Chapter 4
South American Fossil Carnivorans (Order Carnivora)

Abstract Carnivora is a clade of mammalian predators that evolved in northern continents during the Paleocene, and since the Miocene have invaded the southern continents (i.e., Africa and South America). They evolved a large diversity and disparity of body forms and size, which allowed the occupation of many ecological niches. Carnivorans arrived in South America in the late Miocene, when Central America provided a land bridge, or an island chain that facilitated migration of initial mammalian groups including carnivorans. The first carnivorans in South America were procyonids, followed by mustelids and canids in the late Pliocene, and felids, mephitids, and ursids in the Pleistocene. Their high diversity and morphological disparity can be explained through a combination of repeated immigrations and radiations into empty ecological zones. Here we present a synthesis of the systematics, distribution, and paleocology of fossil terrestrial carnivorans of South America.

Keywords Canidae · Felidae · Mustelidae · Procyonidae · Ursidae
Mephitidae · Immigration · Speciation

4.1 Introduction

Like domesticated animals, carnivorans are a very familiar group that has a long history of interactions with hominids during the Pleistocene, where they were both the hunters and the hunted, as depicted by Paleolithic carnivoran representations in cave paintings and sculptures (e.g., Kurtén 1968; Brain 1981; Clutton Brock 1996a; Morey 2010; Figs. 1.2–3). Their place in human life as both prey animals and competitors gave them a symbolic value that explains their inclusion in the cultures, religions, and fables of different times (Clutton Brock 1996a). Their symbolic importance, value as material resources, and the use of domestic carnivorans for different purposes (e.g., dog and cat; Clutton Brock 1996a; Morey 2010) explains the intense interactions between humans and this mammalian clade during the Quaternary. Different kinds of relationships between carnivorans and

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humans are included in art (e.g., cave paintings, pottery; Cardich 1979; Paunero et al. 2005; Gordillo 2010), myths, use of their remains in burials (Prates et al. 2010; Politis et al. 2014), hunting, and taming wild species, like the domestic dog (Schwartz 1997; Prates et al. 2010; Stahl 2013).

Carnivorans are a monophyletic group, and although they are primarily predators that live by hunting and eating other animals, a habit that is thought to have been present in their most recent common ancestor, some descendants became adapted to omnivorous or herbivorous diets (Hunt 1996; Flynn and Wesley-Hunt 2005; Flynn et al. 2010). The key synapomorphy of carnivorans is the presence of a pair of modified teeth (carnassials: upper fourth premolar and lower first molar), with long crests that function as scissors and are optimized for slicing meat (Ewer 1973; Van Valkenburgh 1989) (Fig. 4.1).

Carnivora is the crown group that contains the closest common ancestor of living carnivorans and all its descendants and consists of two large clades of living and fossil taxa. Feliformia includes felids (Felidae), Asiatic linsangs (Prionodontidae), hyaenids (Hyaenidae), "false" sabertooth cats (extinct Nimravidae and Barbourofelidae), palm civets (Nandiniidae), civets (Viverridae), mongooses (Herpestidae), and falanoucs (Eupleridae); Caniformia includes dogs (Canidae), bears (Ursidae), skunks (Mephitidae), weasels, otters, and relatives (Mustelidae), red pandas (Ailuridae), raccoons (Procyonidae), seals (Phocidae), sea lions (Otariidae), walruses (Odobenidae), and bear-dogs (extinct Amphicyonidae) (Hunt 1996; Morlo et al. 2004; Flynn et al. 2010; Eizirik et al. 2010; Nyakatura and Bininda-Emonds 2012). Seals, sea lions, and walruses form a clade that is called Pinnipedia that includes the carnivorans living in the sea. More basal carnivoran groups are the Viverravidae and the paraphyletic Miacidae, which are successive sister taxa of the monophyletic group that includes Feliformia and Caniformia (Flynn et al. 2010; Fig. 1.5). Miacidae and Viverravidae were historically included within the Order Carnivora (e.g., Hunt 1996), but now are excluded from crown-group Carnivora and included in the clade Carnivoramorpha (Flynn and Wesley-Hunt 2005; Flynn et al. 2010).

Recent phylogenetic studies show that carnivorans form a clade with pangolins and Creodonta (an extinct clade of predators), as their successive sister taxa and all are members of Laurasiatheria (including ungulates, bats, and cetaceans) (O'Leary et al. 2013; Fig. 1.5). However, Creodonta is paraphyletic and is divided in Hyaenodonta and Oxyaenodonta, with Hyaenodonta being the closest sister taxon of Carnivora (Solé and Smith 2013; Flynn and Wesley-Hunt 2005; Fig. 1.5).

Carnivorans have a long fossil record that indicates an origin in northern continents. The oldest records concerned viverravids found in the early Paleocene of North America (NA). This group was also present in Asia in the late Paleocene. Most living families of Caniformia are first recorded in the Eocene, while the crown group Feliformia is only recorded since the late Oligocene (Hunt 1996; Flynn and Wesley-Hunt 2005). Carnivorans invaded a wide range of habitats in most continents and seas, and consequently they display great taxonomic diversity, morphological disparity, and size.

The fossil record of taxonomic diversity in SA could be explained by a combination of succesive immigrations from Central America and local radiations

Fig. 4.1 Map of South America showing the localities (black symbols), or states, provinces, departments and regions (white symbols) mentioned in the text, where fossil carnivorans have been recorded. 1 Orocual (Venezuela); 2 La Calera (Ecuador); 3 La Chimba (Ecuador); 4 Cotocallo (Ecuador); 5 Punin (Ecuador); Loma Alta (Ecuador); 7 La Carolina (Ecuador); 8 Talara (Perú); 9 Huánuco department (Perú); 10 Junín department (Perú); 11 Arequipa department (Perú); 12 Tirapata (Perú); 13 Tarija (Bolivia); 14 Piaui state (Brasil); 15 Bahia State (Brasil); 16 Minas Gerais state (Brasil); 17 Mato Grosso state (Brazil); 18 Rio Grande do Sul (Brasil); 19 Formosa province (Argentina); 20 Catamarca province (Argentina); 21 Mendoza province (Argentina); 22 Córdoba province (Argentina); 23 Entre Ríos province (Argentina); 24 Buenos Aires province; 25 Lujan (Argentina); 26 La Pampa province (Argentina); 27 Valdivia (Chile); 28 Tierra del Fuego Island (Chile and Argentina); 29 Beagle Channel (Chile and Argentina). Broken line: northern limit of the Patagonian Region; Point line: northern and western limits of the Pampean Region. Squares: Quaternary; triangles: Pliocene; stars: late Miocene

enabled by the availability of ecological zones, plus later radiation of several clades in SA (Prevosti and Soibelzon 2012). The immigration of carnivorans to SA was facilitated by tectonic changes occurring in Panama that established intermittent terrestrial connections with Central America during the late Miocene (see Chap. 2). The pattern of carnivoran immigration was incremental. Procyonids arrived in the late Miocene, followed by weasels and foxes in the late Pliocene, and felids, otters,

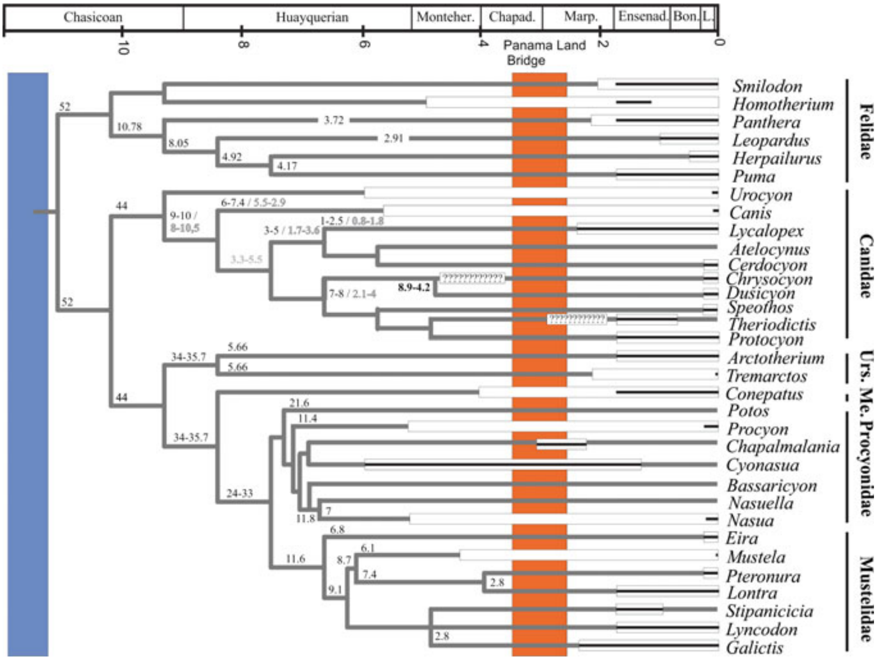


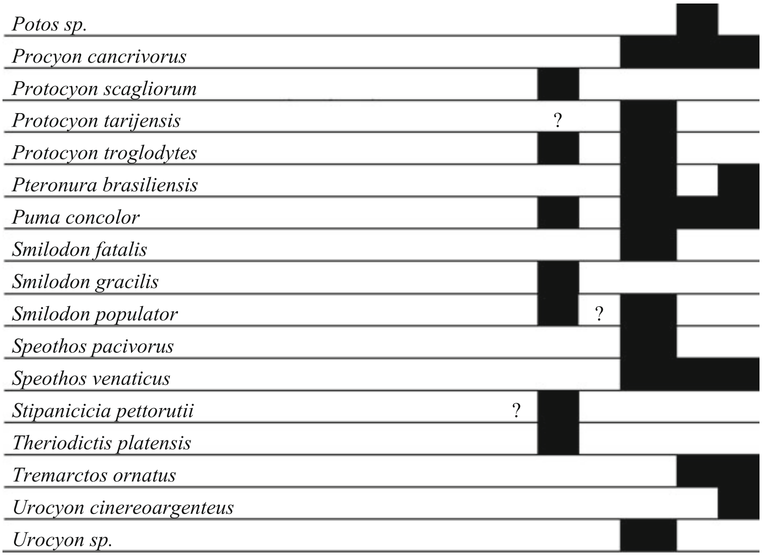
Fig. 4.2 South American carnivore supertree showing the fossil record of each genus in South America (black line) or other continents (white box). The numbers in the nodes correspond to molecular dates of divergence. For canids different estimates of the time of molecular divergence are given (tree nodes do not represent age of divergence). The orange box represents the "traditional" estimate of the establishment of the Panama Bridge, while the purple box indicates new evidence that suggest an early connection between South America and the Panama arc (see Chap. 2)

skunks, large canids, and bears in the Pleistocene (Fig. 4.2; Table 4.1; Soibelzon and Prevosti 2007, 2013; Prevosti and Soibelzon 2012). During the Late Pleistocene, other immigrations are recorded (e.g., *Urocyon* Baird 1857, *Canis dirus* Leidy 1858, *Smilodon fatalis* Leidy 1868), and it is possible that some carnivores originating in South America invaded Central America (e.g., *Speothos* Lund 1839, *Eira* Hamilton Smith 1842, *Procyon cancrivorus*). From the early–Middle Pleistocene (Ensenadan, 1.8–0.5 Ma) onwards, there was a large increase in diversity and morphological disparity, that was caused not only by immigration but also by the high rate of in situ speciation in the Pleistocene (Ensenadan–Lujanian; Prevosti and Soibelzon 2012). Molecular data suggest that the living populations of cougar (*Puma concolor* (Linnaeus 1771)) represent a recent (ca. 10 ka) recolonization of NA from SA (Culver et al. 2000). The fossil record shows a low level diversity, extinctions, speciation, and immigration during the late Miocene–Pliocene, with a substantial increase in these processes in the early–Middle Pleistocene (Ensenadan) and Late Pleistocene (Lujanian; Prevosti and Soibelzon 2012). In summary, most carnivoran groups immigrated to South

Table 4.1 Distribution of carnivorans in the South American Stages/Ages. ?: dubious record

	Huayquerian	Montehermosan	Chapadmalalan	Barrancalobian	Vorohuean	Sanandresian	Ensenadan	Bonaerian	Lujanian	Platan	Recent
"Canis" gezi							■				
"Felis" vorohuensis							■				
Arctotherium angustidens							■				
Arctotherium bonariense								?	■		
Arctotherium tarijense								?	■		
Arctotherium vetustum								?			
Arctotherium wingei									■		
Atelocynus microtis											■
Bassaricyon alleni											■
Bassaricyon bedarddi											■
Bassaricyon gabbi											■
Canis dirus									■		
Canis familiaris										■	■
Canis nehringi									■		
Cerdocyon thous									■	■	■
Chapalmalania altaefrontis			■								
Chapalmalania ortognatha			■		■						
Chrysocyon brachyurus							?		■	■	■
Conepatus chinga							?		■	■	■
Conepatus mercedensis							■		■		
Conepatus primaevus							■	?			
Conepatus semistriatus									■		■
Conepatus talarae									■		
Cyonasua argentina	■										
Cyonasua brevirostris	■										
Cyonasua clausa		■									
Cyonasua groeberi	?	?	?								
Cyonasua lutaria			■								
Cyonasua meranii							■				
Cyonasua pascuali	■										
Cyonasua sp. nov.	■										
Dusicyon australis											■
Dusicyon avus									■	■	

Eira barbara					■		■
Galictis cuja					■	■	■
Galictis hennigi			■				
Galictis sorgentinii	■						
Galictis sp.		■					
Galictis vittata					■		■
Herpailurus sp.				■			
Herpailurus yagouaroundi					?		■
Homotherium venezuelensis			■				
Leopardus colocolo			■			■	■
Leopardus geoffroyi							■
Leopardus guigna							■
Leopardus jacobita							■
Leopardus pardalis					■	■	■
Leopardus tigrinus					■	?	■
Leopardus wiedii					■	?	■
Lontra felina							■
Lontra longicaudis			■		■	■	■
Lontra provocax						■	■
Lycalopex culpaeus					■	■	■
Lycalopex cultridens	■		■				
Lycalopex ensenadensis			■		■		
Lycalopex fulvipes							■
Lycalopex griseus						■	■
Lycalopex gymnocercus			■	?	■	■	■
Lycalopex sechurae					■	■	■
Lycalopex sp.		■					
Lycalopex vetulus					■		■
Lyncodon bosei			■				
Lyncodon patagonicus					■	■	■
Mustela africana							■
Mustela felipei							■
Mustela frenata						■	■
Nasua narica							■
Nasua nasua					■	■	■
Nasuella olivacea							■
Panthera onca			■		■	■	■
Potos flavus							■



America, and speciated there, during the Pleistocene (Ensenadan-Platan). The fauna was further shaped by extinctions of large effect occurring at the end of the Ensenadan and Lujanian (Prevosti and Soibelzon 2012; see also Chap. 5).

