen crossing the Panama Canal, so a coyote presence in SA is expected in the near future (Monroy-Vilchis *et al.*, 2020).

Venezuelan context. Three species of living canids have been registered in Venezuela: *Urocyon cinereoargenteus*, *Cerdocyon thous*, and *Speothos venaticus* (Handley, 1976; Bisbal, 1989; Eisenberg, 1989; Linares, 1998; Sánchez & Lew, 2012). The crab-eating fox, *C. thous*, is the most widely-distributed canid species in the region, found across most of the country, although with gaps south of the Venezuelan Amazon (Lucherini, 2015). *Urocyon cinereoargenteus* is present in the western region, in the plains and swamps of Zulía, the Venezuelan Andes, the Cordillera Central, and part of the Central Llanos (Roemer *et al.*, 2015). Observations of *S. venaticus* are rare in Venezuela; this is consistent with Bisbal (1989) and Linares (1998), who showed several gaps in the distribution of this species, especially in the region of the Llanos and the Falcón basin. By contrast, DeMatteo *et al.* (2011) indicated that this canid is present throughout the country.

In addition, Hershkovitz (1961) stated “without a doubt” regarding the presence of the short-eared dog (*Atelocynus microtis*) in Venezuela, south of the Orinoco River (see also Bisbal, 1989; Linares, 1998). There are no confirming data at present. Later, for the post-Hispanic colonization age, Berry (1939) indicated the presence of *C. familiaris* (cited by Von der Osten, 1947 as *C. vulgaris*) from marginal sediments of Lake Tacarigua (Valencia Lake) in the Carabobo State. Linares (1987) reported pre-Hispanic domestic dogs from the archaeological sites El Cuartel (445 ¹⁴C years BP) and Puerto Santo (425 ¹⁴C years BP) in Sucre State, together with remains of *C. thous*. Although evidence of domestic dogs is recent in SA, this canid is distributed widely over the region, and in some cases, it became feral.

Fossil canids in Venezuela (Fig. 1) evidence a diversity

different from the past. The Swiss paleontologist H.P. Schaub in 1938 collected remains of a glyptodontid, some indeterminate mammals, and an incomplete distal extremity (without the epiphysis) of a femur from Cerro la Cruz (Quebrada de Agua Viva del Totumo), near Valera city, Trujillo State (Carrillo, 2015; J. Carrillo, pers. comm.). The latter specimen may belong to a large canid. Fossils of *Aenocyon dirus* have been reported from the late Pleistocene of the Mene de Inciarte deposit at Zulía State and Muaco at Falcón State (Royo y Gómez, 1960; Bocquentin, 1979; Prevosti & Rincón, 2007). Also, from Inciarte, gray fox (*Urocyon* cf. *U. cinereoargenteus*) were found (Prevosti & Rincón, 2007). Several specimens of *Protocyon* also have been reported from this deposit, and from the field of El Breal de Orocuál at Monagas State (Rincón *et al.*, 2009; Solórzano *et al.*, 2015; Ruiz-Ramoni, 2016).

In addition to these previous reports, our team (AR, AS, DRR) at the Instituto Venezolano de Investigaciones Científicas (IVIC) made new discoveries in the Orocuál, Inciarte, and Central Llanos regions, during 2016 and 2017 (Fig. 1). Preliminary assessments indicated that these materials provide new data about the past diversity and evolution of canids in the context of the GABI in SA (Ruiz-Ramoni, 2016). Our objective here is to report these new discoveries and the reinterpretations of previous material from Venezuela, with the aim to increase the knowledge of this group of carnivores at the northern tip of SA. Canids from this region have received less attention than those from the south of the continent, such as in Argentina (Gervais & Ameghino, 1880; Berta, 1988; Prevosti & Forasiepi, 2018). We present a comprehensive revision of the taxonomy of the canid specimens discovered in Venezuela.

Institutional abbreviations. CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina; EBRG, Museo de la Estación Biológica Rancho Grande, Aragua, Venezuela; FLSCN, Fundación La Salle de Ciencias Naturales, San Carlos, Venezuela; IBUNAM, Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México, CDMX, México; IGM, Colección Nacional de Paleontología, Museo María Del Carmen Perrilliat, Instituto de Geología, Universidad Nacional Autónoma de México, CDMX, México; INAH, Instituto Nacional de Antropología e Historia, CDMX, México; IVIC, Instituto Venezolano de

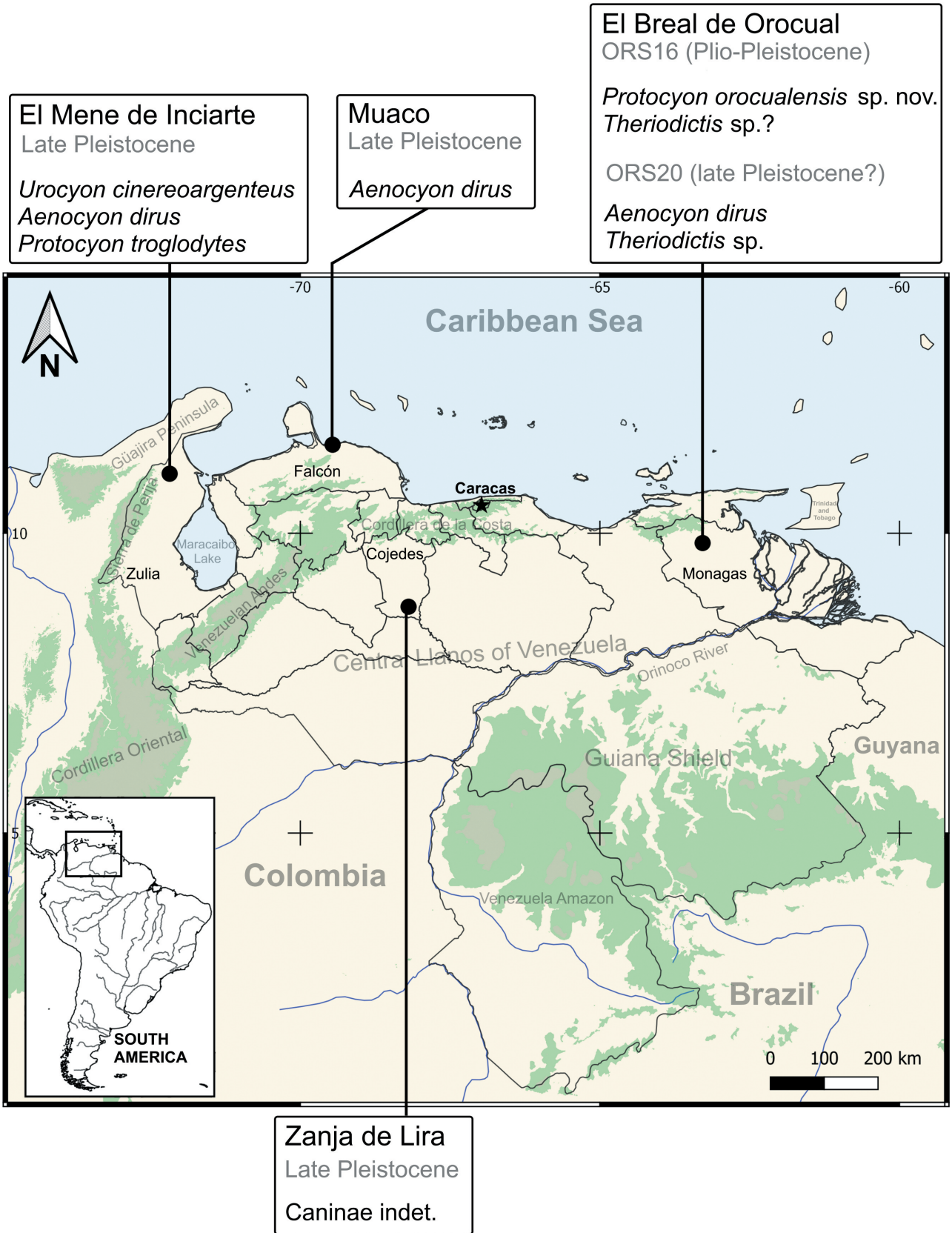


Figure 1. Paleontological localities with canid remains in Venezuela.

Investigaciones Científicas, San Antonio de Los Altos, Venezuela; **IVICP**, Colección Paleontológica del IVIC, San Antonio de Los Altos, Venezuela; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **LACM**, Natural History Museum Los Angeles County and La Brea Tar Pit and Museum, Los Angeles, United States; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MBLUZ**, Museo de Biología de La Universidad del Zulia, Maracaibo, Venezuela; **MG**, Natural History Museum, Geneva, Switzerland; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN**, Muséum National D’Histoire Naturelle, Paris, France; **MPS**, Museo Paleontológico “Fray Manuel de Torres”, San Pedro, Argentina; **OR**, Collection El Breal de Orocuá oil pit well ORS16, and **ORS20**, Collection El Breal de Orocuá oil pit well ORS20 (**ORS** means Orocuá Shell), both housed in Laboratorio de Paleontología, Centro de Ecología, IVIC, San Antonio de los Altos, Miranda, Venezuela; **PDVSA**, Petróleos de Venezuela, S.A., Venezuela; **ROM**, Royal Ontario Museum, Toronto, Canada; **UCV**, Universidad Central de Venezuela, Caracas, Venezuela; **UF**, University of Florida Collection, Florida, United States; **UNAM**, Universidad Nacional Autónoma de México, CDMX, México; **VF**, Vertebrados Falcón, Museo Royo y Gómez at the UCV, Caracas, Venezuela.

Anatomical abbreviations. **I/i**, upper/lower incisor; **C/c**, upper/lower canine; **P/p**, upper/lower premolar; **M/m**, upper/lower molar; **d**, desiduous, when it is before dental abbreviation. The numbers that accompany dental abbreviations mean the position of the tooth in the dental series.

Other abbreviations. **GABI**, Great American Biotic Interchange; **NA**, North America; **NALMA**, North American Land Mammals Age; **ORS**, Pozo Orocuá Shell; **SA**, South America; **SALMA**, South American Land Mammals Age.

MATERIAL AND METHODS

Material

We review the fossil material assigned to the subfamily Caninae that have been discovered in Venezuela. We based this report on material included in Ruiz-Ramoni (2016), on additional unpublished material, and on some notes about previous reports by Royo y Gómez (1960), Bocquentin (1979), Prevosti and Rincón (2007), Rincón *et al.* (2009), and

Solórzano *et al.* (2015). The materials are curated at the FLSCN, MBLUZ, UCV (VF), and IVIC.

Methods

We conducted morphological and morphometric comparisons of the fossilized canids, using specimens that are curated at the indicated collections. Descriptions are provided in the specialized bibliography. We focused on dental and mandibular elements due to their abundance in the paleontological record. The Supplementary Online Information includes the measurements of the newly-identified canids from Venezuela (Tables S1 and S2); the list of specimens used for comparison (Table S3); and the morphometric analyses that support the taxonomic assignments (Figs. S1 and S2). The body mass of the large canids (> 13 kg) was estimated using Van Valkenburg’s (1990) equation, based on the anteroposterior length of m1. Because only one small canid was recorded in the context of the material from Venezuela, its body mass was not calculated here.

