

THE EVOLUTION OF SOUTH AMERICAN CARNIVORE FAUNA: A  
PALEONTOLOGICAL PERSPECTIVE

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Abstract: Although the history of placental carnivores (Order Carnivora) in South America is relatively short, they are a successful and diverse group. Carnivores, like many other taxa, enter South America from North America in the event called “Great American Biotic Interchange” (GABI). Most families, genera and species are recorded since the early Pleistocene ( $\approx 1.8$  Ma), but the oldest records are represented by procyonids found in Late Miocene levels (6-7 Ma), followed by mustelids and canids in the Late Pliocene ( $\approx 2.5$  Ma). We review the fossil record of South American carnivores using the latest taxonomic, phylogenetic and biostratigraphic studies, in order to investigate their patterns of origin and diversification. During the Miocene-Pliocene the diversity of carnivores is lower than in the Pleistocene and most species were small sized and omnivorous, but in the Early Pleistocene diversity increases, reaching levels somewhat lower than in the present. Size and diet disparity also augment in the Early Pleistocene with the presence of hypercarnivore, omnivore, mesocarnivore and piscivore species of different sizes (ranging between 1 to 1000 kg). The lacks of records or low diversity observed in several ages (e.g. Barrancalobian, Bonaerian and Platan) are mostly related to taphonomic or analytic biases. The bias against tropical areas is a key problem in the South American record, since almost all pre-Late Pleistocene records come from the southern part of the continent. Beyond this bias, the available information suggests that Recent and fossil carnivores invaded South America from Central America through several independent events, but that local South American speciation also provided many species and several genera.

Keywords: Carnivora, South America, Fossil record, Systematic,

## Introduction

South America possesses a rich eutherian carnivore (Mammalia, Carnivora) fauna, composed of  $\approx 47$  species, with a large diversity of canids, felids and procyonids (Wilson and Reeder, 2005). Most of these species are endemic to South America, while others have a Neotropical distribution (e.g. *Eira barbara*), and a few are Pan-American (e.g. *Puma concolor*). This diversity is amazing, especially taking into account that the Order Carnivora is a relatively recent group in South America. Like many other taxa of holarctic origin, most of the carnivores arrived in South America through the Panamian Isthmus as part of the biogeographic event called the "Great American Biotic Interchange" (GABI, Marshall et al, 1982). However, this biogeographic event started before the marine barrier that separated South America and North America disappeared, around the Pliocene–Pleistocene boundary ca 4-2.5 Ma (see Woodbourne et al. 2006) as it is indicated by the fossil record of Procyonidae in South America. Thus, carnivores are recorded in South America from Late Miocene to recent times, with representatives of the families Felidae, Canidae, Ursidae, Mustelidae and Procyonidae (Soibelzon and Prevosti 2007). Previous authors (Cione and Tonni, 1995; Woodburne et al., 2006; Prevosti et al., 2006; Soibelzon and Prevosti, 2007) have suggested that immigration of Carnivora to South America occurred in a "step-like" pattern. The first record corresponds to the Huayquerian (late Miocene) procyonids, then at the end of the Pliocene (Vorohueian) the canids (Caninae) and mustelids (Mustelinae) appear. After the Plio-Pleistocene boundary (Ensenadan) the carnivore guild in South America experienced a peak in diversity, when Ursidae, Felidae, Mephitinae, Lutrinae and large canids are first recorded (Fig. 1).

Before the GABI the mammalian carnivore guild in South America was composed by metatherians. The last record of a large metatherian carnivore corresponds to *Parahyaenodon argentinus* and *Thylacosmilus atrox* in the Early and middle Pliocene, respectively (Forasiepi et al., 2007). The following record of large eutherian carnivores (Canidae, Felidae and Ursidae) has given rise to several interpretations about the ecological role of eutherian carnivores in relation to that of metatherian carnivores and the causes of extinction of sparassodont carnivores (eg. “competitive displacement,” “replacement,” “enrichment;” see Simpson, 1950, 1980; Patterson and Pascual, 1972; Reig, 1981; Marshall, 1982; Marshall et al. 1982; Webb, 1985; Forasiepi et al. 2007). Recent works have not supported “competitive displacement” and agree with a replacement scenario (Forasiepi et al., 2007; Prevosti et al., 2009).

