

First description of milk teeth of fossil South American procyonid from the lower Chapadmalalan (Late Miocene–Early Pliocene) of “Farola Monte Hermoso,” Argentina: paleoecological considerations

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Abstract The first record of milk teeth of South American fossil procyonids comes from the Late Miocene–Early Pliocene at “Farola Monte Hermoso,” Buenos Aires Province, Argentina. Five extant genera of Procyonidae inhabit South America (*Bassaricyon* Allen, *Nasuella* Hollister, *Potos* Geoffroy Saint-Hilaire and Cuvier, *Procyon* Storr, and *Nasua* Storr). Of these only *Procyon* and *Nasua* are present in the fossil record (Late Pleistocene–Holocene), in several localities in Brazil, Uruguay, and Bolivia. In addition, six other fossil genera were named, but only two are considered valid: *Cyonasua* and *Chapadmalania*. Thus, *Cyonasua* encompasses ten formally named species and *Chapadmalania* two. The new specimen, MLP 09-X-5-1, is assigned to cf. *Cyonasua*. In addition, anatomical evidence implies a much more carnivorous diet in Late Miocene–Early Pleistocene procyonids than that of extant South American taxa. Finally, I examine and discuss the “competitive displacement” hypothesis regarding the extinction of native marsupial carnivores after the arrival of immigrant placental carnivores in South America.

Keywords Procyonidae · Fossil · Milk teeth · *Cyonasua* · South America

Kurzfassung Ich beschreibe hier zum ersten Mal Milchzähne von südamerikanischen fossilen Procyonidae. Diese acht Zähne (MLP 09-X-5-1) kommen aus dem späten

Miozän–frühen Pliozän von “Farola Monte Hermoso”, Provinz Buenos Aires, Argentinien. Fünf rerente Gattungen von Procyonidae leben in Südamerika (*Bassaricyon* Allen, *Nasuella* Hollister, *Potos* Geoffroy Saint-Hilaire & Cuvier, *Procyon* Storr und *Nasua* Storr). Von diesen Gattungen sind nur *Procyon* und *Nasua* im Fossilbericht (spätes Pleistozän–Holozän) aus verschiedenen Lokalitäten in Brasilien, Uruguay und Bolivien bekannt. Außerdem wurden sechs fossile Gattungen benannt, aber nur zwei werden noch heute als gültig anerkannt: *Cyonasua* und *Chapadmalania*. *Cyonasua* umfasst damit zehn formell benannte Arten und *Chapadmalania* zwei. Nach der Beschreibung und dem Vergleich von MLP 09-X-5-1 ordne ich die Zähne cf. *Cyonasua* zu. Außerdem zeige ich anatomische Hinweise, die eine stärker räuberische Lebensweise und carnivore Ernährung der Procyonidae aus dem späten Miozän als die der heutigen Taxa in Südamerika anzeigen.

Schlüsselwörter Procyonidae · *Cyonasua* · Südamerika · Fossilien · Milchzähne

Introduction

Five extant genera of Procyonidae inhabit South America (*Bassaricyon* Allen, *Nasuella* Hollister, *Potos* Geoffroy Saint-Hilaire and Cuvier, *Procyon* Storr, and *Nasua* Storr). Of these only *Procyon* and *Nasua* are present in the fossil record (Late Pleistocene–Holocene), in several localities in Argentina, Brazil, Uruguay, and Bolivia (Soibelzon et al. 2009a, in press). In addition, five fossil genera have been named (*Cyonasua* Ameghino, *Oligobunis* Burmeister, *Pachynasua* Rovereto, *Brachynasua* Ameghino and Kraglievich, and *Chapadmalania* Ameghino) of which only two are considered valid today (*Cyonasua* and *Chapadmalania*,