4.2 Systematics, Distribution, and Paleoecology

Here we present a synthesis of the diversity, paleoecology, temporal and geographic distribution, and paleoecology of South American carnivores at the generic level (4.1). With regard to fossil occurrences of living taxa, we used known ecological aspects of living representatives to infer their paleoecology (Table 4.1). The large body of pertinent archeological works was not exhaustively searched, and some carnivoran records for the Holocene were probably missed. One issue with archeological papers is that they usually lack enough information to confirm the alleged taxonomic determinations.

Mammalia Linnaeus 1758
Carnivora Bowdich 1821
Feliformia Kretzoi 1945
Felidae Fischer 1817

Felids are highly specialized terrestrial apex predators with a hypercarnivorous diets (Ewer 1973; Wilson and Mittermeier 2009). They have a very short snout, powerful jaw muscles, and a reduced dentition that is specialized for shearing meat (Ewer 1973; Radinsky 1981; Biknevicius and Van Valkenburgh 1996). The oldest record of the family is dated between 35–28 Ma from Europe and spread to other

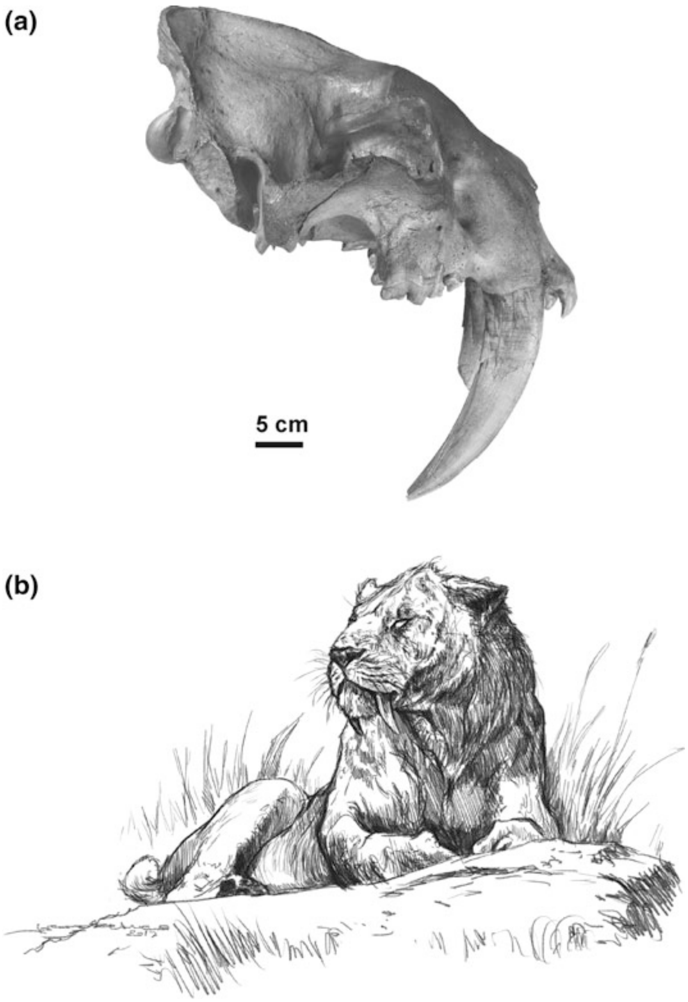


Fig. 4.3 Lateral view of the skull of *Smilodon fatalis* (LACM-HC2001) (**a**) and life reconstruction of *Smilodon populator* (**b**). Scale = 5 cm

continents during the Miocene–Pleistocene (Hunt 1996; Werdelin et al. 2008). South American felids are included in the two subfamilies Machairodontinae and Felinae, which correspond to “sabre-toothed” and “conical-toothed” cats, respectively (Fig. 4.2; Werdelin 1996; Werdelin et al. 2008). Two phylogenies were recently published that include fossil taxa (Sakamoto and Ruta 2012; Christiansen 2013), but the relationships of most fossil felids are still poorly understood.

Machairodontinae Gill 1872

Smilodon Lund 1842

(Fig. 4.3; Tables 4.1 and 4.2)

Table 4.2 Diet and body mass of the South America carnivorans. The criterion for diet classification was taken from Prevosti et al. (2013). RGA: relative grinding area of lower carnassial (m1)

Taxa	RGA	Diet	Body mass (kg)	Commentaries
Smilodon populator	0	Hypercarnivore	290.00	Data from Prevosti et al. (2013)
Smilodon fatalis	0	Hypercarnivore	220.00	Data from Prevosti et al. (2013)
Smilodon gracilis	0	Hypercarnivore	77.50	Data from Prevosti et al. (2013)
Homotherium venezuelensis	0	Hypercarnivore	190.00	Data from Prevosti et al. (2013)
Panthera onca	0	Hypercarnivore	71.20	Data from Prevosti et al. (2013)
Puma concolor	0	Hypercarnivore	52.53	Data from Prevosti et al. (2013)
Herpailurus sp.	0	Hypercarnivore	5.20	Data from Prevosti et al. (2013)
Herpailurus yagouaroundi	0	Hypercarnivore	5.20	Data from Prevosti et al. (2013)
"Felis" vorohuensis	0	Hypercarnivore	3.77	Data from Prevosti et al. (2013)
Leopardus colocolo	0	Hypercarnivore	4.92	Data from Prevosti et al. (2013)
Leopardus geoffroyi	0	Hypercarnivore	2.89	Data from Prevosti et al. (2013)
Leopardus jacobita	0	Hypercarnivore	9.17	Data from Prevosti et al. (2013)
Leopardus guigna	0	Hypercarnivore	2.20	Data from Prevosti et al. (2013)
Leopardus pardalis	0	Hypercarnivore	10.08	Data from Prevosti et al. (2013)
Leopardus tigrinus	0	Hypercarnivore	3.00	Data from Prevosti et al. (2013)
Leopardus wiedii	0	Hypercarnivore	2.85	Data from Prevosti et al. (2013)
Lycalopex gymnocercus	0.54	Mesocarnivore	4.98	Data from Prevosti et al. (2013)
Lycalopex cultridens	0.55	Mesocarnivore	3.33	Data from Prevosti et al. (2013)
Lycalopex sp.	0.56	Mesocarnivore	4.20	Data from Prevosti et al. (2013)
Lycalopex culpaeus	0.49	Mesocarnivore	7.28	Data from Prevosti et al. (2013)
Lycalopex griseus	0.55	Mesocarnivore	3.33	Data from Prevosti et al. (2013)

(continued)

Table 4.2 (continued)

Taxa	RGA	Diet	Body mass (kg)	Commentaries
Lycalopex vetulus	0.68	Omnivore	3.35	Data from Prevosti et al. (2013)
Lycalopex fulvipes	0.59	Mesocarnivore	2.71	Data from Prevosti et al. (2013)
Lycalopex sechurae	0.60	Omnivore	3.60	Data from Prevosti et al. (2013)
Lycalopex ensenadensis	0.59	Omnivore	4.98	Data from Prevosti et al. (2013)
Cerdocyon thous	0.58	Hypercarnivore	5.70	Data from Prevosti et al. (2013)
Atelocynus microtis	0.56	Mesocarnivore	9.50	Data from Prevosti et al. (2013)
Chrysocyon brachyurus	0.51	Omnivore	25.00	Data from Prevosti et al. (2013)
Speothos venaticus	0.45	Hypercarnivore	6.50	Data from Prevosti et al. (2013)
Speothos pacivorus	0.45	Hypercarnivore	6.50	Data from Prevosti et al. (2013)
Dusicyon australis	0.48	Mesocarnivore	11.00	Data from Prevosti et al. (2013)
Dusicyon avus	0.48	Mesocarnivore	14.65	Data from Prevosti et al. (2013)
Theriodictis platensis	0.40	Hypercarnivore	36.00	Data from Prevosti et al. (2013)
“Canis” gezi	0.38	Hypercarnivore	36.00	Data from Prevosti et al. (2013)
Protocyon scagliorum	0.40	Hypercarnivore	25.00	Data from Prevosti et al. (2013)
Protocyon troglodytes	0.40	Hypercarnivore	25.00	Data from Prevosti et al. (2013)
Protocyon tarijensis	0.45	Hypercarnivore	30.00	Data from Prevosti et al. (2013)
Canis dirus	0.44	Hypercarnivore	51.00	Data from Prevosti et al. (2013)
Canis nehringi	0.40	Hypercarnivore	34.54	Data from Prevosti (2006b)
Canis familiaris	0.49	Omnivore	15.00	Data from Prevosti et al. (2013)
Urocyon cinereoargenteus	0.62	Omnivore	3.65	Data from Prevosti et al. (2013)
Urocyon sp	0.62	Omnivore	3.65	Data from Prevosti et al. (2013)
Arctotherium angustidens	0.79	Omnivore	900.00	Data from Prevosti et al. (2013)

(continued)

Table 4.2 (continued)

Taxa	RGA	Diet	Body mass (kg)	Commentaries
Arctotherium wingei	0.66	Omnivore	250.00	Data from Prevosti et al. (2013)
Arctotherium vetustum	0.66	Omnivore	300.00	Data from Prevosti et al. (2013)
Arctotherium tarijense	0.71	Omnivore	500.00	Data from Prevosti et al. (2013)
Arctotherium bonariense	0.69	Omnivore	600.00	Data from Prevosti et al. (2013)
Tremarctos ornatus	0.73	Omnivore	175.00	Data from Prevosti et al. (2013)
Mustela frenata	0.36	Hypercarnivore	0.12	Data from Prevosti et al. (2013)
Mustela africana	0.41	Hypercarnivore	0.19	Data from Prevosti et al. (2013)
Mustela felipei	0.41	Hypercarnivore	0.14	Data from Prevosti et al. (2013)
Eira barbara	0.46	Mesocarnivore	4.23	Data from Prevosti et al. (2013)
Galictis cuja	0.35	Hypercarnivore	1.90	Data from Prevosti et al. (2013)
Galictis sorgentinii	0.55	Hypercarnivore	2.12	Data from Prevosti et al. (2013)
Galictis vittata	0.47	Hypercarnivore	2.34	Data from Prevosti et al. (2013)
Galictis hennigi	0.35	Hypercarnivore	2.12	Data from Prevosti et al. (2013)
Galictis sp.	0.35	Hypercarnivore	2.12	Data from Prevosti et al. (2013)
Lyncodon bosei	0.47	Hypercarnivore	0.23	Data from Prevosti et al. (2013)
Lyncodon patagonicus	0.44	Hypercarnivore	0.23	Data from Prevosti et al. (2013)
Stipanicicia pettorutii	0.41	Hypercarnivore	2.12	Data from Prevosti et al. (2013)
Lontra longicaudis	0.87	Hypercarnivore	10.33	Data from Prevosti et al. (2013)
Lontra provocax	0.68	Hypercarnivore	7.50	Data from Prevosti et al. (2013)
Lontra felina	0.86	Hypercarnivore	4.40	Data from Prevosti et al. (2013)
Pteronura brasiliensis	0.70	Hypercarnivore	26.00	Data from Prevosti et al. (2013)
Conepatus chinga	1.11	Omnivore	1.92	Data from Prevosti et al. (2013)

(continued)

Table 4.2 (continued)

Taxa	RGA	Diet	Body mass (kg)	Commentaries
Conepatus mercedensis	1.22	Omnivore	2.36	Data from Prevosti et al. (2013)
Conepatus talarae	1.27	Omnivore	2.36	Data from Prevosti et al. (2013)
Conepatus semistriatus	1.13	Omnivore	4.00	Data from Prevosti et al. (2013)
Conepatus primaevus	1.07	Omnivore	4.00	RGA: this work; Body mass of *C. semistriatus*
Nasua nasua	1.23	Omnivore	5.00	Data from Prevosti et al. (2013)
Nasua narica	1.23	Omnivore	5.00	Data from Prevosti et al. (2013)
Nasuella olivacea	1.23	Omnivore	4.00	Data from Prevosti et al. (2013)
Procyon cancrivorus	0.87	Omnivore	9.00	Data from Prevosti et al. (2013)
Potos flavus	2.08	Omnivore	3.00	Data from Prevosti et al. (2013)
Potos sp.	2.08	Omnivore	3.00	Data from Prevosti et al. (2013)
Bassaricyon gabbi	1.34	Omnivore	1.20	Data from Prevosti et al. (2013)
Bassaricyon bedarddi	1.34	Omnivore	1.20	Data from Prevosti et al. (2013)
Bassaricyon alleni	1.34	Omnivore	1.20	Data from Prevosti et al. (2013)
Cyonasua argentina	0.88	Omnivore	12.97	This work
Cyonasua pascuali	0.88	Omnivore	11.37	This work
Cyonasua groeberi	0.95	Omnivore	14.73	This work
Cyonasua brevirostris	0.95	Omnivore	14.19	This work
Cyonasua clausa	0.86	Omnivore	15.32	This work
Cyonasua lutaria	0.77	Omnivore	14.26	This work
Cyonasua meranii	0.88	Omnivore	13.49	This work
Chapalmalania ortognatha	0.79	Omnivore	88.13	This work
Chapalmalania altaefrontis	0.75	Omnivore	88.13	This work

Species in South America: *Smilodon fatalis* Leidy 1868, *S. gracilis* Cope 1880, and *S. populator* Lund 1842.