Geographic and geological provenance

Mene de Inciarte. In Venezuela, ‘mene’ refers to asphalt pit. The assemblage comes from a tar pit at the foothills of the Sierra de Perijá, near the Cachirí River and the homonymous town, at the northeast of the La Paz oil field in Zulia State (Fig. 1). The outcrops are formed by unconsolidated sedimentary rocks corresponding to terraces with horizontal Pleistocene strata, some of which are impregnated with asphalt of Cretaceous origin (Urbani & Galarraga, 1991). Currently, the field of Inciarte presents active gas and asphalt deposits at various localities of the area, where some emissions have degrees of fluidity (Arnold *et al.*, 2008). The tar pits act as animal traps, where a massive vertebrate accumulation occurred over time, with exceptional preservation (McDonald *et al.*, 1999; Rincón, 2005; Rincón *et al.*, 2006; Prevosti & Rincón, 2007; Steadman *et al.*, 2015). The age of the deposit has been determined by radiocarbon analyses, providing dates between 25.5 ± 0.6 and 27.9 ± 0.4 ka ^{14}C years BP (late Pleistocene) (McDonald *et al.*, 1999; Jull *et al.*, 2004).

Muaco. The faunal assemblage comes from a sequence of sedimentary strata near the Muaco and Carrizal towns, Falcón State (Fig. 1). Muaco belongs to the El Jobo paleon-

tological-archaeological complex. This complex also is associated with the Cucuruchú and Taima-Taima sites, with accumulations of archaeological and paleontological material (Royo y Gómez, 1960). The radiocarbon method provided ages between 14.3 ± 0.5 and 16.4 ± 0.4 ka ^{14}C years BP (late Pleistocene) (Cruxent & Ochsenius, 1979; Ochsenius, 1980). **El Breal de Orocuál.** The Orocuál region includes multiple fossil assemblages in tar pits, located 20 km northeast of Maturín city, Monagas State (Fig. 1). In the area, two different massive accumulations of fossil vertebrates have been discovered: ORS16 and ORS20, separated by 300 m (Rincón *et al.*, 2009; Solórzano *et al.*, 2015). ORS16 is composed of dusty sediment mixed with traces of petroleum hydrocarbon, which is currently inactive. By comparison, ORS20 has an active petroleum flow. Both deposits overlay a collapsed structure called “La Hoya de Orocuál” in the Mesa Formation. The latter consists of fluvial-deltaic strata deposited by the Orinoco River during the early to middle Pleistocene (González de Juana, 1946; Carbón *et al.*, 1992). Thermoluminescence data suggest a middle Pleistocene age for the Mesa Formation (Carbón *et al.*, 1992), although the ages of the tar pits have been determined by biochronology. Rincón *et al.* (2009, 2011) and Czaplewski and Rincón (2020) reported taxa recognized primarily from the late Miocene and Pliocene, such as *Neocavia* sp., *Phugatherium* sp., and a Tetrastylinae rodent. Still, other taxa are characteristic of the Pliocene and middle Pleistocene, revealing *Smilodon gracilis* and *Pachyarmatherium leiseyi*. These data suggest an age close to the late Pliocene to early Pleistocene.

On the other hand, ORS20 has been assigned to the late Pleistocene due to the presence of *S. populator*, *Equus* sp., *Platygonus* sp. (Solórzano *et al.*, 2015). Some of these taxa also were present during the middle Pleistocene. In this work, we report remains of *Aenocyon dirus* that is considered typical of the late Pleistocene (see discussion).

Zanja de Lira. The fossil assemblage comes from a sedimentary sequence on the margins of the Caño Igües, southeast of El Polvero, Cojedes State. In this locality, fossil materials of megafauna have been found, including Gomphotheriidae, Megatheriidae, Glyptodontoidea, and Macraucheniiidae, with evidence of human presence (A. Rincón, pers. obs.). The fauna association has been assigned to the late Pleistocene (Carrillo *et al.*, 2008; Chávez, 2012).

SYSTEMATIC PALEONTOLOGY

Authorship of taxa mentioned in this section are listed in Supplementary Online Information 1.

Family CANIDAE Fischer de Waldheim, 1817

Subfamily CANINAE Fischer de Waldheim, 1817

Tribe VULPINI Hemprich & Ehrenberg, 1830

Genus *Urocyon* Baird, 1858

Type species. *Urocyon cinereoargenteus* (Schreber, 1775). Current fox of the eastern United States and California.

Urocyon cinereoargenteus (Schreber, 1775)

Figure 2.1–2.5

1775 *Canis cinereo argenteus* Schreber, p. 92.

1775 *Canis virginianus* Schreber, p. 585.

1784 [*Vulpes*] *pensylvanicus* Boddaert, p. 97.

1830 *Canis nigrirostris* Lichtenstein, p. 106.

1899 *Urocyon parvidens* Miller, p. 276.

1899 *Urocyon guatemalae* Miller, p. 278.

1929 *Urocyon seminolensis* Simpson, p. 575.

1960 *Urocyon atwaterensis* Getz, p. 363–364.

List of synonymies modified from Fritzell and Haroldson (1982) and Prevosti and Rincón (2007).

Referred material. Mene de Inciarte. IVICP 3531, left M1 (Fig. 2.1).

IVICP 3528, a nearly complete right hemimandible (the mesial part is absent from the alveolus of the lower canine); only m1 is present (Fig. 2.2–2.3). IVICP 3530, left c (Fig. 2.4). IVICP 3529, a fragment of right hemimandible, lacking the ascending process and the anterior part of the corpus; dentition that includes roots of c and p1; p2 that preserves the posterior root and part of the crown; p3, p4, and m2 are complete (Fig. 2.5).

Geographic occurrence. In SA to date, the gray fox has been discovered only in the Mene de Inciarte tar pit. Most *Urocyon cinereoargenteus* fossil material comes from the southern and eastern regions of the United States. Currently, this species is distributed from the eastern border between Canada and the United States to Venezuela and Colombia (Fritzell & Haroldson, 1982).

Stratigraphic occurrence. Late Pleistocene to Present.

Description and comparison. IVICP 3531 is an M1 of a small

canid (Tabs. S1 and S2) with the paracone slightly larger than the metacone. The parastyle is small. The paraconule is present but poorly differentiated from the cristid that connects the protocone to the parastyle, whereas this cusp is well-differentiated in the genus *Lycalopex*. A continuous ingulum covers the anteromedial border of the molar

(also called the mesial cingulum), as in modern *Urocyon cinereoargenteus*. By comparison, in *Atelocynus microtis*, *Cerdocyon thous*, and *Lycalopex* spp. (but not in *Lycalopex griseus*), there is a slight evagination at the level of the protocone. The medial cingulum is thick at the posterolingual corner, and the hypocone is not present.

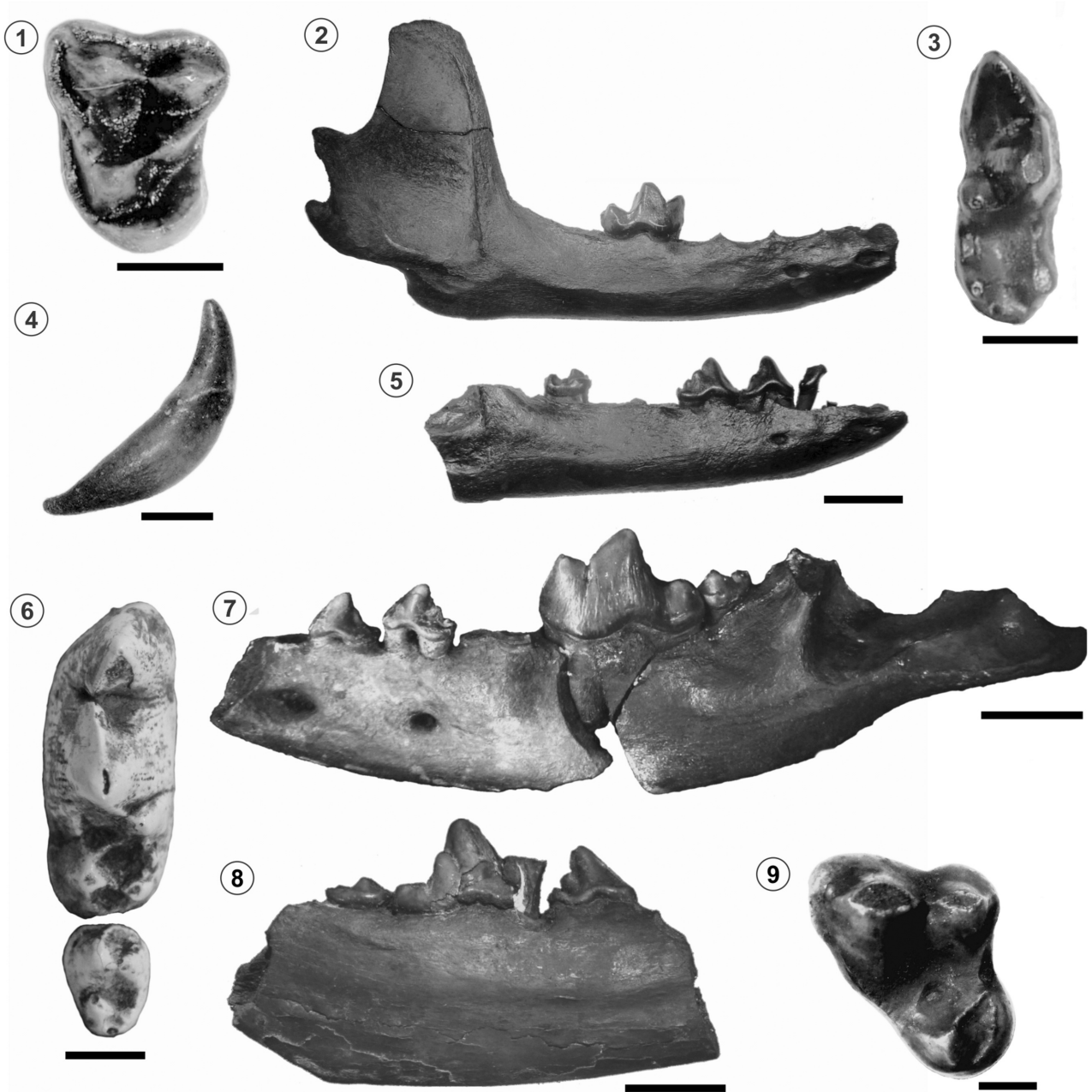


Figure 2. 1–5, *Urocyon cinereoargenteus* from El Mene de Inciarte; 1, IVICP 3531, left M1 in occlusal view; 2, IVICP 3528, right hemimandible in labial view; 3, IVICP 3528, occlusal view of the m1; 4, IVICP 3530, left lower canine in lateral view; 5, IVICP 3529, right hemimandible in labial view. 6–8, *Aenocyon dirus* from El Breal de Orocuál (ORS20); 6, ORS20 418, molars in occlusal view; 7, ORS20 418, left hemimandible in labial view; 8, ORS20 420, left hemimandible in lingual view. 9, *Protocyon* aff. *P. troglodytes* from El Mene de Inciarte, IVICP 3521, left M1 in occlusal view. Scale bars equal 5 mm (1, 4, 9), 10 mm (2, 3, 5, 7), 20 mm (6, 8).

