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Stratigraphic range of the large canids (Carnivora, Canidae) in South America, and its relevance to quaternary biostratigraphy

F.J. Prevosti^{a,*}, E.P. Tonni^b, J.C. Bidegain^c^a División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", CONICET, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina^b Departamento Científico Paleontología Vertebrados, Museo de La Plata, B1900FWA La Plata, Argentina^c LEMIT, Calle 52 e/121 y 122, B1900FWA La Plata, Argentina

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ABSTRACT

The fossil record of large canids is reviewed in order to improve the current South American biostratigraphic chart. This analysis is based on the recent systematic revision of those taxa performed by one of the authors and new field and paleomagnetic works. The first occurrences of large canids are limited to the Early–Middle Pleistocene (Ensenadan stage/age). *Theriodictis platensis*, "*Canis*" *gezi*, and *Protopcyon scagliorum* are restricted to the Ensenadan. Most *T. platensis* specimens came from late Ensenadan levels (0.78– \approx 0.5 Ma), but the oldest one is between 0.78 Ma and 1 Ma old. The biochron of *Protopcyon troglodytes* spans the Ensenadan–Lujanian interval, and its youngest remains are associated with ¹⁴C dates of 25–27/20–10 ka BP. Most individuals of *Protopcyon tarijensis* could be between 1 Ma and 10 ka, but one specimen comes from a level surely younger than 0.78 Ma, and probably younger than 28 ka. The oldest records of the living species *Chrysocyon brachyurus* are between ca. 0.3 Ma–9 ka BP. The first record of *Canis dirus* (and *Canis* by extension) in South America is limited to the latest Pleistocene (<25–27 ka).

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1. Introduction

Both evolutionary and biogeographic events constrain the fossilization and preservation of taxa at different stratigraphic levels and places. These are the raw material used for the elaboration of local and regional biostratigraphical charts that contribute to larger scale regional correlations and chronostratigraphic schemes, along with other sources of information (e.g., Cione and Tonni, 1995; Woodburne, 2004).

As for other carnivores (e.g., Felidae, Ursidae), the family Canidae possesses a wide geographic and stratigraphic range that comprises the majority of the Cenozoic and most of the continents. Several events of migration and origination of these taxa have been found in the fossil record and used in biostratigraphic studies on many continents (e.g., Woodburne, 2004; Cione and Tonni, 2005). For example, the Pliocene–Pleistocene transition in Europe is recognized by the first occurrence of three large canids, an event named the "*Canis* event" (see Martínez-Navarro and Rook, 2003).

The family Canidae is a late immigrant in South America and reached this continent in several independent invasions (see Berta, 1987, 1988; Wayne et al., 1997; Prevosti, 2006). It is first recorded in the late Pliocene (Sanandresian Subage/Substage; see Cione and

Tonni, 2005), but most species are restricted to the Pleistocene and recent.

In the past some species have been used to characterize biostratigraphic units. Two examples are *Theriodictis platensis*, considered to be restricted to the *Mesotherium cristatum* biozone (Prevosti et al., 2004a, 2004b; Cione and Tonni, 2005), and the first occurrence of *Dusicyon cultridens* which occurs in the *Akodon (Akodon) lorenzinii* biozone (Cione and Tonni, 2001, 2005). Prevosti et al.'s (2004a, 2004b) analysis suggests that *Theriodictis* is restricted to the Ensenadan. The same is true for *Protopcyon scagliorum*, while the biochron of *Protopcyon troglodytes* comprises Ensenadan–Lujanian time, and a third species, *Protopcyon orcesi* (= *P. troglodytes* in this work) was found in "Lujanian" beds of Ecuador, but the lack of dates and accurate biostratigraphic charts in Ecuador raises some doubts about the Lujanian age of those beds (see Prevosti et al., 2005).

At the time those works were published, the fossil record of the group was based in an old systematic revision, made more than 20 years ago, and published in 1988 by Berta. Recently, a new systematic revision (Prevosti, 2006), anchored in a phylogenetic framework, has modified and expanded the work of Berta (1988), and provided new results that modified the conclusions of those earlier papers.