Temporal and geographic distribution: In South America, *Smilodon* is recorded from the Ensenadan to the Lujanian, from Tierra del Fuego in Chile to Venezuela, covering almost all of South America (Berta 1985; Kurtén and Werdelin 1990; Cartelle 1999; Ubilla and Perea 1999; Hadler Rodríguez et al. 2004; Rincón 2006; Prevosti and Pomi 2007; Prevosti et al. 2013; Fariña et al. 2014; Lindsey and Seymour 2015).

Paleoecology: *Smilodon* was a very large hypercanivore that predated on large mammals (Christiansen 2008; Slater and Van Valkenburgh 2008; Prevosti et al. 2010), using a stalk and ambush strategy (Akersten 1985; Van Valkenburgh and Hertel 1998; Coltrain et al. 2004; Prevosti and Vizcaíno 2006; Wroe et al. 2013; Prevosti and Martin 2013; Morales and Giannini 2014). *Smilodon* may have been a social predator (Carbone et al. 2009; Van Valkenburgh et al. 2009; Bocherens et al. 2016; but see McCall et al. 2003; Kiffner 2009). Using stable isotopes, Coltrain et al. (2004) suggested that *S. fatalis* hunted ruminants in North America (Rancho La Brea), while Prevosti and Martin (2013) and Bocherens et al. (2016) stated that *S. populator* consumed horses, ground sloths, and camelids in southern Patagonia and large mammals from open habits (e.g., macrauchenids and ground sloths) in the Pampean Region, respectively. The estimated body mass is between 55 kg and 100 kg for *S. gracilis*, 160 kg–280 kg for *S. fatalis*, and 220 kg–400 kg for *S. populator* (Christiansen and Harris 2005; Prevosti and Vizcaíno 2006; Prevosti and Martin 2013). The ambush strategy would have resulted in a bite to the throat of the prey powered by the massive jaw and neck muscles (Akersten 1985; Andersson et al. 2011). The robust forelimbs were important to fix the prey during the bite, and would have contributed to the bite power, generating a class 1 lever (McHenry et al. 2007; Meachen-Samuels and Van Valkenburgh 2009; Brown 2014).

Comments: *Smilodon* initially appeared in the late Pliocene of North America with the species *Smilodon gracilis* (Berta 1985, 1995). The immigration of this genus to South America is obscured by the limited fossil record of Central America and northern South America (Rincón et al. 2011). The characters used to separate *S. fatalis* from *S. populator* are variable, and some specimens have a mix of them, indicating that the genus needs a systematic review.

Recently, Chimento (2016) questioned the synonymy between *Smilodontidium riggii* Kraglievich 1948, and *Smilodon* (see Prevosti and Pomi 2007) and considered it a pantherine. This conclusion, however, was based on only two specimens of *S. populator*, without considering the intraspecific variation (or intrageneric in this case) among *Smilodon* and other felids. They utilized a selection of characters of unproved systematic value, ignoring other relevant features (e.g., length of the head of the astragalus; depth of the medial groove for the astragalar trochlea on the distal articular tibial facet in anterior view, robustness of the tibia diaphysis) that are shared with *Smilodon* (Prevosti and Pomi 2007).

Homotherium Fabrini 1890
(Fig. 4.4; Tables 4.1 and 4.2)

Fig. 4.4 Lateral view of the skull of *Homotherium venezuelensis* (IVIC OR 1352, Holotype) Scale = 5 cm

Species in South America: *Homotherium venezuelensis* Rincón, Prevosti and Parras 2011.

Temporal and geographic distribution: The South American species is restricted to the early–Middle Pleistocene of eastern Venezuela (Rincón et al. 2011).

Paleoecology: The morphology of *H. venezuelensis* is similar to its Holarctic congeners, and indicates that it had a body mass of ca. 190 kg and preyed on large mammals (Van Valkenburgh and Hertel 1998; Antón and Galobart 1999).

Comments: An incomplete mandible from Uruguay, with imprecise age, was assigned to cf. *Xenosmilus* (Mones and Rinderknecht 2004). The specimen clearly represents Homotheriini, but its generic attribution is uncertain (Rincón et al. 2011).

Felinae Fischer 1817
Panthera Oken 1816
(Fig. 4.5a; Tables 4.1 and 4.2)

Species in South America: *Panthera onca* (Linnaeus 1758).

Temporal and geographic distribution: In South America, *Panthera* is recorded from the Ensenadan to Present, and from Tierra del Fuego in Chile to northern South America (Cabrera 1934; Ochsenius and Gruhn 1979; Seymour 1983; Hoffstetter 1986; Cartelle 1999; Ubilla and Perea 1999; Pomi and Prevosti 2005; Martin 2013; Prevosti and Martin 2013).

Paleoecology: Living jaguars are the largest predators (30 kg–120 kg) in South America, hunting large- and medium-sized mammals (Wilson and Mittermeier 2009). During the Pleistocene, a much larger jaguar, with a body mass of about 190 kg, was present in Peru, Argentina, and southern Chile (Cabrera 1934; Seymour 1983; Pomi and Prevosti 2005). The Patagonian Jaguar has been given different names (the most common is *Panthera onca mesembrina* coined by Angel Cabrera 1934). A recent paleoecological study combining morphology, stable isotopes, and taphonomy demonstrated that the Patagonian Jaguar was able to hunt horses, camelids, and ground sloths (*Mylodon*) (Martin 2013; Prevosti and Martin 2013). A similar conclusion can be inferred for the Late Pleistocene jaguars found in the Pampean Region (Prevosti and Vizcaíno 2006). Recent isotopic data indicate

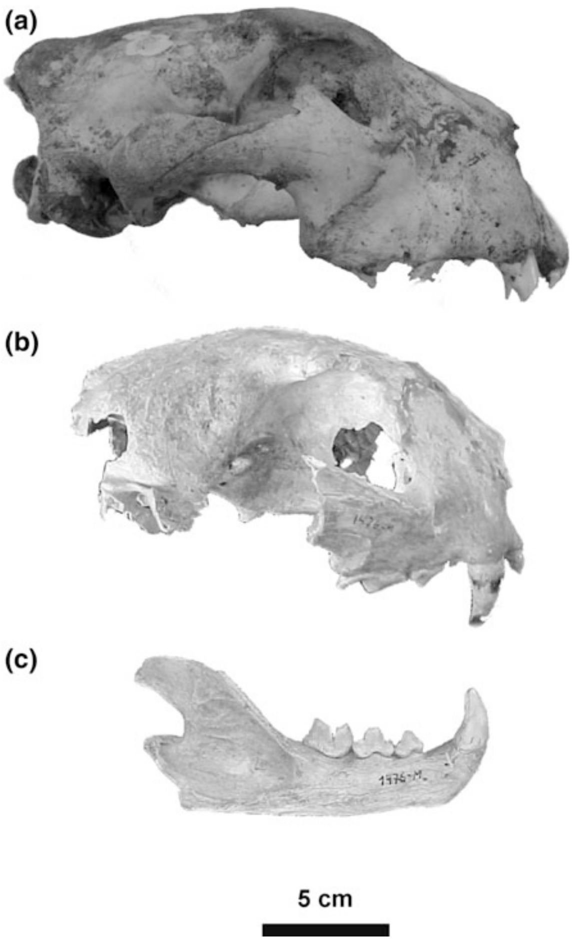


Fig. 4.5 Lateral view of the skull of a juvenil specimen of *Panthera onca mesembrina* (BM M20893) (**a**), lateral view of the skull (**b**), and mandible (**c**) of *Puma concolor* (MMP 1476 M). Scale = 5 cm

that it hunted macrauchenids, ground sloths, chinchillids, and equids; the first two groups in lower proportion, and the last two in larger proportion than in *Smilodon populator* and *Protocyon troglodytes* (Lund 1838) (Bocherens et al. 2016). This implies lower competition between these large felids than between *Smilodon fatalis* and *Panthera atrox* (Leidy 1853) from the Late Pleistocene of North America, probably related to the larger size of the South American species (Bocherens et al. 2016).

Comments: The oldest records of *Panthera onca* in South America are from the early–Middle Pleistocene (Ensenadan, 1.8–0.5 Ma) of the Pampean Region (Berman 1994; Ubilla and Perea 1999; Soibelzon and Prevosti 2007; Prevosti and Soibelzon 2012). In North America, the oldest records are of similar age (middle Irvingtonian, 1–0.6 Ma; Seymour 1993; Turner and Antón 1996; Woodburne 2004). Some authors have suggested that jaguars originated in Africa (Hemmer et al. 2010), while others suggested that the Old World, early Pleistocene taxon (e.g., *Panthera gombaszoegensis* (Kretzoi 1858)) was related to or should even be included in *P. onca* (Seymour 1993; Turner and Antón 1996). These hypotheses are based only on a comparative qualitative approach and should be tested using cladistic methodology. With the same approach mentioned above, and claiming the authority principle, Chimento (2016) considered that "*Felis*" *longifrons* Burmeister 1866 is not a synonym of *P. onca* (see Pomi and Prevosti 2005) but a different taxon. Unfortunately, omission of a complete discussion of previous systematic arguments, that support the synonymy, do not help to resolve the systematic position of this fossil (Pomi and Prevosti 2005).

Puma Jardine 1834
(Fig. 4.5b, c; Tables 4.1 and 4.2)

Species in South America: *Puma concolor* (Linnaeus 1771).

Temporal and geographic distribution: This species has been present in South America since the Ensenadan (1.8–0.5 Ma). The fossil record suggests a broad distribution in the continent (e.g., Hoffstetter 1952; Berta and Marshall 1978; Berman 1994; Ubilla and Perea 1999; Cartelle 1999; Shockey et al. 2009; Soibelzon and Prevosti 2007; Prevosti and Martin 2013), as is the case at present, with a species range covering all SA (Wilson and Mittermeier 2009). An excellent skull of *Puma concolor* (MMP 1476 M) found in Ensenadan levels of the sea-cliffs placed north of Mar del Plata city (Buenos Aires, Argentina) is shown in Fig. 4.5.

Paleoecology: *Puma* is one of the largest predators (34 kg–120 kg) in SA today and is distributed over a wide range of environments, such as cold steppes and tropical rainforests, where they hunt medium- and large-sized mammals, including domestic animals (e.g., cows and horses; Wilson and Mittermeier 2009). Larger pumas, with a body mass of about 140 kg, were recorded in Southern Patagonia as well as elsewhere (Prevosti and Vizcaíno 2006) during the Late Pleistocene, where they were able to prey on native horses (*Hippidium* and *Equus* (*Amerhippus*)) and camelids (Prevosti and Martin 2013).

Comments: Pumas, together with the small jaguarundi (*Herpailurus* Severtzov 1858), are related to the cheetah (*Acinonyx*) and represent another felid lineage that invaded SA during the Pleistocene. Its phylogenetic relationship, and the inclusion of the North American and Old Word fossil species in the same genus, was suggested by morphological and morphometric analyzes (Seymour 1999; Hemmer et al. 2004; Madurell Malapeira et al. 2010) but still has no cladistic support. The fossil record of *Puma concolor* is older in SA than in NA, since the oldest record in North America is 0.4 Ma (Van Valkenburgh et al. 1990). Living NA populations apparently constitute a re-migration from SA that occurred in the Late Pleistocene (10 ka; Culver et al. 2000).