The lower canine has a tenuous vertical crest on the lingual side that ends in a cingulum that runs along the base of the crown. The premolars are not sharp, as seen in some specimens of *Urocyon littoralis*. The p2 (the posterior half preserved) is present only in IVICP 3529, and no accessory cusp is observed. In IVICP 3529, the p4 has two posterior accessory cusps and a cingulum (see Fig. 2.5). The presence of a second posterior accessory cusp on p4 is not frequent in *Urocyon* nor in many fox species. However, Szuma (2002) recognized the presence of multiple accessory cusps on the lower premolars in the Eurasian *Vulpes vulpes* as intraspecific variability, which leads us to believe that this feature is not a novelty in our specimen. The m1 has a well-developed metaconid. The entoconid is a conspicuous cusp, but it is less developed than the hypoconid, and connects to it by a transversal crest. A protostylid is present but barely visible. The hypoconulid projects posteriorly as a shelf, as in *Urocyon* (not seen in *Urocyon webbi*), *Cerdocyon*, and *Lycalopex*.

Other small canids, such as *A. microtis* and most of North American foxes (excluding *Urocyon*), have a small hypoconulid, or it is not present. The m2 has a well-defined mesiolabial cingulum that surrounds the protoconid to the anterior region of the molar. This morphology has been observed in living *U. cinereoargenteus*, while in *C. thous*, the cingulum is more restricted to the labial side. The m2 is elongated; the metaconid is reduced and located posterior to the protoconid. In *Urocyon minicephalus*, the m2 is less elongated, and the metaconid is directly opposite to the protoconid (Tedford *et al.*, 2009).

The hemimandibles have a straight corpus. This morphology also is observed in *Atelocynus*, *Cerdocyon*, *Lycalopex*, and *Urocyon* (*U. cinereoargenteus*, *U. minicephalus*, and *U. littoralis*), but it differs from *Vulpes* and the extinct *Metalopex* with a semi-curved corpus. The subangular lobe is well-marked and presents a caudal expansion or spine (only visible in IVICP 3528) that is typical of *U. cinereoargenteus*, *U. minicephalus* (Ruiz-Ramoni *et al.*, 2020), and *U. littoralis*. The angular process is hook-like, as in the members of the tribe Vulpini, while in South American foxes, this structure is more rounded. In *Lycalopex gymnocercus*, the angular process also is hook-like but very pronounced, differing from IVICP 3528. On the medial side of the angular process, the insertion of the lower branch of the pterygoid internus

muscle is more expanded than in other *U. cinereoargenteus*, but not as large as in *C. thous*, and similar to the species of genus *Lycalopex*. This feature likely reflects intraspecific variability. The insertion of the lower branch of the pterygoid internus muscle is more developed than in *Lycalopex*, although it is shallow compared to other species. The masseter fossa is deep and extends beyond the alveolus of m3. The mandibular condyle is tilted slightly toward the lingual side with respect to the anteroposterior axis of the corpus. On IVICP 3528, the coronoid process is wider at the upper end than in other species of *Urocyon*, like living specimens of *U. cinereoargenteus* and *U. littoralis*. This feature could be affected by intraspecific variability and should be evaluated with a larger sample. A diastema between premolars can be seen, although the size of each is difficult to determine because of the absence of some dental pieces.

In summary, the morphology of the m2, the subangular lobe, and the m1 hypoconulid of IVICP 3528, allow us to recognize this specimen as the gray fox, *U. cinereoargenteus*. IVICP 3529 has no characteristics against this determination, except for the p4, but as discussed above, multiple cusps are possible intraspecific expressions.

Previous reports in Venezuela. Prevosti and Rincón (2007) reported fossil material from the Inciarte deposit that they classified as *Urocyon* cf. *U. cinereoargenteus*. Their report consisted of the left temporal with the tympanic bulla, the petrosal, the mastoid process (MBLUZP 2235), a fragment of the right parietal (MBLUZP 2824), and an incomplete occipital (MBLUZP 2903).

Tribe CANINI Fischer de Waldheim, 1817
Subtribe CANINA Fischer de Waldheim, 1817

Genus *Aenocyon* Merriam, 1918

Type species. *Canis dirus* (Leidy, 1858). Pleistocene of Evansville, Indiana, United States.

Aenocyon dirus (Leidy, 1858)

Figure 2.6–2.8

1854 *Canis primaevus* Leidy, p. 200.

1858 *Canis dirus* Leidy, p. 21.

1869 *Canis indianensis* Leidy, p. 368.

1876 *Canis mississippiensis* Allen, p. 49.

- 1916 *Canis ayersi* Sellards, p. 121–140.
 1918 *Aenocyon dirus* Merriam, p. 531–533.
 1959 *Canis (Aenocyon) dirus* Churcher, p. 564.
 1960 *Aenocyon* sp. nov.? Rojo y Gómez, p. 156.
 1979 *Canis armbrusteri* Nowak, p. 93.
 2021 *Aenocyon dirus* Perri et al., p. 1.

List of synonymies modified from Bocquentin (1979) and Tedford *et al.* (2009).

Referred material. El Breal de Orocuál ORS20. ORS20 418, partial left hemimandible with the alveolus of p1, complete p2–p3, p4 (roots only), complete m1–m2, and the alveolus of m3 (Fig. 2.6–2.7). ORS20 419, incomplete right hemimandible with p2 (posterior root only) and complete p3–m2. ORS20 420, fragment of left hemimandible with p4–m2 (Fig. 2.8). ORS20 6455, left m2. ORS20 418 and 419 are associated and probably belong to the same individual (see below).

Geographic occurrence. Fossil distribution extends from Alberta, Canada, to Tarija, Bolivia (Dundas, 1999), possibly extending to the Argentine Pampas (see below). In Venezuela, it has been discovered in Muaco, Inciarte, and ORS20.

Stratigraphic occurrence. Middle(?) Pleistocene to Holocene.

Description and comparison. ORS20 418, 419, and 420 have a premolar pattern commonly seen in canids, especially large canids. The p1 has one root (seen in the alveolus of ORS20 418), while other premolars have two roots. The p2, p3, and p4 have a similar morphology, with a principal cusp and a ridge that runs along with the tooth in a mesiodistal direction. The p2 does not have an accessory cusp, but the p3 and p4 have it. It is more marked on p4 as well as the posterior cingulum. Tedford *et al.* (2009) describe the p3 with an accessory cusp that is characteristic of the dire wolf and allows differentiation from its relative species, "*Canis*" *armbrusteri*, although they pointed out some exceptions.

In the Orocuál material, some variability can be seen. ORS20 419 has a p3 with two small posterior cusps. Nowak (1979) also suggested that p3 could have a second and third cusp (*i.e.*, accessory cusp) in some individuals of *Aenocyon dirus*. The m1 has a robust paraconid and protoconid. The metaconid is present, but the mesoconid is absent, unlike "*C.*" *armbrusteri*. The hypoconid is the most developed cusp of the talonid, and it joins to the basal section of the metaconid by a crest. Berta (1988) described a transverse crest as a diagnostic feature of *A. dirus*, but the

feature also is present in "*C.*" *armbrusteri* and some Eurasian species of *Canis*, including *C. lupus*. The entoconid is present but lower and less developed than the hypoconid, a feature that is characteristic of *A. dirus* and "*C.*" *armbrusteri* (Tedford *et al.*, 2009). In ORS20 418, at least three small cusps are observed between the entoconid and metaconid; Berta (1988) mentioned them for *A. dirus*. The hypoconulid is present as a shallow ridge that forms a back shelf on the molar.

The m2 paracone is absent, but there is a crest from the protoconid to the anterior region of the molar. The anterolabial cingulum is reduced in Orocuál specimens. We made the same observation in members of *A. dirus* from NA and SA. However, the loss of this cingulum has been described for North American specimens of *A. dirus* (Tedford *et al.*, 2009) and is used to differentiate it from "*C.*" *armbrusteri*. The entoconid is absent.

The m3 was not preserved in any recovered specimen from Orocuál, but only one alveolus is observed for this molar. ORS20 418 is the only specimen that preserves the mandibular corpus almost completely. It has a slight curvature in the ventral mandible region and the masseter fossa behind the m3 alveolus. In this specimen, the angular process is robust and projects to the posterior. There is a very deep insertion for the superficial branch of the pterygoid internus muscle, but it is less developed than the inferior branch of this muscle.

In summary, dental characters, such as the p3 with a posterior accessory cusp, m1 and m2 entoconid absent, and the m2 anterolabial cingulum reduced, indicate that ORS20 418, 419, and 420 have the same morphology of North and South American specimens of *A. dirus*. In addition, the most distinctive feature of *A. dirus* is its large size with respect to other species of contemporary canids (Nowak, 1979; Anyonge & Roman, 2006; Tedford *et al.*, 2009; Ruiz-Ramoni & Montellano-Ballesteros, 2019). This body conformation also can be seen in El Breal de Orocuál specimens (Fig. 3 and Tab. S2). The body mass estimates for ORS20 418 and 419 were 38.1 and 37.3 kg, respectively; these results support being specimens from the same individual. These estimates fall outside the range of gray wolves and only match with the size of bigger *A. dirus* individuals. The body mass of ORS20 420 was 33.3 kg, corresponding to a large individual that was close to modern *C. lupus*.

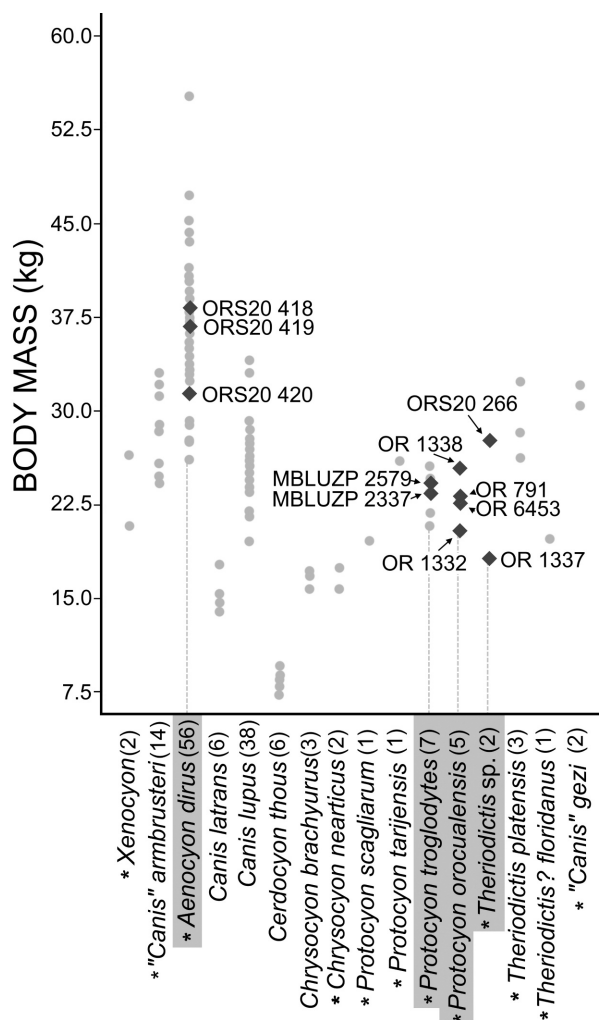


Figure 3. Body mass (in kg) of fossil (*) and living canids from North and South America, highlighting the specimens from Venezuela (rhombi). Each point corresponds to an individual analyzed (numbers in parentheses).