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Berman 1994; Soibelzon 2007). A thorough taxonomic study is in progress by the author. Thus, *Cyonasua* encompasses ten species: *C. argentina* Ameghino, *C. brevirostris* (Moreno and Mercerat), *C. longirostris* (Rovereto), *C. pascuali* Linares, *C. groeberi* Kraglievich and Reig, *C. lutaria* (Cabrera), *C. clausa* (Ameghino), *C. robusta*, *C. argentinus* (Burmeister), and *C. meranii* Ameghino and Kraglievich, whereas *Chapadmalania* includes two species: *Ch. ortognatha* Ameghino and *Ch. altaefrontis* Kraglievich and Ameghino. *Cyonasua* and *Chapadmalania* are mainly recorded during the late Tertiary (Late Miocene to Pliocene); nevertheless, there are scarce records of *Cyonasua* (*C. meranii*) in the Quaternary of Argentina (Ensenadan, Early to Middle Pleistocene). Despite the great number of species of *Cyonasua* described, it is relatively scarce, and most specimens remain unpublished.

Procyonids were the first placental carnivores that arrived in South America after the marine barrier separating North and South America disappeared ca. 4–2.5 Ma (see Woodburne et al. 2006; Soibelzon and Prevosti 2007). It is important to note that recent South American procyonids represent a second invasion from North or Central America during the Latest Pleistocene–Holocene and are not directly related to *Cyonasua* or *Chapadmalania* (Prevosti and Soibelzon in press). Therefore procyonids are recorded in South America from Late Miocene to Recent times but with a record gap of ~900 Ky between the Early and the Latest Pleistocene.

Milk teeth of this genus (dI3, dC1, dP1–4; belonging to one specimen) are described for the first time herein. These specimens from the Late Miocene–Early Pliocene at Farola Monte Hermoso (Buenos Aires, Argentina) are assigned to cf. *Cyonasua*. Also some paleoecological issues in relation to the Mio-Pleistocene South American carnivore guild (integrated by placental and marsupial carnivores) are discussed.

Locality and age

Eight milk teeth (MLP 09-X-5-1) were exhumed from the marine cliff at the Farola Monte Hermoso locality (see Fig. 1a), Buenos Aires, Argentina. Farola Monte Hermoso is of historical interest because it was one of the paleontological localities visited by Charles Darwin during 1832; he was the first to study the geology and paleontology of this site. Farola Monte Hermoso is particularly attractive because of abundant and diverse Mio-Pliocene fossils; additionally this is the type locality of the Monte Hermoso Formation. Interestingly, Farola Monte Hermoso was the

first Argentinean lighthouse; it was inaugurated in November 1881.

The bearing level of MLP 09-X-5-1 is known as “Miembro de las Limolitas claras” (Bonaparte 1960) and corresponds to the *Neocavia depressidens* Biozone (Cione and Tonni 1996) included in the Monte Hermoso Formation, which is Chapadmalalan in age [Late Miocene–Early Pliocene, Cione and Tonni (1996)]. MLP 09-X-5-1 was found in association with fragmentary remains of the notoungulate *Paedotherium* and the rodents *Actenomys* and *Neocavia* (Sergio Bogan, pers. comm. 2008).