Herpailurus Severtzov 1858
(Tables 4.1 and 4.2)

Species in South America: *Herpailurus yagouaroundi* (E. Geoffroy Saint-Hilaire 1803).

Temporal and geographic distribution: *H. yagouaroundi* is today distributed from southern NA to northern Patagonia, mainly in forested areas (Wilson and Mittermeier 2009). Its fossil record in SA is very incomplete and limited to the "Lujanian" of Minas Gerais and Bahia, Brazil (10–200 ka) and cf. *Herpailurus* from the Bonaerian (0.5–0.125 Ma) of the Pampean Region, Argentina (Prevosti 2006a). It is also mentioned in a faunal list of the Lujanian of Piaui; Brazil (48.5–12 ka BP; Guérin et al. 1993).

Paleoecology: Extrapolation of the ecological habits of the living species suggests that fossil *Herpailurus* were small predators (3 kg–7.6 kg) of small mammals (mainly rodents) (Wilson and Mittermeier 2009).

Comments: The long genetic separation of *Puma* and *Herpailurus* and their large morphological differences support the view that *Herpailurus* independently invaded South America after the establishment of the Panama Bridge (Prevosti 2006a; Rincón et al. 2011; Prevosti and Soibelzon 2012). Recently, Chimento et al. (2014) suggested that "*Felis*" *pumoides* Castellanos 1958, a species previously referred to *Puma concolor* (Berman 1994), is valid. The authors included the taxon in *Herpailurus* and assigned it to the Pliocene. However, the characters used to justify their taxonomic attribution are variable among felids or taxonomically irrelevant (Seymour 1999; Prevosti *pers. obs.*). For example, the minor palatine foramen has the same development in some of the living specimens of *P. concolor* (e.g., MACN 13054) studied by Chimento et al. (2014). Instead, the size and morphology of this fossil are close to the living *Puma*, as indicated by Berman (1994). At least one feature is different from the living specimens of *Puma concolor* studied, the shape of the P3 (see Castellanos 1958), which is narrower and has a less developed lingual cingulum in its distal portion (Prevosti *pers. obs.*). Importantly, the author did not provide evidence in support of a much earlier age than the accepted Ensenadan or younger age.

Leopardus Gray 1842
(Tables 4.1 and 4.2)

Species in South America: *Leopardus colocolo* (Molina 1782), *L. geoffroyi* (d'Orbigny and Gervais 1844), *L. guigna* (Molina 1782), *L. jacobita* (Cornalia 1782), *L. pardalis* (Linnaeus 1758), *L. tigrinus* (Schreber 1775), *L. wiedii* (Schinz 1821), and "*Felis*" *vorohuensis* Berta 1983.

Temporal and geographic distribution: *Leopardus* is dispersed across the continent. *Leopardus tigrinus*, *L. wiedii,* and *L. pardalis* are also present in Central America and southern NA (Wilson and Mittermeier 2009). The oldest records in SA are *L. colocolo* and "*Felis*" *vorohuensis* from the late Ensenadan (0.78–0.5 Ma) of the Pampean Region (Prevosti 2006a). *Leopardus tigrinus*, *L. wiedii,* and *L. pardalis* are recorded from the Late Pleistocene–early Holocene ("Lujanian") of Minas Gerais, Brazil, *L. pardalis* from the "Lujanian" of Bahia, Brazil, the Lujanian of Talara, Peru (ca. 13 ka BP), and the late Holocene of Ecuador (Cartelle 1999;

Prevosti 2006a; Stahl 2003). *Leopardus wiedii* and *L. pardalis* have also found in the Late Pleistocene of southern USA (Werdelin 1985; Seymour 1999; Prevosti 2006a). Remains of *L. geoffroyi* are from the Holocene, whereas the living species *L. guigna* and *L. jacobita* do not have a definitive fossil record (Prevosti 2006a). Linares (1998) mentioned the presence of *L. pardalis* in archaeological sites of Margarita Island, Central and Oriental Cordilleras, and *L. tigrinus* in the Central Cordillera, and the San Pedro Archipelago in Venezuela, but he did not figure or describe these remains, and the attributions were not justified. *Leopardus pardalis* was recently reported from the Sopas Formation (27–58 ka BP) in Uruguay (Perea et al. 2015). *Leopardus colocolo* is also cited for the Platan of Buenos Aires, Argentina, and southern Patagonia in Chile (Clutton Brock 1988; Quintana 2001; Alvarez 2009; see also Prevosti 2006a).

Paleoecology: According to the ecology of the living species, it is possible that the fossil taxa were small to mid-size predators (1.3 kg–15 kg) of small mammals, mainly rodents (Wilson and Mittermeier 2009).

Comments: Two alternative hypotheses can be drawn for *Leopardus*. The genus invaded SA after the development of the Panama Bridge, where it was diversified into several species in relation to different biogeographic areas and prey sizes, later re-invading Central and North America. Or several species might have invaded SA independently (Prevosti 2006a; Eizirik 2012; Prevosti and Soibelzon 2012; Prevosti and Pardiñas, in press). The last hypothesis could be supported by the fact that *L. pardalis* and *L. wiedii* are sister taxa that have been separated from other species of the genus for as much as 2 and 4.25 Ma (see Johnson et al. 2006) and have Late Pleistocene fossils in southern NA (Werdelin 1985; Seymour 1999). Diversity in specialization to different environments was an important factor in the evolution of this genus (Prevosti and Pardiñas, in press).

Recently, *L. guttulus* (Hensel 1872) was recognized as a full species separate from *L. tigrinus* based on genetic data (Trigo et al. 2013); this hypothesis should be also evaluated with morphological data and tested with more evidence.

Caniformia Kretozoi 1938

Canidae Fischer 1817

Living canids (Caninae) have quite generalized habits. They retain a more complete dentition than do Felidae, a long rostrum, and cursorial locomotion (Ewer 1973; Wang and Tedford 2008; Tedford et al. 2009). However, extinct canid groups demonstrate much larger morphological disparity and diverse ecological habits (Wang and Tedford 2008; Tedford et al. 2009). The family has a long history in NA, where they are recorded from the late Eocene (36 Ma) onwards. Later, between the middle and late Miocene (16 and 7 Ma), they reached the Old World (Wang and Tedford 2008; Tedford et al. 2009). The family experienced several radiations in NA that resulted in wide morphological disparity and ecomorphs, with omnivorous, insectivorous, scavenging and hypercarnivorous diets, and scansorial and cursorial locomotor types (Wang 1993; Wang et al. 1999). Canids invaded South America in different waves during the Pleistocene, and their diverse specialization to different environments was an important feature of their radiation (Prevosti 2010; Eizirik 2012; Prevosti and Soibelzon 2012; Prevosti and Pardiñas, in press; Moura Bubadué et al. 2015). *Atelocynus* is the only living genus that lacks confirmed fossils.

Lycalopex Burmeister 1854
(Tables 4.1 and 4.2)

Species in South America: *Lycalopex culpaeus* (Molina 1782), *L. cultridens* (Gervais and Ameghino 1880), *L. ensenadensis* (Ameghino 1888), *L. fulvipes* (Martin 1837), *L. griseus* (Gray 1837), *L. gymnocerus* (Fischer 1814), *L. sechurae* Thomas 1900, and *L. vetulus* (Lund 1842).

Temporal and geographic distribution: The oldest record of *Lycalopex* is *L. cultridens* from the Vorohuean (late Pliocene) of Buenos Aires, Argentina. This species disappeared in the Ensenadan (Berman 1994; Soibelzon and Prevosti 2007, 2013). Also in Buenos Aires, a fox similar to but larger than *L. gymnocercus* was found in Sanandresian levels (late Pliocene–earliest Pleistocene). Fossil remains confidently assigned to *L. gymnocercus* are known since the Ensenadan (early–Middle Pleistocene) (Berman 1994; Soibelzon and Prevosti 2007, 2013). *Lycalopex gymnocercus* is also found in the Lujanian of Entre Ríos, Argentina; Salto, Uruguay; "uncertain" levels in Tarija, Bolivia; the "Lujanian" of Minas Gerais, Brazil (Berta 1987; Soibelzon and Prevosti 2007, 2013), and the Platan of Buenos Aires and Santiago del Estero, Argentina (Ameghino 1889; Bonomo 2005; Alvarez 2009; Quintana 2001; del Papa 2012). *Lycalopex ensenadensis* is to date exclusively from Ensenadan and Lujanian levels in Buenos Aires, (Ramirez and Prevosti 2014). *Lycalopex culpaeus* is present in Lujanian–Platan sites of Southern Chile and Patagonia in Argentina, the "Lujanian" of La Carolina and Punin, Ecuador; and the Lujanian of Huánuco and Junín, Peru (Caviglia 1986; Clutton-Brock 1988; Massoia 1992; Trejo and Jackson 1998; Soibelzon and Prevosti 2007, 2013; Amorosi and Prevosti 2008; Shockey et al. 2009; Méndez et al. 2014). Berman (1994) described a specimen from the Ensenadan of Buenos Aires as *L. culpaeus,* but the specimen is very fragmentary and does not preserve the diagnostic features of the species. *Lycalopex sechurae* was found in Talara, Peru (Lujanian, 13–14 ka BP), and La Carolina, Ecuador ("Lujanian"), *L. vetulus* in the "Lujanian" of Minas Gerais, Brazil, and *L. griseus* in the Holocene of Patagonia, and possibly also Córdoba and Santiago del Estero, Argentina (Ameghino 1889; Kraglievich and Rusconi 1931; Berta 1987; Clutton-Brock 1988; Massoia 1992; Soibelzon and Prevosti 2007, 2013; Amorosi and Prevosti 2008; Méndez et al. 2014). *Lycalopex sechurae* and *L. culpaeus* are also included in faunal lists of Holocene archaeological sites in Ecuador (Stahl and Athens 2001; Stahl 2003). The presence of *L. griseus* and *L. culpaeus* in the Quaternary of Buenos Aires, Argentina, is not corroborated (but see comments for the taxonomic status of *L. gymnocercus* and *L. griseus*).

Paleoecology: *Lycalopex* is a small to middle-sized canid (1.8 kg–13.8 kg) with mesocarnivorous-omnivorous habits. In particular, *L. culpaeus* is the more carnivorous species, hunting rodents and hares (Wilson and Mittermeier 2009).

Comments: The genus *Lycalopex* originated in SA, where it diversified into at least seven species, occupying different geographic areas and environments (Prevosti and Soibelzon 2012; Prevosti and Pardiñas, in press). Morphological studies suggest that *L.griseus* is a junior synonym of *L. gymnocercus* (Zunino et al. 1995; Prevosti et al. 2013), but this should be corrroborated with DNA studies and other sources of information. The extinct *L. cultridens* has a morphology and size intermediate between *L. gymnocercus* and *L. griseus* (Berman 1994), thus this fossil should be included in *L. gymnocercus* if this synonymy is accepted. "*Canis*" *peruanus* Nordenskiöld 1908 (Late Pleistocene of Peru; Nordenskiöld 1908) has a cranial and dental anatomy that agrees with *L. culpaeus*, a species also present in the region since the Late Pleistocene.

Cerdocyon Hamilton Smith 1839
(Tables 4.1 and 4.2)

Species in South America: *Cerdocyon thous* (Linnaeus 1766).

Temporal and geographic distribution: The recent distribution of this species covers most of north and central SA, across forested environments with the exception of Amazonia (Wilson and Mittermeier 2009). Few fossils are assigned to this genus, which is limited to the "Lujanian" of Minas Gerais and Bahia, Brazil, and the Lujanian of the Pampean Region, Argentina (Berta 1987; Cartelle 1999; Ramírez 2014).

Paleoecology: *Cerdocyon thous* is a small fox (4.5 kg–8.5 kg) with an omnivorous diet composed of fruits, insects, and small mammals (Wilson and Mittermeier 2009).

Comments: Some molecular studies suggest a SA origin for *Ce. thous* (Eizirik 2012). However, the long molecular divergence between *Cerdocyon* and other SA canids suggests that the genus could have differentiated outside South America (i.e., Central and/or North America; Prevosti 2010; Prevosti and Soibelzon 2012; Prevosti and Pardiñas, in press). But the supposed records of *Cerdocyon* in the NA Pliocene (Tedford et al. 2009) are incorrect because the specimens in question appear to be more closely related to Vulpini (Prevosti 2010).

Chrysocyon Hamilton Smith 1839
(Tables 4.1 and 4.2)

Species in South America: *Chrysocyon brachyurus* (Illiger 1815).

Temporal and geographic distribution: Extant populations *Ch. brachyurus* are present in northeastern Argentina, Uruguay, South and Central Brazil, Paraguay, and Bolivia, inhabiting grasslands, crop fields, "Cerrado" and other forested areas (Wilson and Mittermeier 2009). Fossil remains are known from the "Lujanian" of Minas Gerais, Brazil, and the Holocene of Buenos Aires and Entre Ríos, Argentina (Prevosti et al. 2009a). Other material comes from Tarija, Bolivia, but its stratigraphic location in the Ensenadan of that locality is doubtful (Prevosti et al. 2009a).