The aim of this contribution is to review and update the fossil record of continental Carnivora in South America in order to infer the origination and evolution of the Order in this continent. We base this review on a quantification of the diversity of the group through time, its first and last taxon records, and ecological “characters” (diet and body mass), taken from the latest taxonomic and biostratigraphic studies. We also explore the quality of the fossil record of the group. Our data suggest that the diversity of fossil and recent carnivores in South America is a consequence of several independent immigrations from North America (also within subfamilies and genera), and the local diversification of these immigrants. Two important extinction events are identified, one at the beginning of the Middle Pleistocene (Ensenadan), and other at the end of the Pleistocene (Lujanian), when the largest mammals, or megamammals, disappeared. The South American carnivoran fossil record has several biases, with no or limited representation in the Barrancalobian (Late Pliocene), Bonaerian (Middle-Late Pleistocene) and Holocene. During most of the duration of carnivoran occurrence in

South America the fossil record is restricted to the southern cone, and only in the Late Pleistocene-Holocene does it cover most of the continent.

**[Figure 1 about here]**

**Materials and methods**

We used the chronostratigraphy and biostratigraphy of Cione and Tonni (2005, modified by Woodburne et al., 2006; Fig. 1). The information on the fossil taxa included in the analyses was taken from the literature (e.g. Berman, 1994; Seymour, 1999; Soibelzon, 2002, 2004, Soibelzon et al., 2005; Prevosti, 2006a, 2006b; Prevosti and Rincón, 2007; Soibelzon and Rincón, 2007, Soibelzon et al., 2008), or from data associated with specimens deposited in several institutions (e.g. CEHA: Centro de Estudios del Hombre Austral, Chile. GALY: Grupo de Arqueología del Liceo de Young, República Oriental del Uruguay. GP: Instituto de Geociencias, Universidade de Sao Paulo, Brasil. IGC: Instituto de Geociencias, Universidade Federal de Minas Gerais, Brasil. MACN: Vertebrate Paleontology, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina. MACN-zool: Mastozoology, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina. MARC: Museo y Archivo Regional Castelli, Argentina. MBLUZ: Museo de Biología de la Universidad del Zulia, Venezuela. MHJ: Museo Histórico de Junín, Argentina. MHNLP: Museo de Historia Natural de La Paz, Bolivia. MLP: Vertebrate Paleontology, Museo de La Plata, Argentina. MLP-M: Mastozology, Museo de La Plata, Argentina. MMMP: Museo Municipal de Mar de Plata “Lorenzo Scaglia“, Argentina. MMPH: Museo Municipal “Punta Hermengo“, Argentina. MNHNP-PAM: Museum National de Histoire Naturelle, Pampean Collection, Francia. MPD: Museo Paleontológico de Daireux, Argentina. MPS: Museo Paleontológico de San Pedro, Argentina. MPV: Museo Paleontológico de Valencia, Spain. NHM: Natural History Museum, London, England. PIMUZ:

Paläontologisches Institut und Museum der Universität Zürich, Switzerland. UZM: Zoological Museo University of Copenhagen, Denmark. VF: Museo Royo y Gómez, Universidad Central de Venezuela, Venezuela).

We calculated diversity as the number of species per age, and also first and last species records. Several authors have suggested that raw diversity quantified in this way may be affected by different biases (Foote, 2000; Palombo et al., 2008), but since this revision is a large scale analysis, covering all of South America, this is not a problem. We used the number of “Lazarus taxa” (a taxon absent in an age or strata, but present in the overlying and underlying ones; Foote, 2000; Palombo et al., 2008) to detect possible biases in the South America carnivore fossil record.