Materials and methods

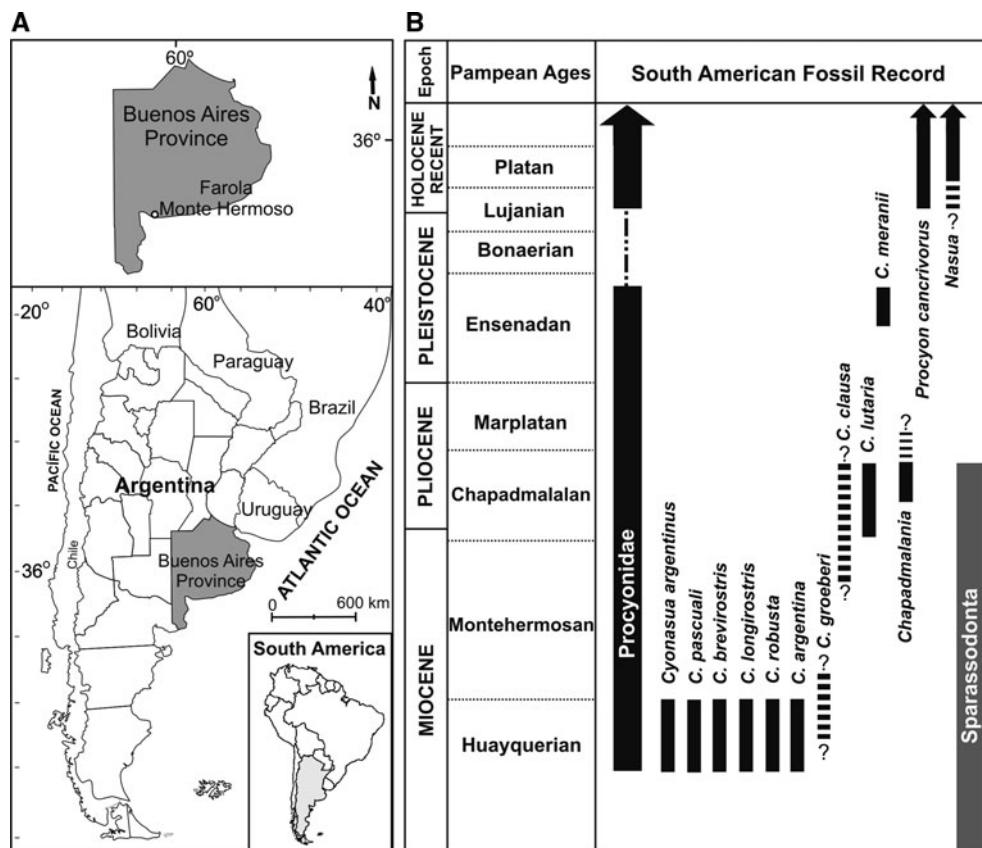
Material used for comparisons. Juveniles: MACN 34-47 (*Procyon cancrivorus*), ETMNH 301 (*P. lotor*). Adults: MLP 34-VI-20-6 holotype of *Pachynasua lutaria* (=*Cyonasua lutaria*); MLP 29-IV-15-1 holotype of *Amphinasua brevirostris* (=*Cyonasua brevirostris*); MACN 8209 holotype of *Amphinasua longirostris* (=*Cyonasua longirostris*); AMNH 45985 holotype of *Cyonasua pascuali*; MACN 6687, MACN 6689, MACN 6688, MMMP 362, MMMP 1004, MMMP 971, MMMP 1120 (*Cyonasua* sp.); MLP-zool 1-I-03-25 (*Procyon cancrivorus*), AMNH 30748 (*Bassaricyon gabii*), MLP-zool 6026 (*Nasua nasua*), ETMNH 516 (*Potos flavus*), ETMNH 516 (*Bassaricyon astutus*).

Morphological terms and definitions of measurements follow Soibelzon and Carlini (2004) and papers cited therein. We numbered the deciduous premolars mesiodistally as Terzea (1969) and all recent authors (i.e., the last deciduous premolar is dP3/dp4) to facilitate comparisons. The chronostratigraphic/geochronologic units used herein follow the usage by Woodburne et al. (2006). Measurements were taken with a Vernier caliper.

Abbreviations

AMNH American Museum Natural History, USA; ETMNH East Tennessee Museum of Natural History, USA; GHUNLPam Geología Histórica, Universidad Nacional de La Pampa, Argentina; MACN-zool: Mastozoology collection, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina; MACN: Vertebrate paleontology collection, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina; MLP: Vertebrate paleontology collection, Museo de La Plata, Argentina; MLP-zool: Mastozoology collection, Museo de La Plata, Argentina; MMMP Museo Municipal de Mar del Plata, Argentina. Ky. Kilo Years (1,000 years). Ma. Million Years.

Fig. 1 **a** Map showing the locality Farola Monte Hermoso where cf. *Cyonasua* was recovered. **b** Chronological chart of the late Cenozoic in South America, showing the biochrons of all procyonids with fossil record and the biochron of Sparassodonta (chronostratigraphic units according to Woodburne et al. 2006)



Results

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Procyonidae Gray, 1825

cf. *Cyonasua* Ameghino, 1885

Figure 2a–n, Table 1

Type species: *Cyonasua argentina* Ameghino 1885.

Temporal range: Late Miocene to Middle Pleistocene (Huayquerian to Ensenadan) (Fig. 1b).