Paleoecology: *Chrysocyon brachyurus* is a large canid (20.5 kg–30 kg), with an omnivorous diet composed of fruits, insects, and rodents (Wilson and Mittermeier 2009). The functional relevance of its long legs is a matter of discussion. Some authors have suggested that the long legs are useful for locomotion in flooded areas, or alternatively for locomotion in grasslands, or for rapid pursuit of prey (Hildebrand 1952; 1954; Langguth 1975; Dietz 1985; Andersson 2004).

Comments: *Chrysocyon* has a poor fossil record in SA. The fact that *Ch. nearcticus* was described from the Pliocene of North America suggested that the genus originated in the northern Hemisphere (Wang and Tedford 2008; Tedford et al. 2009). A new phylogenetic analysis resulted in *Ch. nearcticus* Wang, Tedford, and Taylor 1999 being placed together with other SA canids, but not the sister taxon of *Ch. brachyurus*. This could be an artifact of the incompleteness of the fossils, indicating that more material is needed to test this hypothesis (Prevosti 2010). Additionally, if the phylogeny of Prevosti (2006b, 2010; see also Austin et al. 2013) is correct regarding the position of *Theriodictis*? *floridanus* (see below), the *Chrysocyon* clade could well have originated in North America. The presence of *Ch. brachyurus* in the Pampean Region during the Holocene, beyond the southern limit of its current distribution, was explained by the presence of warmer temperatures at that time (Prevosti et al. 2004).

Speothos Lund 1839
(Tables 4.1 and 4.2)

Species in South America: *Speothos venaticus* (Lund 1842) and the extinct *Sp. pacivorus* Lund 1842.

Temporal and geographic distribution: *Speothos* occurs today from eastern Panama to northeastern Argentina in humid forests (Berta 1984; Wilson and Mittermeier 2009). Fossils of *Sp. venaticus* and *Sp. pacivorus* are few and restricted to the “Lujanian” of Brazil and a mention of *Speothos* sp. in the faunal list of the late Holocene site of Loma Alta, Ecuador (Stahl 2003).

Paleoecology: *Speothos venaticus* is a small canid (5 kg–8 kg.) with a long body, short legs, short tail, and a reduced and specialized dentition associated with a hypercarnivorous diet (Kraglievich 1930; Hildebrand 1952, 1954; Langguth 1980; Berta 1984; Prevosti 2006b). A good swimmer, it hunts large rodents (e.g., *Dasyprocta* sp.) and armadillos (e.g., *Dasypus* sp.), that it can pursue in their burrows or in the water (Cabrera and Yepez 1940; Wilson and Mittermeier 2009; Lima et al. 2009).

Comments: The putative fossil species *Sp. pacivorus* could be a junior synonym of *Sp. venaticus*, and the differences explained by intraspecific variation. Lima et al. (2009) suggested that the anatomy of *Speothos* evolved to hunt mammals inside burrows, while Hildebrand (1954) argued that the short legs are a specialization for the thick undergrowth bordering jungle streams along which it hunts.

Dusicyon Hamilton Smith 1839
(Fig. 4.6b–c, Tables 4.1 and 4.2)

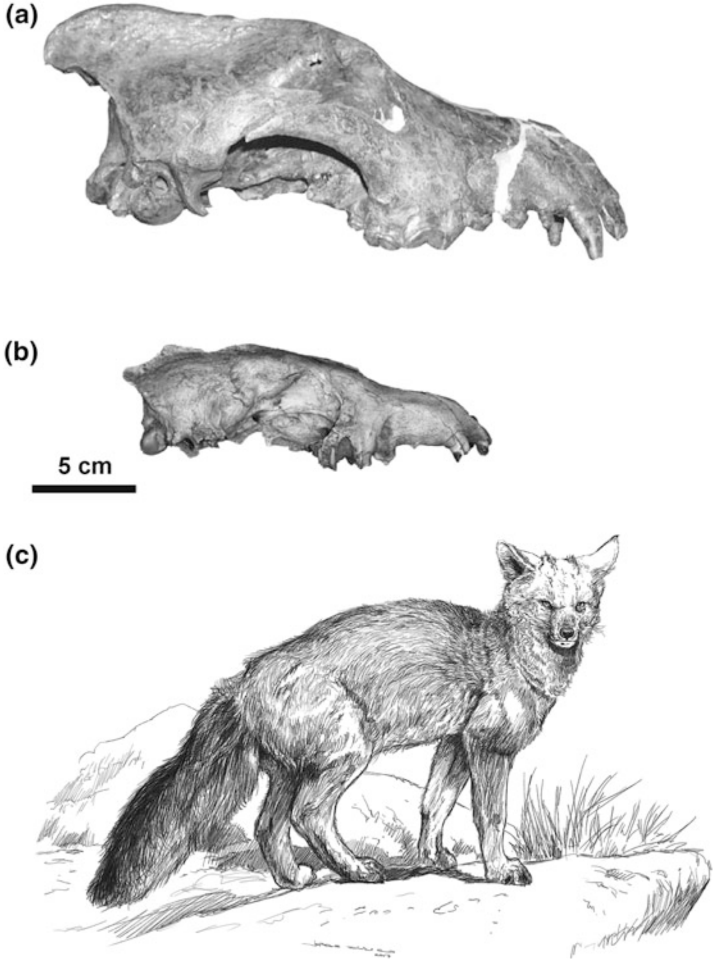


Fig. 4.6 Lateral view of the skull of *Canis dirus* (VF WN) (**a**) and "*Canis*" *peruanus* (NHRM M1952, Holotype) (**b**), and life reconstruction of *Dusicyon avus* (**c**). Scale = 5 cm

Species in South America: *Dusicyon australis* (Kerr 1792), *D. avus* (Burmeister 1866).

Temporal and geographic distribution: *D. australis* was endemic to the Malvinas (= Falkland) islands and was extirpated in the nineteenth century by human hunting. The continental *D. avus* lived in southern Brazil, Uruguay, and the Pampean and Patagonian regions of Argentina during the Late Pleistocene and Holocene (Prevosti et al. 2011, 2015).

Paleoecology: The body mass of *D. avus* was estimated to lie between 13 kg–17 kg. Its diet was apparently more carnivorous than modern SA foxes, which included hunting rodents, armadillos, and juvenile ungulates (e.g., camelids). Stable

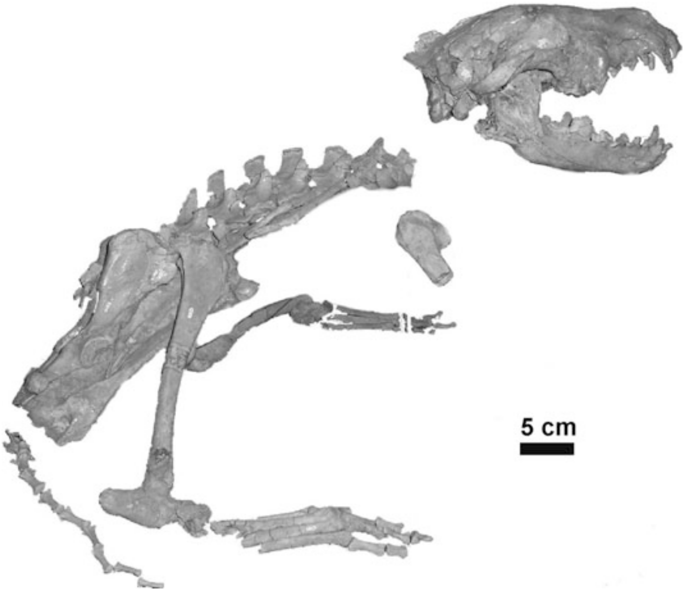


Fig. 4.7 Mounted skeleton of *Theriodictis platensis* (MPS 2). Scale = 5 cm

isotope analysis indicates that *D. avus* could scavenge megammals during the latest Pleistocene and early Holocene in Patagonia (i.e., *Mylodon* sp.; Prevosti and Vizcaíno 2006; Prevosti and Martin 2013).

Comments: Genetic and morphological data indicate that *Dusicyon* is the sister taxon of *Chrysocyon* and is part of the clade that also included *Speothos*, *Protocyon* Giebel 1855, and *Theriodictis* Mercerat 1891(Austin et al. 2013). Available ecological information indicates that *D. australis* hunted birds and ate sea mammals (Cabrera and Yepez 1940). *Dusicyon avus* became extinct around 400–500 years ago, probably by a combination of environmental changes and human impact (Prevosti et al. 2015)

Theriodictis Mercerat 1891
(Fig. 4.7, Tables 4.1 and 4.2)

Species in South America: *Theriodictis platensis* Mercerat 1891.

Temporal and geographic distribution: Ensenadan of the Pampean Region (Prevosti 2006b; Prevosti et al. 2009a).

Paleoecology: *Theriodictis platensis* was one of the largest hypercarnivorous canids from SA (30 kg–50 kg), able to hunt medium- and large-sized mammals (Prevosti and Palmqvist 2001; Prevosti 2006b). The postcranial anatomy suggests that it was cursorial, similar to *Lycaon pictus* (Temminck 1820) (Prevosti 2006b).

Comments: Tedford et al. (2009) tentatively identified the species *Theriodictis*? *floridanus* Wang et al. 1999 from the late Pliocene–early Pleistocene of NA. In a recent phylogenetic analysis, this species was placed as the sister taxon of

Protocyon + *Theriodictis* + *Speothos* + "*Canis*" *gezi* Kraglievich 1928, which may suggest that the origin of this clade was in North America (Prevosti 2010). Unfortunately, *Theriodictis*? *floridanus* is only known by an incomplete mandible and isolated teeth and more complete material is needed to evaluate this hypothesis.

"*Canis*" *gezi* Kraglievich 1928
(Tables 4.1 and 4.2)

Species in South America: "*Canis*" *gezi* Kraglievich 1928.

Temporal and geographic distribution: Ensenadan of the Pampean Region, Argentina (Kraglievich 1928; Berta 1989; Prevosti 2006b; Prevosti et al. 2009a).

Paleoecology: "*Canis*" *gezi* was a large (36 kg–37 kg) hypercarnivorous canid, able to prey on animals between 40 kg–200 kg, or larger including cervids, equids, camelids, peccaries, mesotheriids, large rodents, and armadillos (Prevosti 2006b). The few postcranial remains indicate that it had cursorial habits similar to the living *Canis lupus* or *Lycaon pictus* (Prevosti 2006b).

Comments: Cladistic analysis demonstrated that "*Canis*" *gezi* is not related to *Canis*, but to the clade of *Theriodictis*, *Protocyon,* and *Speothos* (Prevosti 2006b, 2010). "*Canis*" *gezi* is very similar to *Theriodictis*, but has plesiomorphic traits in the dentition, like the presence of a metaconid in the lower carnassial and a more developed hypoconid in the first upper molar (Prevosti 2006b). Since this taxon is known by two incomplete specimens, it is difficult to conclude if it represents another canid or if it could be part of the variation of *Th. platensis*.

Protocyon Giebel 1855
(Tables 4.1 and 4.2)

Species in South America: *Protocyon scagliorum* JL Kraglievich 1952*, Pr. tarijensis* (Ameghino 1902), and *Pr. troglodytes* (Lund 1838).

Temporal and geographic distribution: *Protocyon scagliorum* is known from the Ensenadan (0.78–0.5 Ma BP) of the Pampean Region, Argentina, while *P. tarijensis* is from Tarija, Bolivia, between 1 Ma and ca. 27 ka BP (Prevosti et al. 2009a). *Protocyon troglodytes* is widely distributed during the Late Pleistocene, including Argentina, Uruguay, Bolivia, Brazil, Ecuador, and Venezuela; older records of this species are questionable (Prevosti 2006b; Prevosti and Rincón 2007; Prevosti et al. 2009a; Lindsey and Seymour 2015). The genus *Protocyon* was mentioned from the Middle Pleistocene tar pit of Orocual in eastern Venezuela (Rincón et al. 2009).

Paleoecology: The genus *Protocyon* includes large canids (20 kg–40 kg), with cursorial habits, able to hunt medium- to large-sized mammals (e.g., equids, camelids, deer, tayassuids, and juveniles of megammals) (Cartelle and Langguth 1999; Prevosti 2006b; Prevosti et al. 2009b). Stable isotope analyses indicate that *P. troglodytes* was a hypercarnivore, with equid and megammals carrion probably forming part of its diet (Prevosti and Schubert 2013). A new analysis that includes a larger sample and Bayesian methods (Bocherens et al. 2016) shows that *P. troglodytes* mainly ate macrauchenids and ground sloths, and that had an important overlap in diet with *Smilodon populator*. The exploitation of the same resource could imply an important level of competition between these species.

Comments: *Theriodictis tarijensis* was transferred to *Protocyon* on the basis of the results of phylogenetic analyses (Prevosti 2006b; 2010). A specimen of *Pr. troglodytes* from the Pampean Region provided an age of 17.34 ka BP by AMS 14C (Prevosti and Schubert 2013).

Canis Linnaeus 1758
(Fig. 4.6a; Tables 4.1 and 4.2)

Species in South America: *Canis dirus* Leidy 1858, *C. familiaris* Linnaeus 1758 (domestic dog), and *C. nehringi* (Ameghino 1902).

Temporal and geographic distribution: *Canis dirus* and *C. nehringi* have been found in the latest Pleistocene of Bolivia, Peru, Venezuela, and Argentina (Prevosti 2006b; Prevosti and Rincón 2007; Prevosti et al. 2009a). Domestic dogs are recorded in the continent since the Holocene (Prates et al. 2010).