This paper presents a biostratigraphic analysis of the large canids preserved in the fossil record of South America. This study is based on the recent systematic and phylogenetic analysis of the taxon, new fieldwork, and paleomagnetic analyses that include

* Corresponding author. Tel.: +5411 4982 6670; fax: +5411 4982 1561.
E-mail address: protopcyon@hotmail.com (F.J. Prevosti).

a new paleomagnetic profile. The latter helped constrain the age of several remains of canids (especially *T. platensis*) found in Ensenadan beds. This work will hopefully become a useful tool for future biostratigraphic analysis carried out in South America.

2. Materials and methods

This work follows the biostratigraphic, chronostratigraphic and geochronologic schemes of Cione and Tonni (2005). For chronological purposes, reversals are by far the most important features of the Earth's magnetic field that can be employed as useful tool in biostratigraphic studies. The paleomagnetic records found in present work are interpreted according to the geomagnetic polarity timescale (GPTS) summarized by Cande and Kent (1995).

The specific and generic arrangement of the large canids is based on the phylogenetic analysis and systematic revision performed by one of the authors (Prevosti, 2006) as a part of his doctoral thesis (Table 1). The age of the different fossils studied in the present work was established according to the available bibliography, and through fieldwork. Prevosti (2006) provides a detailed account of these data.

Prevosti's (2006) recent phylogenetic analysis demonstrated that "*Theriodictis*" *tarijensis* (= *Protocyon tarijensis*; Table 1) forms a monophyletic group with the species of *Protocyon*, and consequently that species was removed from genus *Theriodictis*, which in turn became a monotypic genus. "*Canis*" *gezi* is the sister taxon of *Theriodictis*, *Protocyon* and *Speothos*, and not of *Canis* (sensu stricto). For this reason, this species has been excluded from *Canis*, but its generic status could not be resolved.

Oriented samples were taken using a manual square-section sampler made of non-magnetic material (brass/copper–zinc alloy) according to Bidegain (1991). They were transferred to plastic cubic 8 cm³ boxes and non-magnetic plastic glue was added in order to avoid particle movements. The paleomagnetic samples were measured with a Dígico Spinner Magnetometer at Instituto de Física Arroyo Seco (IFAS), Tandil University in Buenos Aires province, Argentina.

NRM for all samples was first measured to obtain the characteristic behaviour of remanence, and AF demagnetization field was applied up to 80 mT peak field. Normal samples were easier to demagnetize than reverse samples, probably due to the presence of minerals with higher coercivity forces in the older layers.

The color of the sediment was established using the Soil Color Charts (Munsell®, 1994). Figs. 1 and 2 illustrate the geographic localities studied.

3. Temporal distribution of large fossil canids in South America

This review shows that the supposedly large Pliocene canids from the south of Buenos Aires province (Argentina), described during the first half of the 20th century (e.g., Frenguelli, 1928, 1929, 1933), lack adequate stratigraphic data to date these specimens. Some, such as the holotype of *Canis* (*Macrocyon*) *chapadmalensis*

(="C." *gezi*), were collected without stratigraphic context. All the other large canids have been found in the layers of Pleistocene age (Prevosti, 2006, see also Kraglievich, 1928).

3.1. *Chrysocyon brachyurus*

Several authors cite the presence of the living species *Ch. brachyurus* in the middle Pleistocene of Tarija (e.g., (Berta, 1988)), but due to the lack of stratigraphic information for the specimen in question, its age could be anywhere between 1 Ma and 10 ka (see above). Other remains of this species have been found in the caves of Lagoa Santa (350–9 ka, see above) and the Holocene of Argentina (Prevosti et al., 2004a; Prevosti, 2006; Fig. 2).