The taxonomy, mainly follows Kraglievich (1930); Berta (1989); Berman, 1994; Seymour (1999); Soibelzon (2004); Prevosti (2006a, 2006b) and other published information (e.g. Berta and Marshall, 1978; Bond, 1986; Mones and Reinderchneck, 2004; Pomi and Prevosti, 2005; Prevosti et al., 2005; Prevosti and Rincón, 2007; Prevosti and Pomi, 2007; Soibelzon and Rincón, 2007; Prevosti and Ferrero, 2008). Some groups, like foxes and procyonids only have old or partial revisions, and thus some dubious taxa (e.g. *Dusciyon peruanus*) were excluded from this review. Unpublished new species (e.g. Zetti, 1972; Berman, 1987, 1994) were also not included.

In order to characterize the ecological diversity of carnivore faunas we used body mass and diet (cf. Van Valkenburgh, 1988; 1991; 2007; Van Valkenburgh and Hertel, 1998). We chose broad dietary classes because they were easiest to apply to any taxa with the available information, but we highlight that these classes are segments of a continuous variation (and not discrete categories). Nevertheless, these categories are adequate to describe the general dietary habits of carnivores, and have been used in several papers (e.g. Berta, 1989; Van Valkenburgh, 1988; 1991; 2007; Van

Valkenburgh and Hertel, 1998). The carnivores were classified as: hypercarnivorous: species that feed mostly on other vertebrates (mammals principally); mesocarnivorous: species with diets mostly composed of vertebrates but incorporating some consistent amount of insects, fruits or other non-vertebrate items; omnivorous: species that incorporate a large proportion of non-vertebrate items like insects or vegetables; piscivorous: species with a diet composed mainly by fishes. The diet and the body mass data of extinct species were taken from the available literature (Berta, 1989; Van Valkenburgh, 1991; Van Valkenburgh and Koepfli, 1993; Berman, 1994; Van Valkenburgh and Hertel, 1998; Prevosti and Vizcaíno, 2006; Prevosti, 2006a; Soibelzon and Tartarini, in press; Figueirido and Soibelzon in press). For those species that lack published data, but have close living representatives of similar size and morphology, the information on the living relatives was used (e.g. *L. griseus* for the extinct *L. cultridens*). In cases where there was more than one recent representative, the data were averaged. Body mass of *Cyonasua* and *Chapalmalania* was estimated following the equation for all carnivora based on m1 mesio-distal length proposed by Van Valkenburgh (1990).

In order to discriminate immigration events we used the following criteria: if the taxon (or its closest relative) has an older record in Central or North America is counted as an immigrant. For example, the presence of *Smilodon* in South America during the Ensenadan is counted as an immigration event, because it has older records and a sister taxon in North America. Conversely the first occurrence of a “South American taxon” was taken as an “in situ” event. To define “South American taxa” we used biogeographic and fossil evidence: these are taxa that are (and were) restricted to South America. For example, the first record of *Smilodon populator* is counted as an “in situ” speciation. Phylogenetic analyses (Bardeleben, 2005; Prevosti, 2006a; Johnson et al.,

2006; Koepfli et al., 2007, 2008; Krause et al., 2008) were also used to classify these taxa. The poverty of the Central America fossil record may be generating some false “in situ” speciation events, and thus we consider this classification as a hypothesis that should be tested in the future with new fossil finds. The distribution, body mass and dietary class of Recent species was taken from Silva and Downing (1995), Sunquist and Sunquist (2002), Sillero Zubiri et al. (2004), Nowak (2005), and Wilson and Reeder (2005).