Paleoecology: *Canis nehringi* and *C. dirus* were one of the larger SA canids (30 kg–38 kg and 30 kg–70 kg, respectively). Horses, cervids, camelids, large rodents, tayassuids, and juveniles of megammals could have been hunted by these canids (Prevosti 2006b; Prevosti and Vizcaíno 2006 and references therein).

Comments: *Canis nehringi* and *C. dirus* were very similar (Berta 1989), possible the same species (Prevosti 2006b). The late presence of *Canis nehringi* and *C. dirus* in South America, and the long history of the last species in NA (Tedford et al. 2009), suggest a younger (Late Pleistocene) immigration to the southern continent (Prevosti 2006b, 2010; Prevosti and Rincón 2007).

Urocyon Baird 1857
(Tables 4.1 and 4.2)

Species in South America: *Urocyon cinereoargenteus* (Schreber 1775).

Temporal and geographic distribution: *Urocyon cinereoargenteus* currently inhabits the northwestern part of SA (Colombia and Venezuela), Central America, and a major part of NA. Its fossil record in SA is limited to the Late Pleistocene of western Venezuela (Prevosti and Rincón 2007).

Paleoecology: *Urocyon cinereoargenteus* is a small canid (2 kg–5.5 kg) with omnivorous diet, including fruits, insects, and small vertebrates, and with scansorial capabilities (Hildebrand 1954; Wilson and Mittermeier 2009).

Comments: The genus *Urocyon* has an extensive record in NA (late Miocene–Present; Wang and Tedford 2008; Tedford et al. 2009), unlike SA with records only as old as the Late Pleistocene (Prevosti and Rincón 2007) that point to a recent immigration.

Ursidae Gray 1825

The bear family includes large terrestrial carnivores with stout legs and fully plantigrade hind feet. Dietary variation in the group encompasses mostly omnivorous (spectacled bear, *Tremarctos ornatus* (Cuvier 1825)), fully herbivorous (giant panda, *Ailuropoda melanoleuca* (Davis 1869)), insectivorous (sloth bear, *Melursus ursinus* (Shaw 1791)), and carnivorous diets (polar bear, *Ursus maritimus* Phipps 1774) (Ewer 1973; Wilson and Mittermeier 2009). Ursidae has an extensive fossil record, starting in the late Eocene of Europe and NA and with a continuous record to the present. In Asia, bears have been recorded from the Oligocene (Hunt 1996; Flynn and Wesley-Hunt 2005), while the family invaded Africa at least three times, the early Miocene (hemicyonines), the late Miocene–early Pliocene (*Indarctos* Pilgrim 1913, *Agriotherium* Wagner 1837), and the Pleistocene (*Ursus* Linnaeus 1758). Ursidae reached SA at least twice during the Pleistocene-Holocene (Hunt 1996; Flynn and Wesley-Hunt 2005; Prevosti and Soibelzon 2012).

Late Eocene–Oligocene ursids are included in a paraphyletic stem group (amphicynodonts) of smaller bears (<15 kg). Hemicyoninae was a group of bears from the Oligocene–Miocene, mainly restricted to northern continents, with long limbs and a digitigrade stance that indicates cursorial habits. Hemicyoninae had a body size range of 5 kg–500 kg and carnassials that retain the shearing function, indicating a more carnivorous diet than modern bears (Hunt 1996). The panda clade is known since the middle Miocene, and the giant panda (*Ailuropoda melanoleuca*) is specialized for a bamboo diet and has a highly modified dentition and skull to suit (Jin et al. 2007; Abella et al. 2012). South American bears belong to the short-faced bear clade (Tremarctinae), recorded since the late Miocene in NA (Hunt 1996; Soibelzon 2004) and since the Pleistocene in the SA.

Arctotherium Burmeister 1879
(Fig. 4.8, Tables 4.1 and 4.2)

Species in South America: *Arctotherium angustidens* Gervais and Ameghino 1880, *A. bonariense* (Gervais 1852), *A. tarijense* Ameghino 1902, *A. vetustum* Ameghino 1885 and *A. wingei* Ameghino 1902 (Soibelzon 2004).

Temporal and geographic distribution: *Arctotherium* is recorded from the Ensenadan to the end of the Pleistocene (Soibelzon and Schubert 2011; Prevosti and Martin 2013). *Arctotherium angustidens* is restricted to the Ensenadan of the Pampean Region, Argentina. Finds of this species in Bolivia lack precise stratigraphic data, as do the records of *A. wingei* and *A. tarijense* (Soibelzon and Schubert 2011). *Arctotherium tarijense* was mentioned in Lujanian beds of southern Patagonia in Chile, Uruguay, and the Pampean Region in Argentina (Soibelzon and Schubert 2011), but the remains from southern Chile are rather fragmentary for a specific determination (Prevosti et al. 2003; Prevosti and Martin 2013; see also López Mendoza et al. 2015). *Arctotherium wingei* has records for the Lujanian of Venezuela and the "Lujanian" of Brazil, and *A. bonaeriense* for the Lujanian of the Pampean Region in Argentina (Soibelzon and Schubert 2011; Rodrigues et al. 2014). The presence of *A. tarijense, A. bonariense*, and *A. vetustum* in the Bonaerian of the Pampean Region is highly questionable and is based on specimens with poor stratigraphic data. A Lujanian Age cannot be excluded for these fossils.

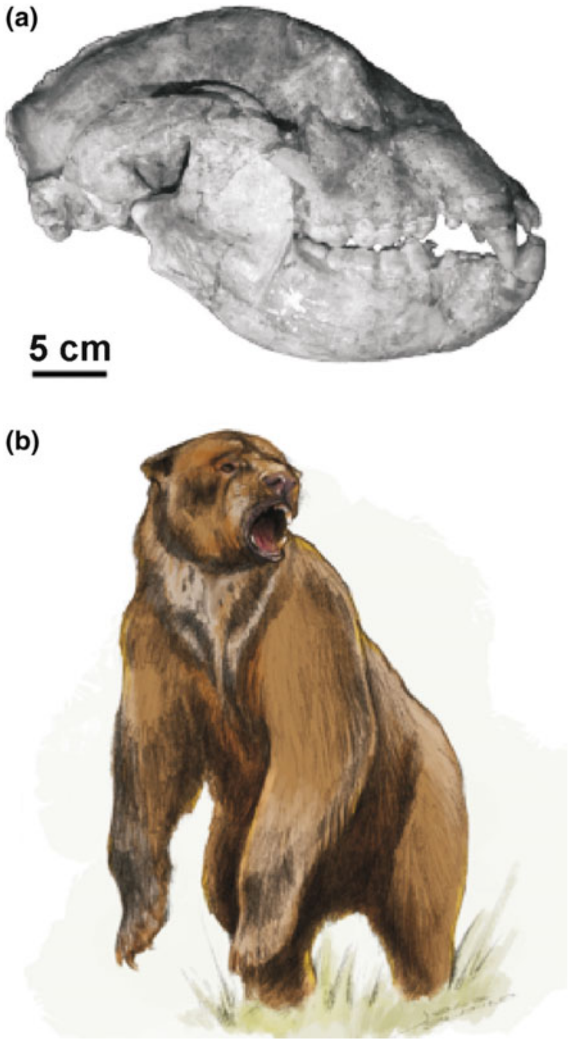


Fig. 4.8 Lateral view of the skull and mandible of *Arctotherium vetustum* (MMP 1233 M) (**a**) and life reconstruction of *Arctotherium* (**b**). Scale = 5 cm

Paleoecology: The largest bear in SA is *Arctotherium angustidens,* with a body mass of about 580 kg–1750 kg (Soibelzon and Schubert 2011). This is followed by *A. wingei*: 42 kg–107 kg; *A. tarijense*: 102 kg–224 kg; *A. bonariense*: 100 kg–545 kg; and *A. vetustum*: 95.5 kg–145 kg (Prevosti and Vizcaíno 2006; Soibelzon and Tarantini 2009). Morphology, pathology, dental wear pattern, and stable isotopes suggest that the large *A. angustidens* was omnivorous, eating also carcasses and bones of large mammals (Soibelzon and Schubert 2011). Other species are interpreted as omnivorous with a larger proportion of vegetable matter in their diets than the Ensenadan species (Figueirido and Soibelzon 2009). A paleoecological study based on southern Patagonian specimens revealed a diet with a large proportion of meat, probably as carrion from large mammals (Prevosti and Martin 2013). Figueirido and Soibelzon (2009), Soibelzon and Schubert (2011) and Soibelzon et al. (2014) correlated smaller sizes with a tendency to a less carnivorous diet with the increase in abundance of large hypercarnivores after the Ensenadan. Unfortunately, the chronological succession of the species of *Arctotherium* is not corroborated by cladistic analysis (i.e., there is no evidence that they represent an evolutionary sequence), and the supposed lower diversity of large hypercarnivores during the Ensenadan is not supported by the available data (see Prevosti and Soibelzon 2012; Prevosti and Pereira 2014).

Comments: *Arctotherium* is endemic to South America and its presence could be explained by a single immigration event from Central America, in the early–Middle Pleistocene (Soibelzon and Prevosti 2007; Prevosti and Soibelzon 2012). A supposed deciduous lower carnassial (dp4) from the late Pliocene of El Salvador assigned to cf. *Arctotherium* was used to support an origin of *Arctotherium* outside South America (Soibelzon et al. 2008). However, the specimen was not compared with other large Neogene bears from NA (i.e., *Agriotherium* and *Indarctos*) and some features of the crown (e.g., shape, thick enamel with furrows) indicate that it may belong to a juvenile mastodont. A recent ancient DNA study indicates that *Arctotherium* is the sister taxa of *Tremarctos*, instead of *Arctodus*, and suggests that the large scavenger morphotype originated independently in North and South America (Mitchell et al. 2016).

Tremarctos Gervais 1855
(Tables 4.1 and 4.2)

Species in South America: *Tremarctos ornatus* (Cuvier 1825).

Temporal and geographic distribution: *Tremarctos ornatus* is currently distributed along the Andean rain forests, from western Venezuela to northwest Argentina (Wilson and Mittermeier 2009; Cosse et al. 2014). Its fossil record is very scarce and includes Holocene material from Peru and Ecuador (Stahl 2003; Stucchi et al. 2009).

Paleoecology: *Tremarctos ornatus* is a medium-sized bear of 60 kg–200 kg, with an omnivorous diet, including a large proportion of vegetables and occasional large mammals obtained by predation (Wilson and Mittermeier 2009).

Comments: The record of *T. ornatus* in SA during the Holocene represents a second wave of bear migration. The fossil record in NA is much more extensive than in SA and goes back to the late Pliocene (Hunt 1996, 1998).

Mustelidae Fischer 1817

Mustelids are small carnivores with elongated bodies, short limbs, and a broad spectrum of diets (omnivores to hypercarnivores). Locomotion (e.g., scansorial, semifossorial, and aquatic) is correlated with their diversity in skeletal shape (Ewer 1973; Wilson and Mittermeier 2009). Today, the group has a near worldwide distribution. They are first recorded in the late Eocene of Europe and North America; the early Miocene produced the oldest records of the living subfamilies

(Wolsan 1993; Hunt 1996; Baskin 1998). South American mustelids represent four subfamilies that originated in northern continents and entered SA independently (Eizirik 2012; Prevosti and Soibelzon 2012). The subfamilies recorded in South America are the aquatic Lutrinae (otters), Guloninae (e.g., wolverine and martens), Mustelinae (weasels), and Ictonychinae (grisons) (see Eizirik 2012; Sato et al. 2012). A supposed early mustelid found in the late Miocene of La Pampa, Argentina (Verzi and Montalvo 2008) was re-identified as a didelphimorphian marsupial (Prevosti and Pardiñas 2009), while the oldest record of this family in SA is from the Vorohuean Subage (Marplatan, late Pliocene; Berman 1994; Prevosti and Soibelzon 2012).

Mustela Linnaeus 1758

(Tables 4.1 and 4.2)

Species in South America: *Mustela africana* Desmaret 1818*, M. felipei* Izor and de la Torre 1978 and *M. frenata* Lichtenstein 1831.

Temporal and geographic distribution: Currently, *Mustela frenata* is distributed from NA to northwestern SA, *M. felipei* is limited to the Andes of Colombia and Ecuador, and *M. africana* is endemic to the tropical forests of Amazonia (Wilson and Mittermeier 2009). The SA fossil record is very scarce, consisting only of an upper P4 referred to *Mustela* cf. *M. frenata* from the middle Holocene site of La Calera, Ecuador (ca. 4.2 ka BP) and a mention for the middle Holocene archaeological site of Cotocallo, Ecuador (Stahl 2003). *Mustela* was also reported from the late Holocene archaeological site of La Chimba, Ecuador (Stahl 2003).

Paleoecology: Living representatives are small hypercarnivores (0.080 kg–0.450 kg) that eat mainly small rodents (Wilson and Mittermeier 2009).