3.2. *Theriodictis platensis*

All the remains of *T. platensis*, the type species of the genus, with enough stratigraphic information have been recovered from Ensenadan levels (see Prevosti et al., 2004b). There are paleomagnetic profiles available for three of these localities (Figs. 1 and 2). One specimen was found at the base of the marine cliffs near Santa Clara del Mar (southeastern Buenos Aires province, Argentina; Fig. 1) at a small stream called Arroyo Santa Elena (37°51'S, 57°30'W). The fossil was collected from the basal beds of this locality, beds that belong to the *M. cristatum* biozone, which indicates an Ensenadan age (Vucetich et al., 1997; Cione et al., 2002; Pardiñas, 2004). The profile is composed of sediments with normal polarity. It was interpreted as the Brunhes chron (<0.78 Ma; Bidegain et al., 2005), and indicates a late Ensenadan age (0.78–≈0.50 Ma) for this specimen. Another specimen found southwest of Arroyo Santa Elena, in a locality called Playa Santa Elena (37°52'S, 57°30'W; see Prevosti et al., 2004b; Fig. 1) presents similar circumstances. A recent paleomagnetic study performed in Playa Santa Elena (see Soibelzon et al., 2009) has shown that the bearing level was deposited during the Brunhes chron, and with the presence of *Mesotherium* supports the late Ensenadan age suggested for this specimen.

A third specimen of *T. platensis* was found in a small quarry (Cantera Vialidad Nacional, 33°47'S, 59°37'W; Fig. 1) near the city of San Pedro, northeastern Buenos Aires province. The geologic profile comprises 3 m of sandy silts, divided into two units (a and b). The lower unit (a) is reddish brown (2.5YR4/4), and contains rhizocretions, calcium carbonate concretions and fine vertical and horizontal calcretes. The unit is 1 m thick and the contact with the upper unit b appears to be sharp. The upper unit (b) is brown (7.5YR5/3) and less compact than unit a. Unit b contains fine prismatic structure at its base, and calcium carbonate as concretions and rhizocretions in its uppermost levels (Fig. 3). Both units (a and b) appear to have been affected by different degree of pedogenesis. The analysis of paleomagnetic samples indicates that the lower unit possesses reverse paleomagnetic levels (i.e., Southern Hemisphere declinations as well as positive inclinations), while the upper one has normal paleomagnetic polarity in all the analysed samples (Northern Hemisphere declinations and negative inclinations; Fig. 3).

The fossil was buried at the base of the unit b. Similar stratigraphic beds have been observed at the base of other quarries where Ensenadan mammals were found. This information indicates that the age of this specimen is late Ensenadan.

Two other *T. platensis* specimens collected in Ramallo (33°29'S, 60°00'W; Fig. 1), a locality near San Pedro, came from levels correlated with the late Ensenadan beds of San Pedro (see Prevosti et al., 2004b; Voglino and Pardiñas, 2005; Prevosti, 2006).

One skull found at the end of the 19th century (Lydekker, 1894) was recovered from an excavation made in the Central Station of

Table 1
Systematic arrangement of the South American large canids followed in this paper (see (Prevosti, 2006)).

<i>Theriodictis platensis</i> Mercerat 1891
" <i>Canis</i> " <i>gezi</i> Kraglievich, 1928
<i>Protocyon troglodytes</i> (Lund, 1838)
<i>Protocyon tarijensis</i> (Ameghino, 1902)
<i>Protocyon scagliorum</i> J. L. Kraglievich, 1952
<i>Chrysocyon brachyurus</i> (Illiger, 1815)
<i>Canis dirus</i> (Leidy, 1858)