**[Figure 2 about here]**

## **Results**

The diversity curve (Fig. 2A; Table 1) shows that eutherian carnivores were rare during the interval Late Miocene-Pliocene (Huayquerian-Sanandresian), with four species or less. There is no record of eutherian carnivores during the Barrancalobian (Late Pliocene). Throughout the Early-Middle Pleistocene (Ensenadan) the diversity increased steeply to nearly 20 species, and then to more than 35 species in the Late Pleistocene (Lujanian). Between the Lujanian and Ensenadan the number of species dropped to seven. Another drop to just over 20 species was observed from the Lujanian to the Holocene (Platan), reaching a figure similar to that of the Ensenadan. Finally, the living fauna (composed of 46 species) surpasses the fossil one of any age.

The first and last records follow more or less the same pattern as the diversity curve (Fig. 2B). First records were very low during the interval Late Miocene-Pliocene, but increased to almost 20 in the Early-Middle Pleistocene and nearly 30 in the Late Pleistocene (Lujanian). During the Bonaerian and Holocene (Platan) the records fell down to four and five, respectively. The present fauna includes 15 "new" species (first records, ie. species without fossil representatives). Last records (extinctions) are roughly

equal to first records during Late Miocene-Pliocene; during the Pleistocene the two curves are similar in shape, but last records are fewer than new ones. It is notable that there is only one last record in the Holocene, and another in the present fauna (recent extinction). We obtained the same pattern when first and last records were calculated as a percentage of diversity (Fig. 2.C). During almost Late Miocene-Pliocene first and last records have similar numbers for each age, and reach the 100 % during Huayquerian, Montehermosan, and Chapadmalalan (only first records). During Pleistocene-Recent the first records had higher numbers than last records, but only reach the 100% in the Ensenadan. The percentage of last record is highest in the Ensenadan.

The first immigration event was recorded in the Late Miocene. Then in the Late Pliocene (Vorohuean) two new immigration events are recorded, but is in the Early to Middle Pleistocene (Ensenadan) and Late Pleistocene (Lujanian) that the immigration events increased abruptly to eight (Fig. 2D). No immigration was recorded in the Middle Pleistocene (Bonaerian). Since Late Pleistocene (Lujanian) the immigrations decreased to two in the Holocene, and two in recent times. The “in situ” originations follow the same pattern as the immigration events, but the numbers are higher for the Pleistocene and Recent, and lower for the Holocene. The percentage of immigration events and “in situ” speciations (Fig. 2E), in relation to diversity, show the same pattern. “In situ” speciation is the only one to reached 100%, which occurred from the Huayquerian through the Chapadmalalan. During pre-Pleistocene ages both variables have similar numbers, but “in situ” speciation has higher numbers in the Pleistocene-Recent.

Although omnivorous species are the only eutherian carnivores during the interval Late Miocene-Middle Pliocene (Huayquerian-Barrancalobian) their diversity is noticeably low (five species) (Fig. 3A). This situation changes in the Late Pleistocene

(Lujanian) when 13 species are recorded. During the Holocene this number falls to eight, a drop that also affects other diet categories, but to different degrees. In the present, there are 14 omnivorous species. The first hypercarnivorous eutherian carnivores occur in the Late Pliocene (Vorohuean-Sanandresian), when only one species is recorded, but in the Ensenadan and Lujanian 12 and 17 species are recorded, respectively. During the Bonaerian the number of hypercarnivores is limited to two. Currently, the number of hypercarnivores inhabiting South America is similar to that of the Lujanian. The first mesocarnivorous species are recorded in the Late Pliocene (Vorohuean-Sanandresian). Later (the beginning of the Pleistocene) mesocarnivore diversity starts to increase (three species in the Ensenadan, four in the Bonaerian, 13 in the Lujanian), while a noticeable drop occurs in the Holocene (eight species), followed by a recovery in the present, with a total of 18 species. Piscivorous species are restricted to the Pleistocene-Holocene, but only in the Late Pleistocene (Lujanian) is there more than one species (two).