Comments: *Mustela* migrated into South America at least two times. One event included *M. frenata*, with fossils in NA since the late Pliocene (Anderson 1984). The second event resulted in the entry of the common ancestor of *M. africana* and *M. felipei,* an endemic SA clade. The scarce fossil record of *Mustela* in SA is probably related to a bias of the fossil record against tropical forests (Chap. 5).

Eira Smith 1842

(Tables 4.1 and 4.2)

Species in South America: *Eira barbara* (Linnaeus 1758).

Temporal and geographic distribution: *Eira barbara* currently occurs from Veracruz, Mexico, to northwestern Argentina and southern Brazil and northeastern Argentina to northern Uruguay across tropical and subtropical forests (Wilson and Mittermeier 2009). The fossil record of *Eira* is limited to the "Lujanian" of Brazil, and a dubious mention for Tarija, Bolivia (Lessa et al. 1998; Cartelle 1999; Soibelzon and Prevosti 2007; Prevosti and Soibelzon 2012). A record of *Eira* cf. *E. barbara* from Bahia state in Brazil was dated to between 22–8 ka BP (Castro et al. 2014).

Paleoecology: *Eira barbara* is a medium-sized carnivore (2.7 kg–7 kg) with an omnivorous diet including insects, fruits, and small mammals (Wilson and Mittermeier 2009).

Comments: *Eira* is the only gulonine in SA (Eizirik 2012; Sato et al. 2012), but it is not clear if the genus originated in South America, and later invaded Central America, or if it originated in Central America (Prevosti and Soibelzon 2012).

Galictis Bell 1826
(Fig. 4.9c, Tables 4.1 and 4.2)

Species in South America: *Galictis cuja* (Molina 1782), *G. hennigi* (Rusconi 1931), *G. sorgentinii* Reig 1958, and *G. vittata* (Schreber 1776).

Temporal and geographic distribution: *Galictis vittata* currently inhabits tropical forests from Mexico to northeastern Argentina and *G. cuja* more open environments from northeast Brazil to southern Patagonia (Wilson and Mittermeier 2009; Bornholdt et al. 2013). The extinct species *G. sorgentinii* and *G. hennigi* are limited to the Vorohuean (late Pliocene) and Ensenadan (early–Middle Pleistocene) of Buenos Aires, Argentina, respectively (Reig 1957; Berman 1994; Soibelzon and Prevosti 2007). *Galictis vittata* was found in the "Lujanian" of Minas Gerais and northern Brazil (Cartelle 1999; Rodrigues et al. 2016). Other fossils similar to *G. vittata,* with a metaconid in the lower carnassial, come from the late Pliocene of Buenos Aires, and one without metaconid in the lower carnassial from the "Ensenadan" of Tarija, Bolivia (Werdelin 1991; Berman 1994; Soibelzon and Prevosti 2007). *G. cuja* was recorded in the Late Pleistocene of Minas Gerais, Brazil, and the Holocene of Argentina (Buenos Aires, Jujuy, Neuquén, and Río Negro provinces) and probably Chile (Ultima Esperanza; Massoia 1992; Prevosti and Pardiñas 2001; Quintana 2001; Prevosti and Soibelzon 2012; Rodriges et al. 2016).

Paleoecology: The genus *Galictis* includes small carnivores (1 kg–3.3 kg) with hypercarnivorous habits, hunting small mammals, mainly rodents; Wilson and Mittermeier (2009).

Comments: The taxonomic validity of the fossil species (e.g., *G. hennigi)* and some informally recognized taxa (see Berman 1994) are pending review. The fossil record suggests that this genus originated in SA and, if so, *G. vittata* secondarily migrated to Central America (Prevosti and Soibelzon 2012).

Lyncodon Gervais 1845
(Tables 4.1 and 4.2)

Species in South America: *Lyncodon bosei* Pascual 1958 and *L. patagonicus* (de Blainville 1842).

Temporal and geographic distribution: *Lyncodon bosei* is only known from the type specimen found in the Ensenadan of Buenos Aires (ca. 1 Ma BP). The living species *L. patagonicus* has records in the Lujanian and Platan (Late Pleistocene–Holocene) of Patagonia and the Pampean Region (Pascual 1958; Prevosti and Pardiñas 2001). Currently, this species is distributed in Patagonia (southern Chile

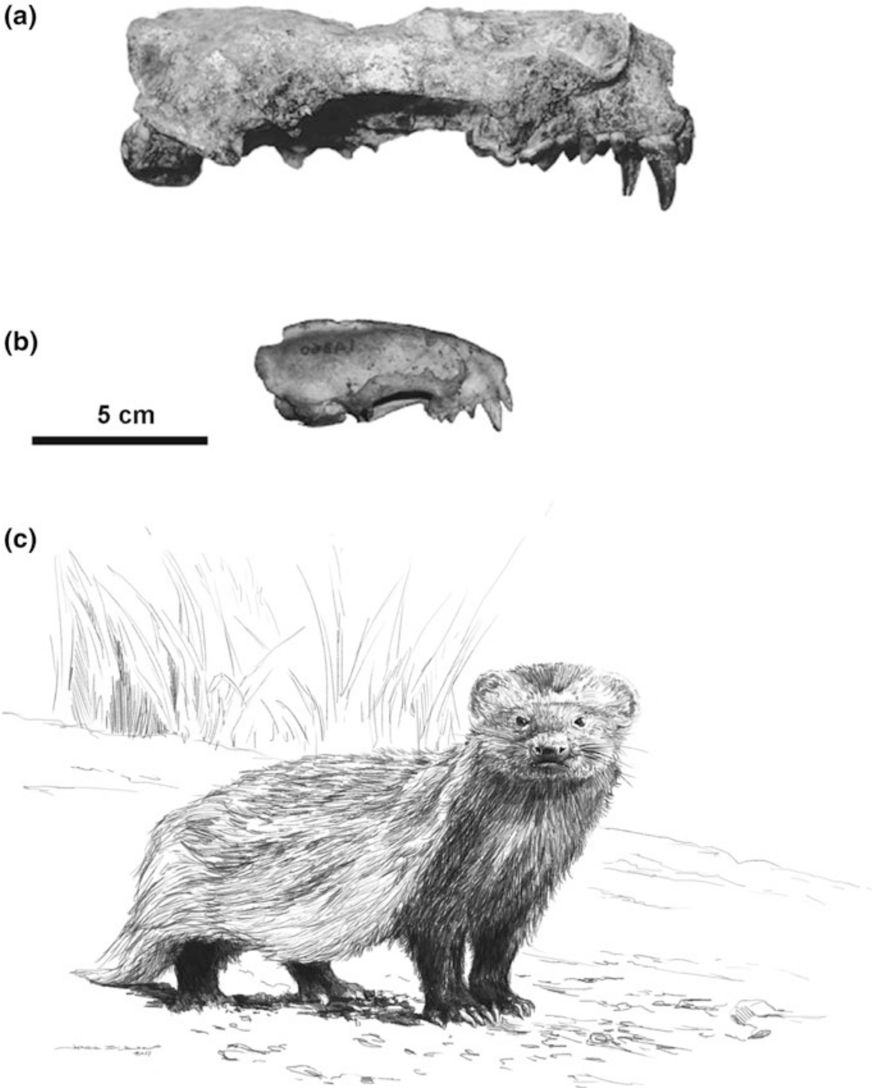


Fig. 4.9 Lateral view of the skull of *Pteronura brasiliensis* (CICYTTP-PV-M-1-21) (**a**), lateral view of the skull of *Stipanicicia pettorutii* (MACN Pv 14260, Holotype) (**b**), and life reconstruction of *Galictis* (**c**). Scale = 5 cm

and Argentina), central areas of Argentina and along the Andes (Wilson and Mittermeier 2009). The fossil record shows that, in connection with climatic changes during the Late Pleistocene and Holocene glaciations, *L. patagonicus* expanded its range to the northeast, including the Pampean Region (Prevosti and Pardiñas 2001; Schiaffini et al. 2013a).

Paleoecology: *Lyncodon patagonicus* is a small carnivore (0.200 kg–0.250 kg) with poorly known habits, that predates on birds and rodents and is probably also capable of hunting fossorial rodents (Prevosti and Pardiñas 2001; Wilson and Mittermeier 2009). *Lyncodon patagonicus* has derived dental traits in comparison to *L. bosei* (e.g., reduction of P4 lingual shelf, loss of m2 and P2/p2; Pascual 1958), which could be related to more carnivorous habits.

Comments: Based on the distribution of the living species and its fossil record, *Lyncodon* originated in SA.

Stipanicicia Reig 1956
(Fig. 4.9b, Tables 4.1 and 4.2)

Species in South America: *Stipanicicia pettorutii* Reig 1956.

Temporal and geographic distribution: Ensenadan of the Buenos Aires, Argentina (Soibelzon and Prevosti 2007). The presence of this genus in older (Marplatan) times is not corroborated by the available data.

Paleoecology: *Stipanicicia pettorutii* was a small mustelid, similar in size to *Galictis,* with a dentition that suggests a hypercarnivorous diet. Based on muscle reconstructions, Ercoli (2015, 2017) suggested that *S. pettorutii* was able to hunt rodents larger than its own body size using a roll and curl strategy to access burrows like *Mustela nigripes*.

Comments: Berman (1994) assigned a lower jaw from southern Buenos Aires province to *Stipanicicia*; however, only cranial material is available for comparison, and unfortunately the mandible has been lost. *Stipanicicia* shares some similarities with *Lyncodon* (e.g., reduction of M1, narrow postorbital constriction; absence of P2) that could indicate a close phylogenetic relationship, something which should be tested with a cladistic analysis. The fossil record suggests that this genus originated in South America.

Lontra Gray 1843
(Tables 4.1 and 4.2)

Species in South America: *Lontra felina* (Molina 1782)*, L. longicaudis* (Olfers 1818), and *L. provocax* (Thomas 1908).

Temporal and geographic distribution: *Lontra longicaudis* occurs from Mexico to Uruguay and northeastern Buenos Aires in Argentina; *Lontra felina* lives in the Pacific and the southern parts of the Atlantic coasts of Patagonia in Chile and Argentina, and *L. provocax* inhabits lakes and rivers of Patagonia in Argentina, and the Beagle Channel (Wilson and Mittermeier 2009). *Lontra longicaudis* is known from the Ensenadan–Holocene of Buenos Aires, Argentina (ca. 1 Ma BP), the Lujanian of Uruguay (27–58 ka BP) and the "Lujanian" of Bahia and Minas Gerais, Brazil (Cione and Tonni 1978; Berman 1994; Soibelzon and Prevosti 2007; Prevosti and Ferrero 2008; Acosta et al. 2015). The presence of this species in the Lujanian of the Buenos Aires (Ameghino 1889) has not yet corroborated. *Lontra provocax* was identified from the Holocene of the Beagle Channel, and one archeological site in Neuquén, Argentina (Massoia 1992; Ercoli 2015). Lindsey and

Seymour (2015) mentioned the presence of "*Lutra*" in a Late Pleistocene site in Ecuador.

Paleoecology: The SA species are medium-sized mustelids (3.2 kg–15 kg), with *L. felina* the smallest and *L. provocax* the largest, eating mainly fish, crustaceans, and molluscs (Wilson and Mittermeier 2009).

Comments: Considering the geographic distribution of *L. felina, L. provocax,* and *L. longicaudis,* and that these species form a monophyletic clade, it is possible that *Lontra* reached SA once and *L. longicaudis* later migrated to Central America, or alternatively that the group entered SA twice, as represented by *L. longicaudis* and the common ancestor of *L. felina* and *L. provocax* (Eizirik 2012 for the phylogenetic analysis). The origin of this clade at ca. 3 Ma (see Eizirik 2012) agrees with the first hypothesis and with the conventional time of formation of the Panama Bridge.

Pteronura Gray 1837
(Fig. 4.9a; Tables 4.1 and 4.2)

Species in South America: *Pteronura brasiliensis* (Gmelin 1837).

Temporal and geographic distribution: *Pteronura brasiliensis* inhabits lowland tropical basins of SA, up to northern Uruguay and Entre Ríos in Argentina (Wilson and Mittermeier 2009). Fossils are limited to the last interglacial (ca. 125 ka BP) of Entre Ríos, and the "Lujanian" of Bahia and Mato Grosso in Brazil (Prevosti and Ferrero 2008).

Paleoecology: *Pteronura brasiliensis* is a large mustelid (22 kg–32 kg) that preferentially eats fishes (Wilson and Mittermeier 2009).

Comments: *Pteronura* is the sister taxon of *Satherium* Gazin 1934, an otter from the Pliocene–early Pleistocene of USA. *Pteronura* represents another lineage of otters that invaded the continent from NA (Prevosti and Ferrero 2008).

Mephitidae Bonaparte 1845

Molecular studies indicate that mephitids are distinct from mustelids (Eizirik 2012). Mephitids are small carnivores with an omnivorous diet, aposematic skin coloration, well-developed odor glands, and terrestrial-semifossorial habits (Ewer 1973; Wilson and Mittermeier 2009). Currently they are restricted to the Americas, with the exception of the Asiatic stink badger (*Mydaus* Cuvier 1821) that is the sister taxon of other living mephitids (Wilson and Mittermeier 2009; Eizirik et al. 2010). *Conepatus* Gray 1837, originated in North America, with fossils from the early Pliocene (Baskin 1998; Wang and Carranza-Castañeda 2008) and invaded SA probably in the early–Middle Pleistocene (Berman 1994; Prevosti and Soibelzon 2012).