Geographic distribution: Argentina (Catamarca, Córdoba, Entre Ríos, Buenos Aires, Jujuy, Mendoza, and La Pampa Provinces) and Peru (?). Referred specimen: MLP 09-X-5-1: left dC1, right dl3, right dP1-4, and left dP3-4 (Fig. 2a–e) collected by Sergio Bogan.

Comments

Because the milk teeth described herein were not in association with definitive molars it is impossible to make a secure taxonomic assignation of MLP 09-X-5-1 to *Cyonasua*. However, this identification seems likely because: (1) this is the only genus presently recognized for Late Miocene to Early Pleistocene procyonids in South America

(*Procyon* was reported in the Latest Pleistocene of Argentina by Soibelzon et al. 2009a, *in press*), (2) at a nearby locality the type specimen of *Pachynasua clausa* (Ameghino) (=*Cyonasua clausa*) was found, and (3) the general morphology of dP3–4 is more similar to that of *Cyonasua* than to any other South American Procyonidae. I propose to classify it as cf. *Cyonasua*. Notably, MLP 09-X-5-1 is smaller than all known fossil specimen except the holotype of *Cyonasua pascuali* (a mandible, AMNH 45985) that is the smallest species of *Cyonasua*.

This fossil record is 6° south of the southern limit of recent procyonid distribution (*P. cancrivorus*, Entre Ríos Province), and today the habitat and climatic conditions at Farola Monte Hermoso are far from optimal for procyonids, but wet and warm climatic conditions were inferred at this locality by the Late Miocene-Early Pliocene based on the fossil record (see Tonni et al. 1992 and articles cited therein).

Description: The morphology of the third upper deciduous incisor (dl3, Fig. 2a, b) is quite different from that of the corresponding permanent tooth. In addition, dl3 is straighter, more slender, and smaller than I3. Unfortunately, the apex of the crown is broken. In labial view, the upper margin of the crown is rounded, and the mesial and distal margins join towards the base of the crown. In occlusal view, the tooth is elliptical in section. An enamel