Previous reports in Venezuela. During the International Geological Congress in Copenhagen (Denmark) in 1960, the Spanish paleontologist José Royo y Gómez mentioned the first remains of *A. dirus* discovered in Venezuela. He showed a partial list of vertebrates found along with lithic remains of humans from the late Pleistocene of Muaco, Falcón State (Fig. 1). In this list, he mentioned a complete skull (VF ?; Fig. 4.1) of a canid with the size of a wolf, and classified as "*Aenocyon* sp. nov.?" (Royo y Gómez, 1960). Also, at Muaco a fragment of a right maxilla (VF 988; Fig. 4.2), a right metatarsal (VF 349), and an upper right canine (VF 407) were catalogued, but not published, as "*A. dirus*?" by C.S.C. (as it is written on the collection label of the UCV). The

initials probably refer to the Canadian paleontologist C.S. Churcher. Later, Bocquentin (1979), in his Ph.D. thesis, assigned VF ?, 988, and 407 to *Canis dirus*, leaving aside VF 349. This metatarsal (VF 349) is very robust, with a curved diaphysis that could have come from a large felid. Likewise, the specimen VF 407 has a morphology similar to the short-face bear; it has a low crown and a groove that is not typical of *A. dirus*. In addition, Prevosti and Rincón (2007) identified dire wolf materials from Inciarte based on a right p4 (MBLUZP 2388), a left I3 (MBLUZP 1941), and a fragment of right mandible (MBLUZP 1940).

Comments about the dire wolf. In the late Pleistocene–Holocene of Luján, Argentina, Ameghino (1902) reported cranial material (MACN Pv 500) as *Dinocynops nehiringi*, reclassified later by Kraglievich (1928) as *Canis nehiringi*. Some authors (Berta, 1988; Prevosti, 2006, 2010; Prevosti & Forasiepi, 2018) considered that MACN Pv 500 could be a dire wolf. Based on phylogenetic analyses, Prevosti (2010: 472) wrote "I considered *C. nehiringi* and *C. dirus* as synonyms". We agree with this hypothesis, but no official conclusion has been taken.

Most recently, a specimen (IVPP V25381) assigned to *Aenocyon dirus* was published from China (Lu *et al.*, 2020), but in our opinion, the morphology and size described by the authors are not conclusive for the taxonomic determination.

On the other hand, the resurrection of the genus *Aenocyon* for the dire wolf was based on genomic analyses (Perri *et al.*, 2021). In other phylogenetic proposals (Berta, 1988; Tedford *et al.*, 2009; Zrzavý *et al.*, 2018), *A. dirus* has a sister species, *Canis armbusteri*, although this is not a firm conclusion (see Prevosti, 2010). In light of new evidence, the *armbusteri* wolf should be re-evaluated at the genus level. For this reason, in the present contribution, we question the assignment of *armbusteri* to *Canis*.

Subtribe CERDOCYONINA Tedford,
Wang & Taylor, 2009

Genus *Protocyon* Giebel, 1855

Type species. *Canis spelaeus* (invalidated), *Canis troglodytes* (Lund, 1838). Middle Pleistocene to Holocene of Lagoa Santa, Brazil (Cartelle & Langguth, 1999).

Protocyon aff. *P. troglodytes* (Lund, 1838)

Figure 2.9

1837 *Canis spelaeus* Lund, p. 324.

1840 *Canis troglodytes* Lund, p. 223.

1843 *Canis lycodes* Lund, p. 81.

1843 *Palaeocyon validus* Lund.

1843 *Palaeocyon troglodytes* Lund, p. 50–54.

1880 *Canis spelaea* Gervais & Ameghino, p. 34.

1882 *Canis musculosus* Ameghino, p. 38.

List of synonymies taken from Berta (1988), Cartelle and Langguth (1999), and Prevosti and Rincón (2007).

Referred material. El Mene de Inciarte. IVICP 3521, left M1 (Fig. 2.9).

Geographic occurrence. Mexico, Argentina, Uruguay, Bolivia,



Figure 4. *Aenocyon dirus* from Muaco, Falcón State. 1, VF ?, skull in dorsal and ventral views; 2, VF 988, right maxillary fragment in labial view. Scale bar equal 20 mm.

Brazil, and Ecuador (Prevosti & Forasiepi, 2018; Schubert *et al.*, 2019). In Venezuela, it has been found at El Mene de Inciarte.

Stratigraphic occurrence. Middle to late Pleistocene.

Description. IVICP 3521 is an M1 of a large canid (see Tab. S1), with a morphology similar to MBLUZP 4380 that was identified previously in Inciarte by Prevosti and Rincón (2007) as *Protocyon* sp. The paracone is conical and more developed than the metacone. The parastyle is present. There is no paraconule and metaconule, while in *Chrysocyon*, these structures are well developed. The labial cingulum is narrow, as in *Theriodictis*, *Protocyon*, and *Aenocyon dirus*. The protocone is present and well-developed. A hypocone is absent, and in its place is the lingual cingulum, while in *A. dirus*, this structure is separated from the cingulum. This cingulum extends mesially and embraces the protocone.

Previous reports in Venezuela. Prevosti and Rincón (2007) identified *Protocyon troglodytes* from El Mene de Inciarte, from two fragments of right hemimandible with m1 (MBLUZP 2337 and 2579) and isolated premolars (MBLUZP 2221, 2393, 2541, 2626, 3953, 4351, 4498, 4727). These authors also reported dental (MBLUZP 1763, 2389, 2462, 2556, 2652, 2840, 2846, 2872, 2957, 3042, 3143, 3222, 3335, 3599, 3636, 3652, 3684, 3881, 3896, 3979, 4008, 4116, 4126, 4163, 4169, 4242, 4319, 4380, 4499, 4603, 4613, 4624, 4726, 4777, 4923) and postcranial material (MBLUZP 3711, 4263, 3243, 4283, 2440, 2867, 2915, 1976, 4700) of *Protocyon* sp. from the same locality.

Other mentions of *Protocyon* in Venezuela have been made by Rincón *et al.* (2009), who assigned cf. *Protocyon* to cranial, dental (OR 242, 713, 789, 791, 1332, 1336, 1337, 1338), and postcranial (OR 261) remains of a canid from the ORS16 deposit. This material is re-evaluated in the following sections. Solórzano *et al.* (2015) reported a right p2 (ORS20 076, length 12.4 mm and width 5.1 mm) and assigned it to cf. *Protocyon*. We do not discard the possibility that *Protocyon* existed in the assemblage of ORS20, but ORS20 076 must be seen in the light of evidence that favors the presence of *A. dirus* (see the previous section) or *Theriodictis* sp. (see section below) in the locality.

***Protocyon orocualensis* sp. nov.**

Figure 5.1–5.6

LSID urn:lsid:zoobank.org:act:6D6322D9-25D2-4FBD-9594-AA251F2DB076

2007 *Canis* sp. Rincón *et al.*

2009 cf. *Protocyon* Rincón *et al.*, p. 604–605.

2016 *Canis* sp. nov. Ruiz-Ramoni, p. 61.

Derivation of name. In honor of its discovery in the Orocuál field, at the Monagas State, Venezuela.

Holotype. El Breal de Orocuál ORS16. OR 1332, right and left hemimandibles with multiple fractures. The right one is complete and presents all lower teeth except for the m3 (Fig. 5.4–5.5 upper); the left one has no posterior region (Fig. 5.5 lower).

Referred specimens. El Breal de Orocuál ORS16. OR 6240, right i1. OR 3574, left i1. OR 6241, right i3. OR 6242, 2476, 6248 (incomplete), right canines. OR 3562, 2467 (incomplete), left canines. OR 1978, 2100, right p1s. OR 790 (incomplete), 1597, 2471, 6245, left p4s. OR 791, right m1. OR 1338, 6354 (without paraconid), 6453, left m1s. OR 6356, left m1 (talonid only). OR 722, fragment of right hemimandible with the roots of m1 and m2 inside the alveolus. OR 1336, fragment of left hemimandible with m2 and the alveolus of m3. OR 949 (without the talonid), 1218, left m2s. OR 2470, 3084, right m2s. OR 5424, right m3. OR 6251, left m3.

Diagnosis. Large-sized canid (Fig. 3 and Tab. S2); premolars with acute cusps; m1 entoconid and hypoconulid are significantly reduced (nearly absent), as in *Protocyon*. The m1 metaconid is present, unlike *P. troglodytes*, *P. scagliorum*, and *P. tarijensis*, and the hemimandible is more gracile than in those canids. The specimen differs from *Canis-Aenocyon* in the absence of a transverse crest in the m1 talonid that connects the metaconid to the hypoconid. The specimen differs from *Chrysocyon* and *Theriodictis* in less development of the m1 entoconid and hypoconulid.

Geographic occurrence. El Breal de Orocuál (ORS16), Venezuela.

Stratigraphic occurrence. Late Pliocene–early Pleistocene.

Description and comparison. The remains described here correspond to a large-sized canid, although smaller than the dire wolf (see Tab. S2; Fig. 3). The lower incisors have a lateral accessory cusp. The i3 is bigger than i2 and i1 (Tab. S2). The lower canine is curved slightly. As in the upper premolars, the lower ones have acute cusps. The p1 has only one root. The p2 and p3 are similar in shape, with no posterior accessory cusp. This feature is different in *Protocyon troglodytes* (LAR 46 and MLP 89-XI-20-1) because the p3 of the latter has a posterior cusp. The p4 is slightly

larger than p3, and has a posterior cusp. On the m1, the entoconid is reduced, and instead, a cingulum is present, consistent with *Protocyon* morphology. However, unlike the

typical *Protocyon* morphology and (usually) *Theriodictis*, the metaconid is present (see the next section on the comments about specimen MG 634/14). The hypoconulid is absent.