**[Figure 3 about here]**

Interestingly, the percentage of diet types in each age (Fig. 3B) shows that in the interval Pleistocene-Recent, hypercarnivorous and omnivorous taxa are better represented than mesocarnivorous and piscivorous ones. Omnivorous species dominate in pre-Pleistocene ages, at least until the Vorohuean, when hypercarnivorous and mesocarnivorous species are first recorded. Other remarkable thing is that during the Pleistocene (except in the Bonaerian), hypercarnivores are more abundant than omnivores, but in the Holocene-Recent they are less or equally represented.

Eutherian carnivores were small animals (body mass  $\approx$  2-7 kgs) during the interval Late Miocene-Pliocene, except for the giant procyonid *Chapalmalania* ( $\approx$  25

kg) (Fig. 4; Table 1). The range in body mass at each age during this interval was narrow, probably due to the low diversity and taxonomic uniformity observed prior to the Early Pleistocene. This range increased in the Early to Middle Pleistocene, when a maximum body mass of  $\approx 1000$  kg and a minimum of  $\approx 0.20$  kg was recorded, although most species were in the 4-50 kg range (median = 10.33 kg). Post-Ensenadan faunas present the same pattern, but the median and maximum values were lower (especially in Holocene to Recent faunas). The Bonaerian was an exception because of the higher median values recorded (290 kg), even if the maximum value was lower (600 kg). However, this is an artefact of the low number of species known from this age (seven), plus the presence of four large species (three bears and *Smilodon populator*).

There is one “Lazarus taxon” recorded from the Barrancalobian, another from the Sanandresian, five from the Bonaerian and ten from the Holocene (Fig. 3C). These peaks may be due to a lack of data or drops recorded in earlier variables (e.g. diversity, see above).

## Discussion

The results presented here regarding the diversity of carnivorans through time (Fig. 2A), agree with those published previously (e.g. Cione and Tonni, 1995; Woodburne et al., 2006; Prevosti et al., 2006; Soibelzon and Prevosti, 2007): the first occurrence of the group was in Late Miocene, when it was represented by procyonids, followed by mustelids and canids in the Late Pliocene (Vorohuean), and then by several families (Felidae, Ursidae, Mephitidae), subfamilies (Lutrinae), and genera in the Early-Middle Pleistocene (Ensenadan). The low pre-Pleistocene diversity of carnivores contrasts with the high numbers recorded in Pleistocene-Recent faunas. At first sight, diversity appears to increase gradually during the interval Pleistocene to Recent, but

there were two drops: the first in the Bonaerian and the second in the Holocene. As is discussed below, we believe that these drops are due to biases in the fossil record.

**[Figure 4 about here]**

The first and last records of the pre-Pleistocene ages follow the diversity line in magnitude and pattern; this is because most species are restricted to one age (see Berman, 1989, 1994; Cione and Tonni, 1995; Fig. 2B, 2C). The last records of the Pleistocene-Holocene show two major extinction events: one in the Middle Pleistocene (end of the Ensenadan) and other at the end of the Lujanian. The first corresponds to a sudden change in the composition of the carnivore fauna between the Ensenadan and Bonaerian. Several large hypercarnivorous canids (e.g. *Theriodictis*, *Protocyon scagliarum*, “*Canis*” *gezi*), foxes (e.g. *Dusicyon ensenadensis*), the giant short-faced bear (*Arctotherium angustidens*), some mustelids (e.g. *Lyncodon bosei*, *Galictis henningi*, *Stipanიცია*), and the last member of the procyonid *Cyonasua* “group” (*C. merani*) became extinct at this boundary (Soibelzon et al., 2005; Prevosti, 2006a, 2006b). However, several short-faced bears (*Arctotherium tarijense*, *A. bonariense*, *A. vetustum*, *A. wingei*), mustelids (e.g. *G. cuja*, *L. patagonicus*, *Eira*, *Pteronura*), foxes and wolf like canids (e.g. *Canis dirus*, *D. avus*), procyonids (e.g. *Nasua*, *Procyon*), and mephitids (e.g. *Conepatus semistriatus*, *Conepatus humboldtii*) appeared after it. The extinction recorded at the end of the Lujanian corresponds to the Pleistocene-Holocene mass extinction that affected most American mammals, especially the larger ones (see Borrero, 2009; Cione et al., 2009).