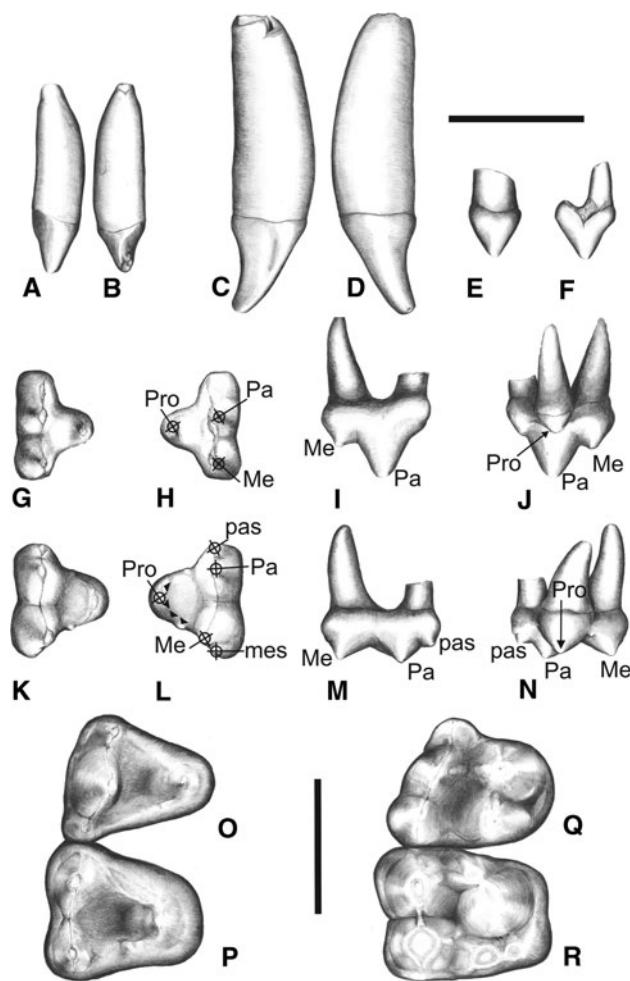


Fig. 2 MLP 09-X-5-1. Right dI3 in **a** distal view and **b** mesial view. Left dC1 in **c** mesial view and **d** distal view. Right dP1 **e**. Right dP2 **f**. Occlusal views of **g** right and **h** left dP3; Right dP3 in labial **i** and **j** lingual views. Occlusal views of right **k** and left **l** dP4. Right dP4 in labial **m** and lingual **n** views. *Cyonasua* (MLP 29-IV-15-1) right P4 **o** and M1 **p**. *Procyon cancrivorus* (MLP 1-I-03-25) right P4 **q** and M1 **r**. *Me* metacone. *mes* metastyle. *Pa* paracone. *pas* parastyle. *Pro* protocone. Black triangle denotes the position of a cusplet. Scale bar = 1 cm

Table 1 Measurements (mm) of MLP 09-X-5-1

Teeth	MDL	LLW
dI3	2.7	3.3
dC1	5.6	4.2
dP1	3.1	2.6
dP2	3.7	2.3
dP3 left	7.05	5.05
dP3 right	7.1	5.1
dP4 left	8.1	7.2
dP4 right	8.2	7.4

MDL mesiodistal length; LLW labiolingual width

crest crosses the lingual margin mesiodistally, and in the middle of this crest a low cusp is developed. The crown would have been implanted obliquely and slightly rotated mesially. The root is mesiodistally compressed and elliptical in section, as is the crown.

The left upper deciduous canine crown (dC1, Fig. 2c, d) is distally curved, and the apex is distolabially directed. Both the crown and the root are labiolingually compressed. The lingual side has a thin enamel edge running from the neck to the crown apex. The distal side is convex, and the mesial side is almost flat. The crown basal margin is at the same height around the tooth. The crown occupies a quarter of the tooth length; in definitive canines of *Cyonasua* it occupies half of the length.

The first upper deciduous premolar (dP1, Fig. 2e) has only one root (as in P1) and its crown is very simple and composed by one low and distally curved cusp. The labial side of this cusp is convex, but the lingual side is almost flat. The general morphology of dP1 is very similar to that of P1, except for the absence of a thin cingulum that runs from the mesial to the distal angle along the lingual-side crown base in definitive P1. It is important to note that P1 is often absent in *Cyonasua*.

The second upper deciduous premolar (dP2, Fig. 2f) has two roots, as does P2. The crown is simple and has one laterally compressed and slightly distally inclined cusp. This tooth is broken near the base of the mesial root, affecting not only the root but also the distal crown base. As in dP1 the labial side of the crown is convex but the lingual side is nearly flat. An enamel ridge ascends on the way to the apex of the crown and descends toward the distal angle running across the mesiodistal axis.

The crown of the third upper deciduous premolar (dP3, Fig. 2g–j) is laterally compressed. Two conspicuous labial cusps are aligned, the mesial cusp (paracone) being much higher and having a wider base than the distal cusp (metacone) (Fig. 2i); a mesiodistally oriented enamel ridge connects both cusps. The labial sides of both cusps are convex, and the lingual is almost flat (Fig. 2g, h). On the lingual side of the crown there is a small cusp (protocone) that lies at the same plane as the paracone apex (Fig. 2g, h, j). The dP3 has three roots (Fig. 2j). MLP 09-X-5-1 dp3 is morphologically simpler in comparison with the same tooth of *Procyon lotor* and *P. cancrivorus*. In these two species the protocone is high, the parastyle is well differentiated, there is a strong cingulum on the lingual border just behind the protocone, the enamel ridge that connects paracone and metacone is very sharp, descending the mesiolingual side of paracone towards the protocone, and at this level there are two small cusps.