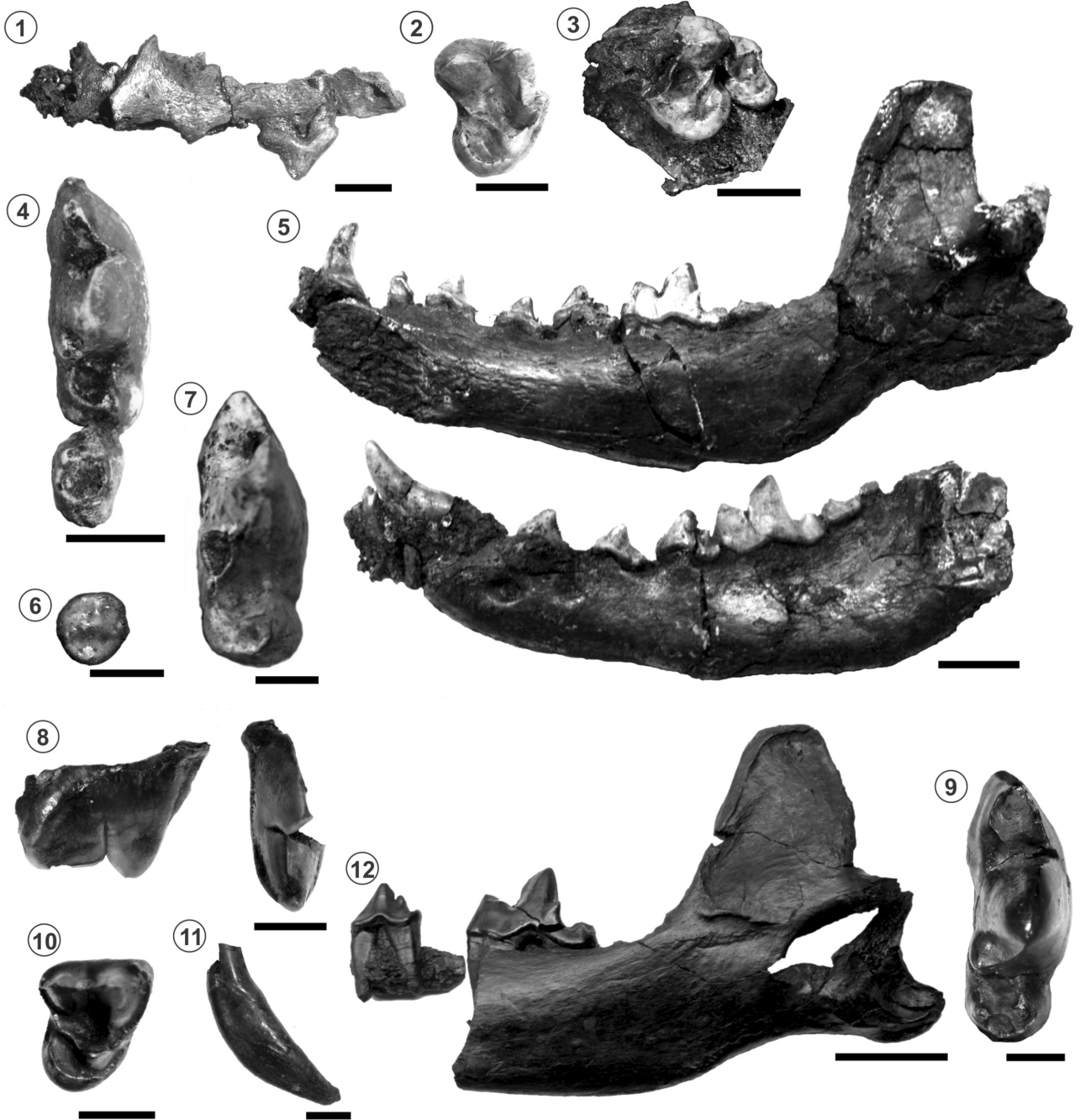


Figure 5. 1–6, *Protocyon orocualensis* sp. nov. from El Breal de Orocuál (ORS16); 1, OR 713, right maxilla with P2 in labial view; 2, OR 262, partial right M1 in occlusal view; 3, OR 6353, maxilla with partial M1 and M2 in occlusal view; 4, OR 1332 (holotype), m1–2 of the right hemimandible in occlusal view; 5, OR 1332 (holotype), right (upper) and left (lower) hemimandibles in lingual and buccal view, respectively; 6, OR 1332 (holotype), left m3 in occlusal view. 1, 2, and 3 is material conferred to *P. orocualensis*. 7, *Theriodictis* sp. from El Breal de Orocuál (ORS20), OR 1337, right m1 in occlusal view. 8–12, *Theriodictis* sp. from El Breal de Orocuál (ORS20 266); 8, left P4 in buccal view; 9,, m1 in occlusal view; 10, right M1 in occlusal view; 11, lower canine in medial view; 12, right hemimandible in lingual view. Scale bars equal 10 mm (1, 2, 3, 4, 7, 8, 9, 10, 11), 20 mm (5, 12), and 2.5 mm (6).

The m2 has a smaller mesiolabial cingulum. The metaconid is absent. The entoconid is reduced to a cingulum, unlike *P. tarijensis*. The m3 is present and has a single cusp.

The mandibular corpus is less robust than in *Theriodictis* and some species of *Protocyon*. The sub-angular lobe is marked. The mandibular condyle is located above the top of m1, although the feature can be seen only in the right hemimandible of OR 1332, which is deformed. The morphology of the angular process it is not well-appreciated because of the degree of deformity, but it is robust and is not in the form of a hook.

In summary, the simplification of the m1 talonid (*i.e.*, strong reduction of the entoconid) is a common condition of large canids (Fig. 3) of the genus *Protocyon* (Berta, 1988). On the other hand, the presence of an m1 metaconid has not been seen in this genus. Since OR 791, 1332, 1338, and 6453 all have metaconids, the latter character does not suggest individual causal variability. In addition, it was found that there is no morphometric relationship between OR 1332 and other large canids of America (see Figs. S1 and S2).

Considering the above-presented evidence, we propose that this taxon belongs to a form different from the known species, *P. troglodytes*, *P. tarijensis*, and *P. scagliorum*, an observation that was considered previously by Rincón *et al.* (2009).

Previous studies. The first report of a fossil canid from ORS16 deposit was made by Rincón *et al.* (2007) during the 67th Annual Meeting of the Society of Vertebrate Paleontology in Texas, United States. The authors mentioned the presence of remains of the genus *Canis* in the faunal association. Later, Rincón *et al.* (2009) described the specimen, mentioning two hemimandibles (OR 1332, holotype described above), a fragment of right mandible (OR 1336), two right and a left m1 (OR 791, 1337, 1338), a right M1 (OR 242), a premolar (OR 789), a maxilla fragment (OR 713), and a metacarpal (OR 261). These authors argued that the morphology of the premolars (with acute cusps) corresponds to the genus *Protocyon*, and by considering the peculiar morphology of the m1, that it could be a new species. However, eventually, they assigned this material to *cf. Protocyon*. Later on, Ruiz-Ramoni (2016) considered the presence of the m1 metaconid to be inconsistent with the diagnosis of *Protocyon* made by Berta (1988), and returned

the specimen to the genus *Canis* as in Rincón *et al.* (2007).

In this report, we provide support for the hypothesis of relationships with *Protocyon*, given the similarities mentioned above and finding that the dental and mandibular morphometry of OR 1332 is different from that of other canids, evaluated using principal component analysis (see Figs. S1 and S2). We consider that the presence of the metaconid in the m1 is a primitive retained character of the *Protocyon* lineage.

Other material. The upper dentition is not included in the diagnosis because there is a probability that it corresponds to another canid. However, see below for the differentiation of these structures with respect to other taxa.

At ORS16, there are other elements of the upper dentition of a canid that are not described above (Fig. 2.1–2.3), including OR 2969 (right I1), OR 905, 2099 (left I2), OR 6243 (left I3), OR 754, 2472, 260, 2098 (left C), OR 262 (right M1), OR 6446 (the paracone of a left M1), OR 6355 (the talonid of an M1), OR 3720 (right P1), OR 713 (a fragment of the right maxilla with the P2 and the alveoli of the P4, P3, and P1), and OR 6353 (a piece of the left maxilla with the M1 and M2).

The upper incisors (I1 and I2) have two accessory cusps on each side of the main cusp. The I3 is caniniform and does not have an accessory cusp, as seen in *Protocyon troglodytes*. The upper canine has a ridge that runs sagittally along with the crown. The premolars have acute cusps, as seen in the South American *Theriodictis* or *Protocyon*. The P1 has a cusp and a single root, while the P2 is wider and double-rooted. On the M1, the labial cingulum is narrow. The paraconule is present, while it is absent in *Theriodictis*, *Protocyon*, and some *Canis-Aenocyon* members. The metaconule is barely visible, differentiating this taxon from "*Canis*" *gezi*. The mesial cingulum is not developed. The hypocone and the lingual cingulum are not differentiated. This cingulum is short in OR 262 and 6353, but smaller in OR 6357. The M2 is present only in OR 6353. This molar has the paracone slightly more robust than the metacone, but both are the same height, as is *Protocyon*. There is no labial cingulum, as "*C.*" *gezi*. The protocone connects only with the paracone by a crest.

We are not certain that these remains correspond to the same canid of OR 1332 (holotype of *P. orocualensis*). The presence in ORS16 of an m1 with the morphology of

Theriodictis sp. (see next section for the description of OR 1337) leaves the possibility that the material belongs to this latter species.

Finally, Ruiz-Ramoni (2016) also reported some premolars and an incisor (OR 324, 728, 759, 789, 2473, 2474, 3588, 5559, 5560, 5570, 6244, 6247, and OR 2475), a fragment of left astragalus (OR 700), some pieces of metapodials (OR 660, 662, 699, 4014, 4953, 5211, 5942), and some phalanges (OR 569, 766, 3711, 4950), that are not considered in the description of the species because, in most cases, their anatomical identification is in doubt and their affinity to the described taxon is not certain.

Genus *Theriodictis* Mercerat, 1891

Type species. *Canis (Theriodictis) platensis* Mercerat, 1891. Late Pleistocene of Gral. Pueyrredón, Mar del Plata, Argentina.

Theriodictis sp. indet.

Figure 5.7–5.12

2016 *Canis* sp. nov. Ruiz-Ramoni, p. 61.

Referred material. El Breal de Orocuál ORS16. OR 1337, a right m1 with the metaconid and the roots fractured (Fig. 5.7). El Breal de Orocuál ORS20. ORS20 266, associated partial left P4 (Fig. 5.8), right p4 and m1 (Fig. 5.9), right M1 (Fig. 5.10), fragment of the left lower canine (Fig. 5.11) and posterior fragment of a right hemimandible (Fig. 5.12).

Geographic occurrence. The genus *Theriodictis* has been reported for Argentina's Pampean Region (Berta, 1988; Prevosti & Forasiepi, 2018). Tedford *et al.* (2009) indicated the presence of a large canid that they classify as *Theriodictis? floridanus* from Florida, in the United States. In Venezuela, remains assigned to *Theriodictis* have been found in El Breal de Orocuál region at the ORS20 deposits. We are uncertain about a possible morphological affinity with remains recovered at ORS16 (see below).

Stratigraphic occurrence. From ORS16? (late Pliocene–early Pleistocene) to ORS20 (late? Pleistocene).

Description and comparison. The M1 lacks the marked labial cingulum, as in other South American canids that include *Protocyon*, *Theriodictis*, *Dusicyon*, and "*Canis*" *gezi*. This structure allows us to differentiate ORS20 266 from *Aenocyon dirus*. The paracone is larger than the metacone.

The parastyle is present but not prominent. The protocone is conical and robust, and connects to the metaconule by a crest (postprotocrista). The metaconule is fused with the distal cingulum as in *Protocyon* and *Theriodictis*; in "*C.*" *gezi* this cusp is isolated. There is no separate hypocone from the lingual cingulum. This cingulum is not as well-developed as in *Protocyon*.

The P4 has a small protocone, a condition also described in *Protocyon*, *Theriodictis* (Berta, 1988), *A. dirus*, "*C.*" *armbrusteri*, and "*C.*" *gezi*. In this premolar, a lingual cingulum is visible, but it is discontinuous, more developed at the level of the metastyle. This morphology is common in other South American canids, except in *Chrysocyon brachyurus*.