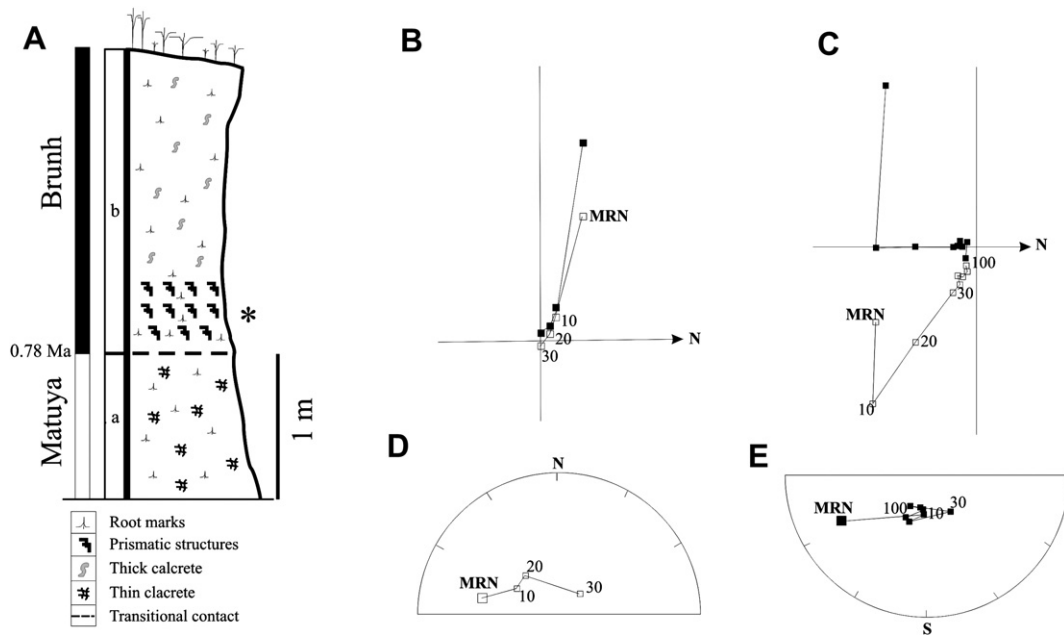


Fig. 3. Geologic profile and paleomagnetic samples of Vialidad Nacional quarry (San Pedro, Buenos Aires, Argentina). A: geologic profile; B: Stereographic diagram of a paleomagnetic sample from stratigraphic unit b; C: Stereographic diagram of a paleomagnetic sample from stratigraphic unit a; D: Zijderveld diagram of a paleomagnetic sample from stratigraphic unit b; E: Zijderveld diagram of a paleomagnetic sample from stratigraphic unit a; and *: provenance of the *Theriodictis platensis* specimen.

2007). This suggests that the fossil is younger than 28 ka, but the correlations between the profiles of MacFadden (2000) and Coltorti et al. (2007) need to be checked. Additionally, Lujanian mammals (*Hoplophorus euphractus*; see Takai et al., 1984; MacFadden, 2000) have also been found in this profile, in agreement with the above mentioned paleomagnetic analysis and ^{14}C dates (Fig. 2).

One *P. troglodytes* specimen came from Unit 10 of San Pedro II, and consequently its age could be between 0.78 Ma and the end of the Pleistocene. The same applies to another *P. troglodytes* individual that was collected in association with other Pleistocene mammals from sediments of the Brunhes chron in the Bolivian locality of Ñuapua (20°52'S, 63°04'W, Fig. 1; see Prevosti et al., 2005).

There are two remains that suggest that *P. troglodytes* could be present in the Ensenadan of Buenos Aires province (Argentina). One came from the lower levels of Playa Quequén (38°32'S, 58°42'W; Fig. 1), where Tonni et al. (1996) described an Ensenadan mammalian assemblage. However, the antiquity of the beds within this stage/age could not be constrained. This remain was previously assigned to *Theriodictis* by Berman (1994), and this criteria was followed by Prevosti et al. (2004a, 2004b), but see Prevosti (2006) for a discussion of its systematic assignment.

The other specimen was found at the lowest level of the cliffs at Camet Norte (37°49'S, 57°29'W; Fig. 1). This level has been correlated with the late Ensenadan bed of Arroyo Santa Elena (see Pardiñas et al., 1998; Prevosti, 2006), which is located a few kilometer to the southwest of the former locality. Unfortunately, no exclusive taxa from the Ensenadan stage/age are known for this bed at present, and consequently the late Ensenadan age of this specimen remains uncertain.