The fourth upper deciduous premolar crown (dP4, Fig. 2k–n) is triangular in occlusal view. The labial margin is slightly curved and longer than the lingual margin, which

is strongly convex. The mesial and distal margins are almost straight and converge towards the lingual side. The two labial cusps are elongated mesiodistally, and both are much larger than the lingual cusps (Fig. 2k, l, n). The mesial cusp (paracone) is larger and slightly more compressed than the distal cusp (metacone). The paracone is vertical, while the metacone is distally inclined (Fig. 2k, l). A large cusp, the parastyle, arises in front of the paracone; also in the right dP4 a small metastyle is situated behind the metacone, but it is not present on the left dP4 (Fig. 2l–n). A deep furrow runs mesiodistally between the labial and lingual cusps. On the lingual margin of the crown there is a large cusp (protocone) with several relatively low cuspules arranged in a mesiodistal series over its apex. These cuspules are more evident on the left than on the right tooth (Fig. 2l). An enamel crest descends on the lingual side of the metacone toward the center of the crown; over this crest and at the valley that divides the lingual and labial cusps there is a cuspule (Fig. 2k, l). No cingulum is observed, apart from a slight widening of the enamel running along the labial side of the metacone (Fig. 2k, l). Contrary to the case of dP3, dP4 of cf. *Cyonasua* is very similar to dP4 of *Procyon* species, the main difference being that dP4 of *Procyon* has two cusps on the lingual side, the largest corresponding to the protocone and the other to the hypocone.

Comparisons

The adult dentition of procyonids is I3/3, C1/1, P4/4, M2/2, total 40. First premolars may be absent, and extra teeth have been reported in several species (Goldman 1913; Guilday and Parmalee 1966; Lotze and Anderson 1979); this is also the dental formula of *Cyonasua* and, as in Recent taxa, the absence of first lower and upper premolars is very frequent. Procyonids' deciduous dental formula is dI2/2, dC1/1, dP4/4 (Gompper 1995). In most mammals the milk dentition is replaced once, a condition called diphyodonty (hemidiphyodontism by Mones 1982), the first set is called primary and the next set secondary (Jernvall 1995); then deciduous teeth and molars are both primary teeth. As Jernvall (1995) pointed out, the last deciduous premolars (dP4/p4 in procyonids) always resemble the first permanent molars. Because we do not have other milk teeth of *Cyonasua* and because dP4 and M1 are both primary teeth we will make comparisons between these two teeth.

The dP4 is triangular in occlusal view, but M1 of *Cyonasua* is always wider than long (Fig. 2p). The cuspule that lies over the enamel crest and between the metacone and protocone in dP4 is always present in M1 of *Cyonasua* (Fig. 2p); in some specimens it presents two apices. There

is no cingulum on dP4, but the M1 of *Cyonasua* always has a lingual cingulum more or less developed (Fig. 2p). Also dP4 has a well-differentiated parastyle that is reduced or absent in the M1 of *Cyonasua* (Fig. 2p).

Paleobiology and paleoecology

Interestingly, dP3 of cf. *Cyonasua* (Fig. 2g–j) and *Procyon* are much more sectorial (i.e., laterally compressed trigonid, high and sharp lingual cusps) than P4 (Fig. 2o, q); in fact they are more similar to the P4 of much more carnivorous procyonids, such as *Bassariscus* Coues. In turn, it is remarkable that the absence of a hypoconid in the dP4 of cf. *Cyonasua* (Fig. 2k–n) corresponds to the absence of this cusp in the M1 of *Cyonasua* (Fig. 2p). On the other hand, its presence in *Procyon*'s dP4 is congruent with its presence in their M1 (Fig. 2r).

The reduction of cingula and the absence of the hypocone in the P4 and M1 of *Cyonasua*, in contrast to the condition observed in Recent South American procyonids (i.e., *Bassaricyon*, *Nasuella*, *Potos*, *Procyon*, and *Nasua*), suggest an omnivorous but mostly carnivorous diet for the former taxon. In turn, *Procyon*, *Nasua*, *Nasuella*, *Potos*, and *Bassaricyon* are mainly frugivores and/or insectivores and only opportunistic predators (Kays 2009), with clearly bunodont molars (e.g., square-shaped P4 and M1 with well-developed hypocone, Fig. 2q–r) in contrast to the much more secodont molars (e.g., P4 and M1 triangular-shaped without hypocone, Fig. 2o–p) observed in *Cyonasua* species.