The p4 has a posterior accessory cusp and a marked cingulum. The principal cusp of this premolar is low, as in *Theriodictis platensis* and *Protocyon troglodytes*. The m1 of ORS20 266 has some similar characteristics as remains that were assigned to *T. platensis*, MG 634/14 and MLP 10-51 from the province of Buenos Aires, Argentina, but also to that of *T.? floridanus*, UF 133922 from Florida, United States. Frequently, the material of *Theriodictis* lacks a metaconid, but MG 634/14 has this cusp slightly more developed than in other specimens assigned to *T. platensis* (Berta, 1988). An even more pronounced metaconid can be seen in UF 133922. In this sense, ORS20 266 looks more like *T.? floridanus*. The talonid is similar to *T. platensis* and *T.? floridanus*, where the entoconid is very reduced, although not as much as in *P. troglodytes*. The absence of a transverse crest between the hypoconid and entoconid indicates that this taxon is different from *Aenocyon-Canis*. The morphology of ORS20 266 is repeated in OR 1337 (see Fig. 5.7 and 5.9), which is an m1 from ORS16. This tooth does not have as reduced entoconid as in *Protocyon*; also, it has a projected hypoconulid that is not seen in any other m1 from ORS16.

ORS20 266 preserves the posterior half of the mandibular corpus, where it is possible to see a marked subangular lobe, a coronoid process with an insertion of the masseter muscle that starts behind the m3, and a robust angular process. The angular process has a depression for the insertion of the superficial branch of the deep pterygoid internus muscle, which is broader than the inferior branch, as in *T. platensis*. On the other hand, ORS20 266 differs from UF 19324 because, in this latter specimen, the area of

insertion of the superficial branch is smaller, while that of the inferior branch is slightly larger. However, specimens of *T. platensis* show variability in the area of these muscular insertions.

It is important to note that some similarities have been observed between ORS 266, *Xenocyon texanus*, and *Xenocyon lycaonoides* from the middle Pleistocene of NA. As in *Xenocyon*, the M1 has a weakly developed labial cingulum and the metaconule is absent. The development of the m1 metaconid is much smaller, the entoconid is smaller, and the hypoconulid is present and placed labially on the talonid (Tedford et al., 2009). The size of *Xenocyon* has a range that is not far from ORS20 266 (Fig. 3). The only obvious difference of ORS20 266 from *X. texanus* and *X. lycaonoides* is the width of the p4; in these *Xenocyon* the p4 is more robust. However, the material is not complete enough to make a more detailed comparison.

Remarks. ORS20 266 was reviewed originally by Ruiz-Ramoni (2016), who assigned it to genus *Canis*, pointing out its resemblance to "*Canis gezi*", based mainly on the absence of a labial cingulum in the M1 and a metaconid on the m1. However, in this work, we recognized close affinity with the genus *Theriodictis*. This assignment is supported morphometrically in Figure S2. On the other hand, OR 1337 was reported by Rincón et al. (2009), who classified it as cf. *Protocyon*. Later, in Ruiz-Ramoni (2016), this molar was included in *Canis* (here named *P. orocualensis*) along with other material of ORS16. Based on our new taxonomic determination, the same species of canids inhabited the Orocuai region during the time of the depositions of ORS16 until ORS20.

Caninae indet.
Figure 6.1–6.5

Referred material. El Mene de Inciarte. IVICP 3533, right dP3 (Fig. 6.1). IVICP 3534, right dP4 (Fig. 6.2). IVICP 3587, right dp4 (Fig. 6.3). IVICP 3540, left m2 (Fig. 6.4). Zanja de Lira. FLSCNP 459 right dP3 (Fig. 6.5).

Remarks. IVICP 3533 is a dP3, with a large paracone and a broad metastyle that is lower than the paracone. The protocone is prominent and is at the paracone level. An ectostyle is present. This tooth initially was classified as *Mustela* in Ruiz-Ramoni (2016) because of its P4-like shape

and small size (length: 6.0 mm; width: 2.3 mm). However, here, it is recognized as a deciduous tooth of a small canid. A similar situation occurs with IVICP 3534 (length: 7.0 mm; width: 6.0 mm), which was classified initially as an M2 of a procyonid because the triangular shape and sharp cusps resembles *Nasua*. Here, we refer it to a dP4 of a small canid. Only *Urocyon cinereoargenteus* has been identified in Inciarte deposits (Prevosti & Rincón, 2007; Ruiz-Ramoni, 2016; this work), but neither IVICP 3533 nor 3534 were compared in-depth with young specimens. Thus, no further taxonomic conclusions are made.

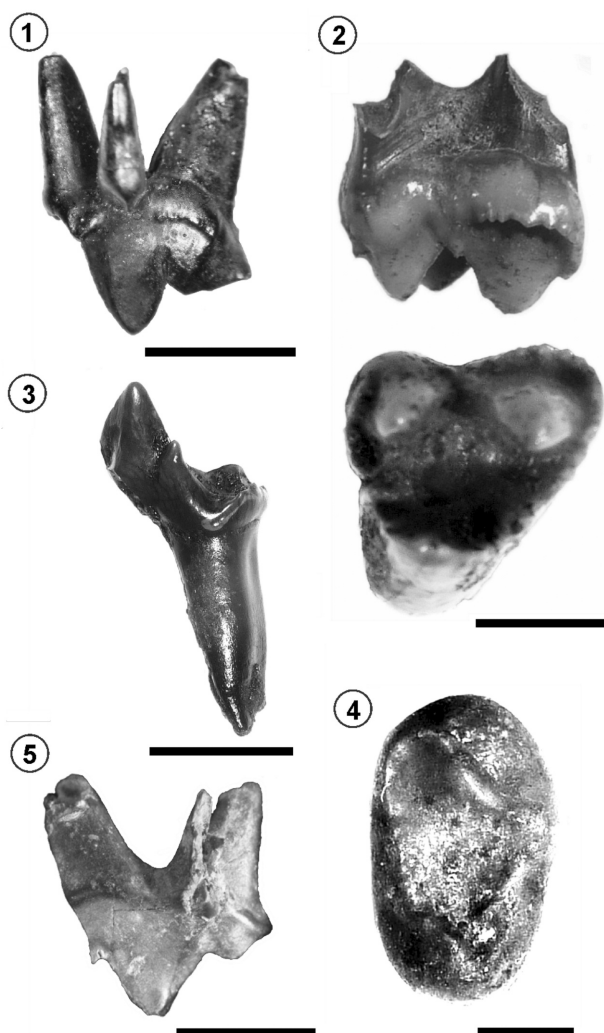


Figure 6. Indeterminate fossils of Canidae from Venezuela. 1–4, from El Mene de Inciarte; 1, IVICP 3533, right dP3 in lingual view; 2, IVICP 3534, right dP4 in lingual (upper) and occlusal (lower) view; 3, IVICP 3587, right dp4 in lingual view; 4, IVICP 3540, left m2 in occlusal. 5, From Zanja de Lira, FLSCNP 459, right dP3 in lingual view. Scale bars equal 5 mm.

A dp4 (IVICP 3587) of a medium-size or large canid also was found at Inciarte. This tooth has the same morphology as MBLUZP 4603 described by Prevosti and Rincón (2007), who classified it as *Protocyon* sp. The latter authors indicated that MBLUZP 4603 is similar to a dp4 of *P. troglodytes* (UZML 6581) housed in the Peter W. Lund Collection, Universitets Zoologiske Museum in Copenhagen (Denmark). However, they indicated also that the metaconid and the lingual cingulum of the talonid in UZML 6581 are further reduced in size. In IVICP 3587, and even in MBLUZP 4603, the metaconid is not smaller. Considering that there are two large canids at the Mene de Inciarte deposit, *Aenocyon dirus* and *P. troglodytes* (Prevosti & Rincón, 2007), no taxonomic conclusions are made about this specimen in this work.

A typical m2 (IVICP 3540) of a possible large canid (length: 7.6 mm; width: 5.0 mm) was found in Inciarte (Ruiz-Ramoni, 2016). It is elliptical in occlusal view, with low cusps. Its morphology does not match with any described canid of the genera *Canis*, *Protocyon*, *Theriodictis*, or *Chrysocyon*.

Finally, a dP3 (FLSCNP 459) was found in the sediments of the Zanja de Lira locality, in Cojedes State. It is slightly longer than IVICP 3533, has a smaller metastyle, and the protocone is located behind the paracone.

DISCUSSION

The diversity of extant canids in Venezuela is quite different from recognized ancient canid taxa, both in species composition and in paleobiological characteristics. Most of the fossilized taxa found in the region are large and hypercarnivorous: *Aenocyon dirus*, *Protocyon troglodytes*, *P. orocualensis*, and *Theriodictis* sp. The gray fox, *Urocyon cinereoargenteus*, is the only small canid that has been identified in the fossil record of the region. However, it is also necessary to consider FLSCNP 459 that belongs to a small canid from Zanja de Lira, and the record of the fox-like *Dusicyon* from the Pleistocene of Boyacá, Colombia (Villarroel *et al.*, 1996).

In this work, we named the new large canid *Protocyon orocualensis* from an age close to the early Pleistocene, based on biochrons of the mammalian association. This species was recognized after our re-evaluation of fossil material from ORS16, discussed previously in Rincón *et al.* (2007), Rincón *et al.* (2009), and Ruiz-Ramoni (2016), and at that time related to *Protocyon* or *Canis*. Based on the new

specimens with consistent morphology, we confirmed its relationship with *Protocyon*, but as a form not recognized previously. This genus is part of the native South American members of the Cerdocyonina clade that is related to *Speothos*, *Theriodictis*, and *Chrysocyon* (Berta, 1988; Prevosti, 2010). Cartelle and Langguth (1999) considered that the genus *Protocyon* should be within the tribe Speothonini; this taxonomic category is not used widely.

On the other hand, this is the first time that genus *Theriodictis* is mentioned for northern SA, thus extending its range from the Argentinian Patagonia to the North of Venezuela (excluding *T.? floridanus* from NA). However, the form discovered in ORS20 has features that likely fall between the South American *T. platensis* and the North American *T.? floridanus* (see "Description and comparison" for *Theriodictis* sp.) due to the presence of a metaconid in m1, being a variant structure in these canids. Genus *Theriodictis* has not been reported previously from the late Pleistocene (Berta, 1988; Prevosti, 2006) that is the age suggested for ORS20 (Solórzano *et al.*, 2015). The most recent records place it biochronologically in the Ensenadan (SALMA, 1.20–0.40 Ma) of the Pampea region in Argentina (Prevosti *et al.*, 2009). However, in ORS20, this canid coexisted with *A. dirus*. Chronologically, the dire wolf is registered from the late Irvingtonian (NALMA, 0.60–0.25 Ma) to Rancholabrean (NALMA, 0.25–0.012 Ma) for NA (Tedford *et al.*, 2009; Ruiz-Ramoni & Montellano-Ballesteros, 2019), and the Lujanian (SALMA, 0.13–0.007 Ma) for SA (Berta, 1988). This leaves two possible hypotheses: (1) this is the most recent record of *Theriodictis*, or (2) the age of ORS20 is closer to the middle Pleistocene, which would mean *A. dirus* in SA is older than has been thought previously. Some authors suggested the origin of the species was close to this age but in NA (Nowak, 1979; Berta, 1988).