Other specimens of *P. troglodytes* are Bonaerian/Lujanian or Lujanian in age, and have been recovered in Ecuador, Brazil, Argentina and Venezuela (see Berta, 1988; Berman, 1994; Oliveira et al., 2005; Prevosti et al., 2005; Prevosti, 2006; Prevosti and Rincón, 2007; Fig. 1). The remains collected in the caves of Lagoa Santa (19°39'S, 43°53'; Fig. 1) and northeastern Brazil (e.g., Bahia, Piauí, and Rio Grande do Norte states) have been referred to the latest Pleistocene, but recent work has shown that the age of these

mammal assemblages is between 350 ka and 9 ka (Auler et al., 2006). Only one specimen described by Cartelle and Langguth (1999) from Toca da Boa Vista (Bahia, 10°09'S, 40°51'W; Fig. 1) has precise stratigraphic data and associated ^{14}C dates that indicate an age between 20 ka and 10 ka. New remains from a site in Venezuela recently studied by Prevosti and Rincón (2007) (see also Prevosti, 2006) (Inciarte, 10°47'N–72°14'W; Fig. 1) are associated with ^{14}C dates of 25.50 ± 0.6 and 27.98 ± 0.37 ka (Jull et al., 2004; Fig. 2).

3.4. "Canis" gezi

Three specimens of "C." *gezi* are known, and two of them were found out of stratigraphic context. The third one, the holotype, was recovered from indistinct Ensenadan levels ("...horizonte pampeano inferior..." Kraglievich, 1928) at the locality of Wilde (Buenos Aires, 34°42'S, 58°18'; see Kraglievich, 1928; Berta, 1988; Berman, 1994; Prevosti, 2006; Figs. 1 and 2).

3.4.1. *Canis dirus*

Because *Canis nehringi* is considered a junior synonym of *C. dirus*, and "C." *gezi* was excluded from the genus, *C. dirus* is currently the only species of *Canis* recorded in the Pleistocene of South America (Prevosti, 2006; Table 1). All the records are late Pleistocene in age. The specimen from Talara (Peru, 4°40'S, 81°60'; Fig. 1) is associated with ^{14}C dates of $13,616 \pm 600$ BP, $14,418 \pm 500$ BP, and 9030 ± 240 BP, while the specimen from Muaco (Venezuela, 11°29'N, 69°32'W) has an age of 16375 ± 400 BP (Dundas, 1999). A third record occurred in the Venezuelan locality of Inciarte, above levels dated between 25 ka and 27 ka (Prevosti, 2006; Prevosti and Rincón, 2007; Fig. 1). The holotype of *C. nehringi* was deposited above the Guerrero Member of the Luján Formation near the Argentinean locality of Luján (Buenos Aires, 34°34'S, 59°06'W; Fig. 1). The lower section of the Salado Member of the Luján Formation have been dated at 10–11 ka BP (Prieto et al., 2004), suggesting that this specimen has a latest Pleistocene age. This suggests that the occurrence of *C. dirus* (and genus *Canis* as a whole) in South America is a late biogeographical event restricted

to the latest Pleistocene (Fig. 2). The arrival of the domestic dog (*Canis familiaris*) was recorded in South America later, during the late Holocene (2–3 ka) (see Schwartz, 1997).

4. Conclusions

The first occurrence of large canids took place in the early-middle Pleistocene (Ensenadan age/stage) and that “C.” *gezi*, *T. platensis* and *P. scagliorum* are exclusive taxa of the *M. cristatum* biozone. Therefore, these taxa yield useful biostratigraphic information. Most of the specimens of *T. platensis* are late Ensenadan in age (0.78–≈0.5 Ma), but one specimen was found in older stratigraphic levels (0.78–1 Ma).

The oldest record of *P. troglodytes* is Ensenadan in age and the younger ones came from the late Pleistocene (25–27 and 20–10 ka). The majority of the *P. tarijensis* remains lack stratigraphic data and could have an age between 1 Ma and 10 ka. One specimen is younger than 0.78 Ma, and probably younger than 28 ka.

The oldest record of *Ch. brachyurus* is between ca. 0.3 Ma–9 ka in age. The age of the specimen collected in Tarija is dubious, and could lie anywhere within the 1 Ma and 10 ka BP temporal lapsus.

The record of *C. dirus*, the only species of *Canis* that was present in South America until the arrival of the domestic dog in the late Holocene, is restricted to the latest Pleistocene. Most of the records of this taxon in South America are between <25/27 ka and 8.5 ka BP. This suggests that the presence of *C. dirus* in South America could be used as a guide fossil for the late Pleistocene–early Holocene.

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