This dietary shift (and consequently ecological niche change) between the first immigrant procyonids and the Recent taxa could have been the result of the peculiar evolution of the carnivore guild in South America, because here the only placental carnivores until the Late Pliocene were procyonids (Forasiepi et al. 2007; Soibelzon et al. 2009b). The other mammalian predators were the Sparassodonta (Metatheria) that became extinct by the Late Chapadmalalan (Forasiepi et al. 2007 and articles cited therein; Fig. 1b).

There is considerable debate as to whether placental carnivores arriving from North America caused the extinction of South American marsupial carnivores by competitive displacement (e.g., Simpson 1950 and subsequent papers, Patterson and Pascual 1968, 1972; Werdelin 1987, 2009) or not (e.g., Forasiepi et al. 2007; Prevosti et al. 2009). The fossil record indicates that Sparassodonta taxa only coexisted with procyonids (Fig. 1b), as they become extinct before the first record of Canidae in the Marplatan age and when procyonids appeared sparassodonts were already in decline (Marshall 1977; Forasiepi et al. 2007).

On the other hand, most sparassodontids were hypercarnivores, thus they occupied a different ecological niche from that occupied by procyonids. Some sparassodonts (e.g., *Stylocinus* Mercerat, “*Prothylacininae*”) show more omnivore molar morphologies (Forasiepi et al. 2007) and could have entered in ecological competition with *Cyonasua*. Although the fossil record indicates that these taxa became extinct shortly after a relatively short coexistence with procyonids (during the Huayquerian, Late Miocene; see Forasiepi et al. 2007), they were larger than *Cyonasua* and presumably occupied a different ecological niche. Noticeably, it was during this time span that *Cyonasua* experienced its greatest diversity (seven species, out of ten described, were present). During a relatively short time span (Middle to Late Pliocene), large procyonids (body mass ~25 kg in contrast to the ~6–7 kg of *Cyonasua*) belonging to the genus *Chapadmalania* Ameghino (closely related to *Cyonasua*; Kraglievich and Olazabal 1959) were recorded in South America, but they quickly became extinct and their fossil record is very poor (Fig. 1b). Noticeably, *Chapadmalania* extinction appears to have been approximately synchronous with the last record of Sparassodonta (family Thylacosmilidae; Fig. 1b).

It was not until the Late Pliocene (Marplatan) that other placental carnivores (e.g., Canidae, Mustelidae) migrated to South America (Prevosti and Pardiñas 2009; for a different view, see Verzi and Montalvo 2008) in the context of the Great American Biotic Interchange (see Woodburne et al. 2006; Soibelzon and Prevosti 2007). By the Early Pleistocene (Ensenadan), the placental carnivores were represented in South America (as today) by six families (i.e., Felidae, Ursidae, Canidae, Mustelidae, Mephitidae, and Procyonidae). Noticeably Procyonidae, with the longest presence in South America, was represented in Ensenadan times by only one species (*Cyonasua meranii* Ameghino and Kraglievich), and according to the fossil record, procyonids disappeared from South America by the Early-Middle Pleistocene boundary (the boundary between Ensenadan and Bonaerian; Fig. 1b).

Therefore, while procyonids were the only placental carnivores in South America, they were diverse and, according to their molar morphology, seemed to have occupied a much more predator niche than today. Nevertheless, when the other placental carnivores arrived they promptly became extinct.

The fossil record indicates that, after the extinction of *Cyonasua meranii*, procyonids were absent from South American ecosystems during nearly 900 Ky, as the next record of a procyonid in South America is from the Latest Pleistocene (Lujanian) when *Procyon cancrivorus* (G. Cuvier) is recorded for first time (Soibelzon et al. 2009a, in press). Remarkably, when Recent taxa (i.e., *Bassaricyon*, *Nasuella*, *Potos*, *Procyon*, and *Nasua*) joined

the South American carnivore guild, they occupied a quite different niche from that occupied by fossil procyonids for almost 6 Ma.

Further studies are needed to understand the role of *Cyonasua* and *Chapadmalania* in the South American Miocene-Pleistocene ecosystems and the possible causes of their extinction; hence, this contribution could be a starting point for future research projects.

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