Berta (1988) indicated a close phylogenetic relationship between the middle Pleistocene "*Canis*" *gezi* and the dire wolf. However, she also clarified that the archaeological record is too limited in SA to draw conclusions (Dundas, 1999). Later, Prevosti (2010) found no close phylogenetic relationship between the dire wolf and "*C.*" *gezi*. In contrast, in Prevosti's proposal, "*C.*" *gezi* is related more closely to the Cerdocyonina (*Chrysocyon*, *Speothos*, *Theriodictis*, and *Protocyon*) than to Canina, to which *A. dirus* belongs (Perri *et*

al., 2021). But, since there is no precise chronological constraint for ORS20, the two hypotheses mentioned above must be evaluated further to resolve the questions.

In any case, the new elements of *A. dirus* from ORS20 extend the range of this species to the eastern part of Venezuela. Previously, *A. dirus* was recognized from the late Pleistocene of Muaco and El Mene de Inciarte (Royo y Gómez, 1960; Prevosti & Rincón, 2007). Berta (1988) and Dundas (1999) mentioned that this canid used the Andean corridor to disperse throughout SA. However, the field of Orocuál is far from this corridor, which indicates that dire wolves were able to move through a wide variety of landscapes. This is consistent with its distribution in NA, without explicit latitudinal or altitudinal constraints (Dundas, 1999; Ruiz-Ramoni & Montellano-Ballesteros, 2019).

Another species that also had a wide range was *P. troglodytes*. The presence of *P. troglodytes* is not novel for the late Pleistocene of Venezuela (Prevosti & Rincón, 2007), but it is the northern-most record of this species on the continent. The presence of this species in northern SA is interesting in light of new evidence in NA. Schubert *et al.* (2019) described well-preserved remains of *P. troglodytes* from the late Pleistocene, together with a typical South American bear, *Arctotherium wingei*, in a cenote in Yucatan, Mexico. The presence of *Protocyon* in Mexico demonstrates an influx of species that inhabited SA in the last moments of the GABI, which indicates that the migratory processes during this biogeographic event were more complex than previously thought.

CONCLUSIONS

In this work, we report a richness of five species of canids from the past of Venezuela. We confirm the existence of the gray fox, *Urocyon cinereoargenteus*, in Venezuela since the late Pleistocene. Similarly, the presence of *Protocyon troglodytes* and *Aenocyon dirus* during this geologic time also is supported by new fossilized remains. *Aenocyon dirus* clearly ranged throughout the region, but its temporal presence is disputed. Genus *Theriodictis* is reported for the first time in the country, with the probability that this record is the most recent biochronologically. A new species of genus *Protocyon* is proposed, *P. orocuálensis*. Although we have discussed the lack of biochronological resolution for El Breal de Orocuál deposits, the new

observations indicate a complex evolution of canids in SA.

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SUPPLEMENTARY ONLINE INFORMATION

CANIDS (CANINAE) FROM THE PAST OF VENEZUELA CÁNIDOS (CANINAE) DEL PASADO DE VENEZUELA

Ruiz-Ramoni *et al.*

TABLE S1. Measurements (mm) of the upper dental material of the fossil canids reported from Venezuela. **Abbreviation:** L, length; W, wide.

	LI1	WI1	LI2	WI2	LI3	WI3	LC	WC	LP1	WP1	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2
<i>Urocyon cinereoargenteus</i>																				
IVICP 3531																	8.0	9.8		
<i>Protocyon</i> aff. <i>P. troglodytes</i>																				
IVICP 3521																	13.9	16.3		
cf. <i>Protocyon orocualensis</i> sp. nov.																				
OR 2969	5.0	4.0																		
OR 905			6.3	4.8																
OR 2099			7.4	5.0																
OR 6243					8.6	5.9														
OR 6249							11.7	12.4												
OR 2098							14.6	9.3												
OR 3720									5.6*	5.2										
OR 713											12.7	5.7	18.7*	7.2*						
OR 262																	14.5*	16.2		
OR 6353																	13.9*	16.9	7.0	10.7
<i>Theriodictis</i> sp.																				
ORS20 266															28.4*		15.3	17.2		

*Estimated value.

TABLE S2. Measurements (mm) of the lower dental material of the fossil canids reported from Venezuela. **Abbreviation:** L, length; W, wide; tri, trigonid; tal, talonid.

	LI1	WI1	LI2	WI2	LI3	WI3	Lc	Wc	Lp1	Wp1	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1tri	Wm1tal	Lm2	Wm2	Lm3	Wm3	
<i>Urocyon cinereoargenteus</i>																								
IVICP 3528																	10.8	4.1						
IVICP 3529													6.5	2.3	8.5	3.1			6.5	4.4				
IVICP 3530							5.2	3.3																
<i>Aenocyon dirus</i>																								
ORS20 418									6.4*	4.1*	14.5	7.7	15.3	7.7	15.0	8.2*	34.6	13.9	11.7					
ORS20 419											6.7	15.4	7.7	18.5	10.0	34.2	12.7	11.6						
ORS20 420														17.6	8.6	32.1*	11.6	11.4	12.2	9.1				
ORS20 6455																				10.3	7.5			
<i>Protocyon orocualensis</i> sp. nov.																								
OR 1332-right					5.5	5.4	13.0	9.3	5.4	4.3	11.6	5.4	11.8	5.4	15.0	6.8	24.5	8.9	8.3	9.5	7.0	5.0	4.7	
OR 1332-left	3.0	2.6	4.2	3.4	4.5	6.0	13.6	8.8			12.5	5.7	12.2	5.3	14.6	7.1	26.3	9.7	8.6	11.0	6.5	5.4*	4.0*	
OR 6240	5.1	3.4																						
OR 6241					6.4	3.7																		
OR 2476							12.8	8.2																
OR 6242							15.3	9.4																
OR 3562							15.3	9.3																
OR 2100									6.4	5.1														
OR 1978									6.4	5.2														
OR 790																7.4								
OR 1597															13.9	7.4								
OR-2471															17.0	7.9								
OR 6245															16.4	8.7								
OR 791																	27.1	11.1						
OR 1338																	27.7	11.5						
OR 6453																	26.1	10.1	9.1					
OR 772																					10.4*	4.7*		
OR 1336																					10.4	8.2	5.5*	5.5*
OR 1218																					9.7	7.4		
OR 2470																					10.3	7.7		
OR 3084																					10.8	8.1		
OR 5424																						5.9	5.3	
OR 6251																						5.3	4.8	
<i>Theriodictis</i> sp.																								
ORS20 266															15.8	7.2	28.1	10.4	8.9	11.8*	7.4*	4.5*	4.6*	
OR 1337																	23.0	11.5						

*Estimated value.

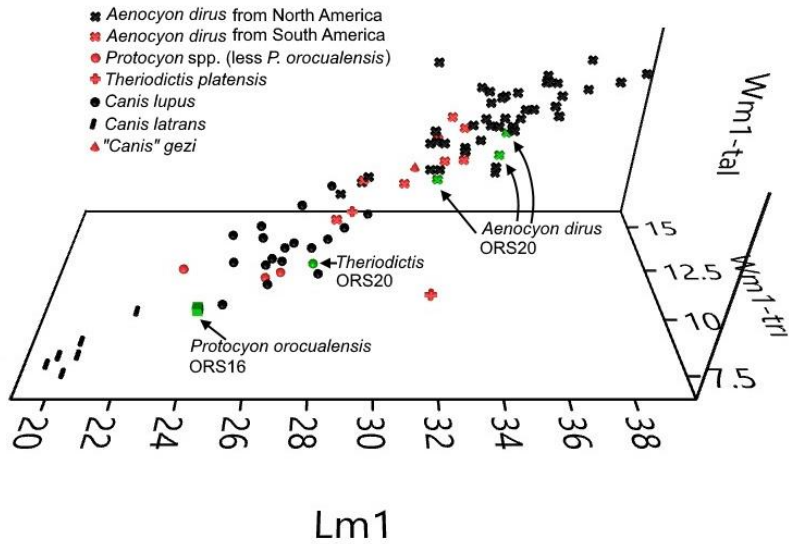


Figure S1. Scatter plot showing the size of the lower first molar (m1) of some living and fossil canids, highlighting the material coming from El Breal de Orocuál (green). Note how the *Aenocyon dirus* from ORS20 (X green) are grouped with the *A. dirus* of North (x black) and South America (x red). *Theriodictis* from ORS20 (dot green) is grouped with *Canis lupus* (black dot) and not far from *T. platensis* (+ red). Something similar occurs with *Protocyon orocualensis* (square green), which is grouped just below the other species of *Protocyon* (dot red). Graphic elaborated with the free software Past 4.06b (Hammer *et al.* 2001). Specimens used for this analysis are listed at the end of the document. Abbreviations: L, length, W, width, tri, trigonid, tal, talonid.

TABLE S3. Specimens used for comparison. * Data taken from Tedford *et al.* (2009), ** Prevosti & Rincón (2007), *** Berta (1988). **AMNH**, Department of Vertebrate Paleontology, American Museum of Natural History, New York, United States; **DP**, Departamento Paleontología del Instituto Nacional de Antropología e Historia, CDMX, México; **F:AM**, Frick Collection, American Museum of Natural History Field Museum of Natural History, Chicago, United States; **IBUNAM**, Colección Nacional de Mamíferos, Instituto de Biología, UNAM; **JWT**, Johnson Collection, West Texas University, United States; **LACM**, Natural History Museum Los Angeles County and La Brea Tar Pit and Museum, Los Angeles, United States; **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; **MBLUZ**, Museo de Biología de La Universidad del Zulia, Maracaibo, Venezuela; **MLP**, Museo de La Plata, La Plata, Argentina; **MMP**, Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Mar del Plata, Argentina; **MNHN**, Muséum National D’Histoire Naturelle, Paris, France; **MPS**, Museo Paleontológico “Fray Manuel de Torres”, San Pedro, Argentina; **ROM**, Royal Ontario Museum, Toronto, Canada; **UA**, University of Arizona, Tucson, United States; **UF**, University of Florida Collection, Florida, United States; **YPM**, Yale Peabody Museum of Natural History, Yale University, Connecticut, United States.