The immigration curve (Fig. 2D, 2E), not only shows the previously recognized events of the Late Miocene, Late Pliocene and Early-Middle Pleistocene, but also another two: Late Pleistocene and Holocene. The peak recorded in the Ensenadan

corresponds to the massive immigration of North American mammals, which included several herbivorous lineages (see Cione and Tonni, 1995; Woodburne et al., 2006). The peak recorded in the Lujanian is a less well-known immigration event, but for carnivores it was numerically similar to the previous one. Sabre-toothed cats (*S. fatalis*), dire wolves (*C. dirus*), the North American grey fox (*Urocyon cinereoargenteus*), procyonids (*Nasua*, *Procyon*), and mustelids (*Eira*, *Pteronura*) were part or results of this immigration (see Kurtén and Werdelin, 1990; Prevosti, 2006a; Prevosti and Rincón, 2007; Prevosti and Ferrero, 2008). The first records of *Tremarctos*, *Mustela*, *Potos*, and *Canis familiaris* in the Holocene of South America may represent post-Pleistocene immigrations (Soibelzon et al. 2005).

As can be seen in Fig. 2E and D, “in situ” speciation explains much more diversity than immigration, but it is clear that both were responsible for the past and present South American carnivore diversity. Thus, South American carnivore faunas are a consequence of several immigration events from Central and North America, plus later speciation “in situ” (see Soibelzon and Prevosti, 2007); successive immigration and speciation events caused an enrichment of the South American carnivore fauna through time (Fig. 2D, 2E). But this pattern was not gradual (Fig. 2A), and can be divided in two phases, one of low diversity before the Pleistocene, and another of high diversity in the Pleistocene-Recent.

There are several taxa that may represent “reverse” cases (i.e. that migrate from South America to Central and North America). For example *Herpailurus*, *Eira barbara*, *Procyon cancrivorus*, and *Speothos* have older records and a wider Recent geographic distribution in South America, and may thus be interpreted as South American invaders into Central and North America. Webb (2004; 2006) postulated a Late Pleistocene invasion of Central America by South American intertropical mammals that might

include these species. However, some of these taxa (e.g. *Herpailurus*) are widely distributed and also occur in temperate habitats, something that could point to a different time of immigration.

Diet and body mass also show a two phase pattern (Figs. 3A, B, 4). Pre-Pleistocene carnivores were mostly omnivorous, while Pleistocene-Recent faunas include taxa of all dietary types. The main difference between Pleistocene and Holocene-Recent faunas is that the former proportionally encompassed more hypercarnivores than the latter. This could be a result of the Pleistocene-Holocene mass extinction, where mainly carnivores of greater than 30 kg body mass disappeared, most of which were hypercarnivores. During pre-Pleistocene ages most species were small (< 10 kg), with the exception of the Late Pliocene (Chapalmalalan-Vorohueian) *Chapadmalania*, which had a body mass of more than 20 kg. Pleistocene-Recent faunas show a wider range of body sizes, spanning from 0.5 to more than 100 kg. Pleistocene faunas have higher maximum body masses than Holocene-Recent ones (600-900 versus 175 kgs), a difference explained by the Pleistocene-Holocene extinction that removed most of the large carnivores (e.g. Van Valkenburgh and Hertel, 1998; Cione et al., 2009). The greater variety of size and diets during Pleistocene-Recent indicates more complex paleosynecological relationships within the terrestrial carnivore guild, and between them and their prey (see Prevosti and Vizcaíno, 2006, Soibelzon et al. 2009).