GEOGRAPHIC ORIGIN	# CATALOG	TAXA
Unknown	F:AM 25509*	<i>Aenocyon dirus</i>
Unknown	UNSM 2912*	<i>Aenocyon dirus</i>
Unknown	UNSM 26117*	<i>Aenocyon dirus</i>
Unknown	UCMP 140265*	<i>Aenocyon dirus</i>
Unknown	UCMP 156047*	<i>Aenocyon dirus</i>
Unknown	UF 9246*	<i>Aenocyon dirus</i>
Unknown	UF 2259*	<i>Aenocyon dirus</i>
El Cedral, Mexico	DP 2500	<i>Aenocyon dirus</i>
El Cedral, Mexico	DP 2499	<i>Aenocyon dirus</i>
El Cedral, Mexico	DP 2497	<i>Aenocyon dirus</i>
El Cedral, Mexico	DP 2504	<i>Aenocyon dirus</i>
El Cedral, Mexico	DP 3671	<i>Aenocyon dirus</i>
El Cedral, Mexico	DP 2498	<i>Aenocyon dirus</i>
El Cedral, Mexico	DP 3672	<i>Aenocyon dirus</i>
Gruta de Loltún, Mexico	DP 269	<i>Aenocyon dirus</i>
San Josecito Cave, Mexico	LAC 9229	<i>Aenocyon dirus</i>
San Josecito Cave, Mexico	LAC 9230	<i>Aenocyon dirus</i>
San Josecito Cave, Mexico	LAC 9231	<i>Aenocyon dirus</i>
San Josecito Cave, Mexico	LAC 9232	<i>Aenocyon dirus</i>
San Josecito Cave, Mexico	LAC 9245	<i>Aenocyon dirus</i>
Maricopa Brea, Arizona, USA	LAC 20864	<i>Aenocyon dirus</i>
Maricopa Brea, Arizona, USA	LAC 18155	<i>Aenocyon dirus</i>
McKittrick Tar Seeps (CIT 138), California, USA	LAC 104927	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-16), California, USA	AMNH 2301-R.14	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-16), California, USA	AMNH 2301-L.88	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-16), California, USA	AMNH 2301-L.179	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-16), California, USA	AMNH 2301-R.167	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-23), California, USA	LACMP23-1408	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-23), California, USA	LACMP23-1360	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-23), California, USA	LACMP23-7502	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-23), California, USA	LACMP23-17604	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2309-32b/2301-L.44	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2300-24/2301-R.12	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2301-R.4	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2300-28/2301-L.12	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2300-32/2301-R.16	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2300-310/2301-L.28	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2300-18/2301-R.8	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-61), California, USA	AMNH 2300-8/2301-R.3	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-67), California, USA	AMNH 2300-325/2301-R.43	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-67), California, USA	AMNH 2300-311/2301-L.29	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-77), California, USA	AMNH 2301-L.375	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-77), California, USA	AMNH 2301-L.377	<i>Aenocyon dirus</i>

Rancho La Brea (Pit-77), California, USA	AMNH 2301-L.462	<i>Aenocyon dirus</i>
Rancho La Brea (Pit-77), California, USA	AMNH 56079	<i>Aenocyon dirus</i>
Talara, Peru	ROM 2049	<i>Aenocyon dirus</i>
Talara, Peru	ROM 2665	<i>Aenocyon dirus</i>
Talara, Peru	ROM 2048	<i>Aenocyon dirus</i>
Talara, Peru	ROM 6405	<i>Aenocyon dirus</i>
Talara, Peru	ROM 6394 (Cast)	<i>Aenocyon dirus</i>
Talara, Peru	ROM 2047 (Cast)	<i>Aenocyon dirus</i>
Florida, USA	ROM 60214	<i>Aenocyon dirus</i>
Cumberland Cave, Tennessee, USA	NMNH 7662*	<i>Canis armbrusteri</i>
Cumberland Cave, Tennessee, USA	NMNH 11881*	<i>Canis armbrusteri</i>
Cumberland Cave, Tennessee, USA	NMNH 8168*	<i>Canis armbrusteri</i>
Cumberland Cave, Tennessee, USA	NMNH 8169*	<i>Canis armbrusteri</i>
Cumberland Cave, Tennessee, USA	NMNH 8172*	<i>Canis armbrusteri</i>
Coleman, Florida USA	UF 12121*	<i>Canis armbrusteri</i>
Coleman, Florida USA	UF 11518*	<i>Canis armbrusteri</i>
Coleman, Florida USA	UF 12121*	<i>Canis armbrusteri</i>
Coleman, Florida USA	UF 12121*	<i>Canis armbrusteri</i>
Coleman, Florida USA	UF 11520*	<i>Canis armbrusteri</i>
Haile 7A, Florida, USA	UF 11845*	<i>Canis armbrusteri</i>
Rock Creek, Texas, USA	JWT 678*	<i>Canis armbrusteri</i>
McLeod Limerock Mine, Florida, USA	F:AM 67286	<i>Canis armbrusteri</i>
McLeod Limerock Mine, Florida, USA	F:AM 67291*	<i>Canis armbrusteri</i>
Wilde, Argentina	MACN 5120	<i>Canis gezi</i>
Miramar, Argentina	MLP 52-IX-27-54	<i>Canis gezi</i>
Present, Mexico	IBUNAM 38219	<i>Canis latrans</i>
Present, Mexico	IBUNAM 14531	<i>Canis latrans</i>
Present, Mexico	IBUNAM 9139	<i>Canis latrans</i>
Present, Mexico	IBUNAM 35161	<i>Canis latrans</i>
Present, Mexico	IBUNAM 38218	<i>Canis latrans</i>
Present, Mexico	IBUNAM 38220	<i>Canis latrans</i>
Present, Columbia, USA	LACM 31248 (3)	<i>Canis lupus</i>
Present, Columbia, USA	LACM 31248 (1)	<i>Canis lupus</i>
Unknown	F:AM 67186*	<i>Canis lupus</i>
Unknown	F:AM 67183*	<i>Canis lupus</i>
Unknown	F:AM 67181*	<i>Canis lupus</i>
Present, Mexico	IBUNAM 32919	<i>Canis lupus</i>
Present, Mexico	IBUNAM 9142	<i>Canis lupus</i>
Present, Mexico	IBUNAM 5255	<i>Canis lupus</i>
Present, Mexico	IBUNAM 567134	<i>Canis lupus</i>
Present, Alaska, USA	LACM 92246	<i>Canis lupus</i>
Present, Alaska, USA	LACM 92249	<i>Canis lupus</i>
Present, Mexico	IBUNAM 24555	<i>Canis lupus</i>
Present, Mexico	IBUNAM 5256	<i>Canis lupus</i>
Present, Mexico	IBUNAM 24553	<i>Canis lupus</i>
Present, Mexico	IBUNAM 567241	<i>Canis lupus</i>
Present, Mexico	IBUNAM 554186	<i>Canis lupus</i>
Present, Mexico	IBUNAM 531293	<i>Canis lupus</i>
Present, Michigan, USA	LACM 92297	<i>Canis lupus</i>
Unknown	AMNH (M) 134940*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 134941*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 134942*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 134943*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 34956*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 34962*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 34959*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 34957*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 34961*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 34958*	<i>Canis lupus nubilus</i>
Unknown	AMNH (M) 4362*	<i>Canis lupus nubilus</i>

Unknown	AMNH (M) 98226*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 130267*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 34447*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 98232*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 130226*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 121469*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 29040*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 16849*	<i>Canis lupus occidentalis</i>
Unknown	AMNH (M) 31624*	<i>Canis lupus occidentalis</i>
Lujan, Argentina	MACN 500	<i>Canis neheringi</i>
Present, Salta, Argentina	MACN-Ma 48.5	<i>Cerdocyon thous</i>
Present, Santa Fe, Argentina	MACN-Ma 33.60	<i>Cerdocyon thous</i>
Present, Salta, Argentina	MACN-Ma 48.10	<i>Cerdocyon thous</i>
Present, Puerto Casado, Paraguay	MACN-Ma 45.34	<i>Cerdocyon thous</i>
Present, Santa Cruz, Bolivia	MACN-Ma 50.61	<i>Cerdocyon thous</i>
Present, Brazil	MACN-Ma 20.32	<i>Cerdocyon thous</i>
Present, Corrientes, Argentina	MACN-Ma 24043	<i>Chrysocyon brachyurus</i>
Present, Corrientes, Argentina	MACN-Ma 25103	<i>Chrysocyon brachyurus</i>
Present, Captive	MACN.Ma 19146	<i>Chrysocyon brachyurus</i>
Unknown	UA 12610*	<i>Chrysocyon nearcticus</i>
Unknown	LACM (CIT) 149*	<i>Chrysocyon nearcticus</i>
Arroyo Santa Elena, Argentina	MMP 164***	<i>Protocyon scagliarum</i>
Talara, Peru	MNHN TAR 658	<i>Protocyon tarijensis</i>
Mercedes, Argentina	MLP 89.XI-20-1	<i>Protocyon troglodytes</i>
El Mene de Inciarte, Venezuela	MBLUZ-P-2337**	<i>Protocyon troglodytes</i>
El Mene de Inciarte, Venezuela	MBLUZ-P-2579**	<i>Protocyon troglodytes</i>
Guamote, Ecuador	MNHN GMT 1	<i>Protocyon troglodytes</i>
Tarija, Bolivia	UF 26911	<i>Protocyon troglodytes</i>
Tarija, Bolivia	UF 27889	<i>Protocyon troglodytes</i>
Ñuapua, Bolivia	MNHN NUA 91	<i>Protocyon troglodytes</i>
RioTala(SanPedro), Argentina	MPS 2	<i>Theriodictis platensis</i>
Mar del Plata, Argentina	MLP 10-80	<i>Theriodictis platensis</i>
Buenos Aires, Argentina	MLP 10-51	<i>Theriodictis platensis</i>
Florida, USA	UF 133922*	<i>Theriodictis? floridanus</i>
USA	F:AM 67180*	<i>Xenocyon lycaonoides</i>
USA	YPM 10058*	<i>Xenocyon texanus</i>

LIST OF CANIDS SPECIES MENTIONED IN THE MAIN TEXT

Aenocyon Merriam, 1918
Aenocyon dirus (Leidy, 1858)
Atelocynus Cabrera, 1940
Atelocynus microtis (Sclater, 1882)
Canis Linnaeus, 1758
“*Canis*” *armbrusteri* Gidley, 1913
Canis familiaris Linnaeus, 1758
“*Canis*” *gezi* Kraglievich, 1928
Canis latrans “Say, 1823”^{*}
Canis lupus Linnaeus, 1758
Cerdocyon Hamilton Smith, 1839
Cerdocyon thous Hamilton Smith, 1839
Chrysocyon Hamilton Smith, 1839
Chrysocyon brachyurus Illiger, 1815
Chrysocyon nearticus Tedford *et al.* 2009
Dusicyon Hamilton Smith, 1839
Dusicyon australis “(Kerr, 1792)”^{*}
Dusicyon avus (Burmeister, 1866)
Lycalopex Burmeister, 1854
“*Lycalopex*” *cultridens* (Gervais & Ameghino, 1880)
Lycalopex griseus (Gray, 1837)
Lycalopex gymnocercus (Fischer 1814)
Metalopex Tedford & Wang, 2008
Protocyon Giebel, 1855
Protocyon scagliorum Kraglievich, 1952
Protocyon tarijensis (Ameghino, 1902)
Protocyon troglodytes (Lund, 1838)
Speothos Lund, 1839
Speothos pacivorus Lund, 1842
Speothos venaticus (Lund, 1842)
Theriodictis Mercerat, 1891
Theriodictis platisis Mercerat, 1891
“*Theriodictis*” *floridanus* Tedford *et al.* 2009
Urocyon Baird, 1858
Urocyon cinereoargenteus (Schreber, 1775)
Urocyon littoralis (Baird, 1858)
Urocyon minicephalus Martin, 1974
Urocyon webbi Tedford *et al.* 2009
Vulpes Frisch, 1775
Vulpes vulpes Linnaeus, 1758
Xenocyon Kretzoi, 1938
Xenocyon lycanoides Kretzoi, 1938
Xenocyon texanus (Troxell), 1915

^{*}Citation not found, reference taken from other authors.

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