**[Table 1 about here]**

This discussion was based in a near literal reading of the fossil record, but as was briefly mentioned earlier, this record possesses several biases that may modify these conclusions in the future.

There is a clear bias against tropical regions (Marshall et al., 1982; Behrensmeier et al., 2000). Most pre-Lujanian sites are from the southern part of South America, especially Argentina, while Lujanian-Platan sites are more evenly distributed. Thus provinciality should increase the diversity (and other variables) of the Lujanian-Recent faunas (Figs. 2, 3). In fact, if we exclude the faunas of Chile, Uruguay and Argentina, the diversity, first records, and number of hypercarnivorous and omnivorous species of the Lujanian are similar to the Ensenadan ones, but last records, immigrations, and “in situ” speciation are lower. Something similar happens with the Recent fauna. As can be seen in Figs. 2 and 3, “Lazarus taxa” indicate that the absence of records during the Barrancalobian, and the low diversity of the Bonaerian (Middle-Late Pleistocene) and Platan (Holocene) are artefacts due to poor preservation conditions or scarcity of sites from these ages. Bonaerian sites are restricted to a few localities of the Buenos Aires province, which explains the low diversity of carnivores in this age. Some of the high numbers of last records of the Ensenadan and high numbers of first records, immigration, and “in situ” speciation of the Lujanian may be the result of the small sample of Bonaerian fossil sites. The same argument could be used for the low diversity (and other variables) of the Platan. Most first records, immigration and “in situ” speciation events recorded for the Recent fauna are probably a byproduct of the preservation bias of the Platan. Another problem is the age of several cave deposits of Brazil that are usually referred to the Lujanian (also in this paper), but that were recently dated to between 10 and 30 ka (Bonaerian-Lujanian; Auler et al., 2006). Excluding these sites produced similar results to those obtained when sites from the northern part of South America were excluded (see above).

This review is a first approach to explore the history of South American carnivores through a quantification of the information in the fossil record. New

systematic revision, fieldwork, revision of biostratigraphic-chronostratigraphic schemes and chronologic assignation of fossil sites should help to improve this database, and may provide a more complete picture of the history of carnivorans in South America. A deeper analysis of this dataset will help to test the effect of the detected biases on its interpretation.

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## Figure and Table legends

Figure 1. Paleomagnetic, biostratigraphic and chronostratigraphic chart of South America, with the first occurrences of carnivores of North American origin during the Late Miocene-Pleistocene. Modified from Prevosti et al. (2006).

Figure 2. Diversity, first and last records, immigration and “in situ” speciation of South American carnivores. A: diversity; B and C: absolute number and percentage of first (solid line) and last (broken line) appearances, respectively. D and E: absolute number and percentage of immigration (solid line) and “in situ” speciation (broken line) events, respectively Huay.: Huayquerian; Mont.: Montehermosan; Chap.: Chapadmalalan; Barra.: Barrancalobian; Voroh.: Vorohueian; San.: Sanandresian; Ense.: Ensenadan; Bona.: Bonaerian; Luja.: Lujanian; Plat.: Platan; Rec.: Recent.

Figure 3. Diet and “Lazarus taxa” through time. A and B: Number and percentage of hypercarnivorous (solid line and empty circles), omnivorous (dotted line and diamonds), mesocarnivorous (broken line and squares), and piscivorous species (broken lines and triangles), respectively; C: diversity (solid line) and “Lazarus taxa” (broken line). Other abbreviations as in Fig. 1.

Figure 4. Carnivore body mass through time. See Fig. 1. for abbreviations.

Table 1. Diversity, first and last records, immigration and “in situ” speciation events, diet, and “Lazarus taxa” of South America for each age. FR: first record; LR: last record; Mig: immigration events; Esp: “in situ” speciation events; Laz: “Lazarus

taxon"; Hyp: hypercarnivores; Mes: mesocarnivores; Om: omnivores; Pisc:  
piscivores; SD: standard deviation.