Conepatus Gray 1837
(Fig. 4.10; Tables 4.1 and 4.2)

Species in South America: *Conepatus altiramus* Reig 1952, *Co. chinga* (Molina 1782), *Co. cordubensis* (Ameghino 1889), *Co. mercedensis* Gervais and Ameghino

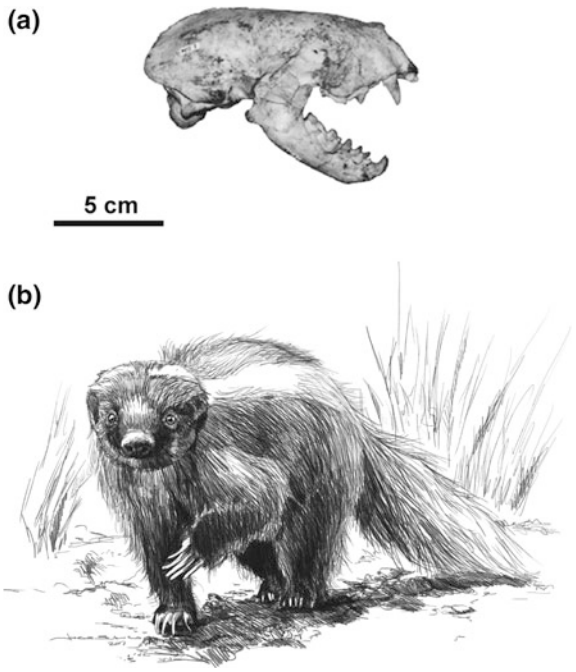


Fig. 4.10 Lateral view of the skull and mandible of *Conepatus primaevus* (MSP 1) (**a**) and life reconstruction of *Conepatus chinga* (**b**). Scale = 5 cm

1880, *Co. primaevus* (Burmeister 1866), *Co. semistriatus* (Boddaert 1785), and *Co. talarae* (Churcher and Van Zyll de Jong 1965).

Temporal and geographic distribution: The two living SA skunks have separate distributions: *Co. chinga* in the southern parts from Peru, Bolivia, Paraguay, and southern Brazil to the Magellan strait in Patagonia and *Co. semistriatus* in the northern part of the continent (Colombia, Venezuela, Ecuador, and North of Peru, and Brazil) and Central America (Wilson and Mittermeier 2009; Schiaffini et al. 2013b). *Conepatus primaevus* is recorded from the Ensenadan and Bonaerian? of Buenos Aires, Argentina (Forasiepi 2003), while *Co. semistriatus* and *Co. talarae* are known from the Lujanian of Muaco, Venezuela and Talara, Peru (13–14 ka. BP; González et al. 2010), respectively. *Conepatus semistriatus* is also found in the “Lujanian” of Bahia, Brazil (Cartelle 1999). *Conepatus mercedensis* occurred in the Ensenadan and, following the stratigraphy of the Luján Basin according to Toledo (2011), the species is also found in the Lujanian of Buenos Aires, Argentina (Berman 1994). *Conepatus chinga* was described from the “Ensenadan” of Tarija, Bolivia, Lujanian–Platan of Buenos Aires, “Lujanian” of Minas Gerais, Brazil, and the late Holocene of Patagonia, Chile, and Argentina (Ameghino 1889; Berman 1994; González et al. 2010). *Conepatus chinga* was also included in the faunal list of the late Holocene archaeological site of La Chimba, Ecuador (Stahl and Athens 2001). *Conepatus cordubensis* is limited to its type locality in the “Bonaerian” of Córdoba, Argentina (Ameghino 1889), but this is probably a junior synonym of *Co. chinga*. Records of *Conepatus* sp. are from the Lujanian of Valdivia, Chile;

Arequipa, Talara, Tirapata, and Huánuco in Peru, and the Ensenadan–Platan of the Buenos Aires and Platan in Patagonia, Argentina (Berman 1994; Tonni et al. 2002; Bonomo 2005; Shockey et al. 2009; Alvarez 2009; González et al. 2010; Lindsey and Seymour 2015). Massoia (1992) and Quintana (2001) mentioned remains of *Co. chinga* from archeological sites of Neuquén and Buenos Aires, respectively. This species probably appears in other archeological sites in Argentina.

The first appearance datum of *Conepatus* in SA is still under debate. *Conepatus altiramus* was described by Reig (1952) and originally suggested that the specimen was recovered from levels 3–5 of the Chapadmalal "Formation" (ca. 3.3 Ma BP), at Barranca de los Lobos, 700 m north of Baliza Caniú (38° 7′ S, 57° 6′ W; Buenos Aires, Argentina) (see Wang and Carranza-Castañeda 2008 who recently defended this age). In 1957, after conversation with Galileo J. Scaglia, who collected the fossil in 1939, Reig suggested that *Co. altiramus* was likely coming from the overlying Barranca de los Lobos "Formation," in view of the fact that this unit is better exposed in the area than the Chapadmalal "Formation." The presence of Pleistocene sediments (Isla et al. 2015) was discounted. In 1958, Reig visited the locality with Galileo J. Scaglia, and re-considered that the holotype of *C. altiramus* effectively was collected from the Chapadmalal "Formation." Additionally, museum label on the type specimen (MMP 173 S) was clearly made by the time of or after the description of *C. altiramus* in 1952, and indicates that it comes from 200 m south of the Punta Mala ("*Costa Atlántica, 200 metros al S. de la bajada de Punta Mala*") from the base of the cliff of the Chapadmalal "Formation." This information is similar to that reported by Reig (1952) and agrees with the information on other fossil labels (Olivares et al. 2012; U.F.J. Pardiñas, pers. comm.), suggesting that there was a change in the geographic point of reference (Baliza Caniú vs. Punta Mala). Considering the likely congruence between the data presented by Reig (1952, 1958) and the MMP label, and evaluating the geological data (e.g., Isla et al. 2015) only the Chapadmalal "Formation" is exposed in the lower section of the locality where *C. altiramus* comes from (but Pleistocene deposits are present in the upper section). Based on the unclear situation about the stratigraphic provenance and the absence of new skunk material from the Chapadmalal "Formation" (or other deposits older than the Ensenadan), several authors considered that the age of this taxon is uncertain and that the confirmed records of skunks in South America are limited to the Ensenadan or younger ages (e.g., Berman 1994; Cione and Tonni 1995; Prevosti and Soibelzon 2012), with whom we agree. The evidence is not clear enough to extend the fossil range of the skunk lineage in SA into the Pliocene (see also Prevosti and Pardiñas, in press) because (1) the fossil was collected in 1939, more than 10 years before the publication of *C. altiramus* and the establishment of the main stratigraphic scheme in the region (Kraglievich 1952); (2) there is no original label in the MMP or field notes written when the fossil was collected to corroborate its provenance; (3) there are no other remains of this taxa or confirmed skunks found in levels older than the Ensenadan. In addition, considering the geographic provenance, it is also possible that the specimen was collected from younger Pleistocene rocks, including a dislocated rocks from upper levels. Wang and Carranza-Castañeda (2008) erroneously indicate that *Co. talarae* is present in the early–Middle Pleistocene of SA, but this taxon is only known from the type locality, which is dated to the Late Pleistocene (see above).

Paleoecology: *Conepatus* group's small carnivores (1–3.5 kg), with an omnivorous diet, are composed of insects, fruits, small vertebrates, and carrion (Wilson and Mittermeier 2009).

Comments: The oldest fossils of *Conepatus* are from the Pliocene of Mexico (4–5 Ma BP) which suggests a NA origin for the clade (Wang and Carranza-Castañeda 2008). The area of origin of *Co. semistriatus* is uncertain (Central or South America); other SA species are clearly from the southern continent by reference to fossil record (Wang and Carranza-Castañeda 2008; Prevosti and Soibelzon 2012). The presence of *Co. primaevus* in the Ensenadan is based on the interpretation of Kraglievich (1934), but at present it is difficult to corroborate this interpretation. On the other hand, the presence of *Co. mercedensis* in the Ensenadan is based on the inclusion of *Conepatus mercedensis praecursor* Rusconi 1932 as a subspecies of this species (Berman 1994).

Procyonidae Bonaparte 1850

Procyonids are, with few exceptions, small- to medium-sized carnivores that inhabit mostly forests, or semiforested habitats, with omnivorous diets and a generalized postcranial structure with scansorial capabilities (Ewers 1973; Wilson and Mittermeier 2009). They are restricted to tropical and subtropical regions of the Americas and are presently absent from other continents (Wilson and Mittermeier 2009). The fossil record shows that their earliest remains are from the Oligocene of Europe, and if Simocyoninae are in fact part of this family, then it was present in other Holarctic continents in the Miocene (Hunt 1996). Miocene–Pliocene NA procyonids were very diverse, including the groups that have invaded South America since the late Miocene (Baskin 1998, 2003). Rodriguez et al. (2013) interpreted that procyonids immigrated twice to South America (in the late Miocene to give rise to *Cyonasua* Ameghino 1885 and *Chapalmalania* Ameghino 1908, and again in the Late Pleistocene for the living taxa), which is inconsistent with phylogenetic reconstructions that indicate multiple immigration events (Prevosti and Soibelzon 2012). The oldest records of *Potos* E. Geoffroy Saint-Hilaire and Cuvier 1795, and *Nasuella* Hollister 1915, are part of the faunal list of the late Holocene archaeological site of La Chimba, Ecuador (Stahl 2003). *Bassaricyon* Allen 1876, has no fossil record.

Nasua Storr 1870
(Tables 4.1 and 4.2)

Species in South America: *Nasua narica* (Linnaeus 1766) and *Nasua nasua* (Linnaeus 1766).

Temporal and geographic distribution: *Nasua narica* currently inhabits Central America and northwest Colombia, while *N. nasua* is distributed from Colombia and Venezuela in the north, to northern Uruguay and northern Argentina in the south (Wilson and Mittermeier 2009). Fossil remains of *N. nasua* has have been found in the “Lujanian” of Minas Gerais and Bahia and Late Pleistocene of Tocantins (Rodrigues et al. 2014), Brazil, and a putative record of *Nasua* from the “Ensenadan” of Tarija, Bolivia (Soibelzon and Prevosti 2007, 2013). *Nasua* cf. *N. nasua* was included in the faunal list of the late Holocene archeological site of La Chimba, Ecuador (Stahl 2003) and described from a late Holocene (ca. 500 years BP) archeological site in northeastern Buenos Aires, Argentina. This record is outside the current geographic distribution of the genus, and could be explained by either anthropic transportation or by a wider distribution of the taxon in the past, associated with recent climatic changes (Ramírez et al. 2015).

Paleoecology: *Nasua* includes small carnivores (2 kg–7 kg) with omnivorous diets, composed mainly of invertebrates and fruit, and with good scansorial capabilities (Wilson and Mittermeier 2009).

Comments: The fossil record of *Nasua*, species distribution, and phylogenetic reconstructions suggest that the genus originated outside SA, with the exception of *N. nasua* (Prevosti and Soibelzon 2012). Molecular data suggest that *Nasuella* is a junior synonym of *Nasua* (Eizirik 2012).

Procyon Storr 1870
(Tables 4.1 and 4.2)

Species in South America: *Procyon cancrivorus* (Cuvier 1798), *Procyon lotor* (Linnaeus 1758).

Temporal and geographic distribution: *Procyon cancrivorus* occurs from Panama to Uruguay and northeastern Buenos Aires (Argentina), while *P. lotor* in SA is only recorded in the Caribbean region of Colombia (Wilson and Mittermeier 2009; Fracassi et al. 2010). Fossil raccoons have been found in the Late Pleistocene of Bahia, Minas Gerais and Tocantins, Brazil and the Lujanian of Formosa, northern Argentina (Soibelzon and Prevosti 2007, 2013; Rodriguez et al. 2013). The latter is associated with a Late Pleistocene fauna, but the correlation made by Soibelzon et al. (2010) with other locality dated ca. 60 ka has no support (see discussion in Prevosti and Schubert 2013). *Procyon* cf. *P. cancrivorus* was listed for the late Holocene La Chimba archaeological site of Ecuador (Stahl 2003), while unpublished *Procyon* remains have been recovered from the Middle Pleistocene Orocual archaeological site in eastern Venezuela (Prevosti *pers. obs.*). As is discussed elsewhere (Soibelzon and Prevosti 2007), the absence of a stratigraphic context or dates associated with the Brazilian fossils does not allow us to confirm their Lujanian Age.

Paleoecology: *Procyon* includes small- to medium-sized carnivores (3.1 kg–7.7 kg), with omnivorous diets (invertebrates, fruits, small vertebrates) and scansorial habits (Wilson and Mittermeier 2009). Currently, *Procyon* inhabits different kind of forested habitats, but also was observed in the South American Llanos.

Comments: The oldest record of *Procyon* is from the late Miocene–Pliocene of NA (Baskin 1998). Soibelzon (2011) and Rodriguez et al. (2013) inferred that raccoons migrated to SA in the Late Pleistocene; however, this could be an artifact of the bias against tropical areas in the fossil record, especially before the Late

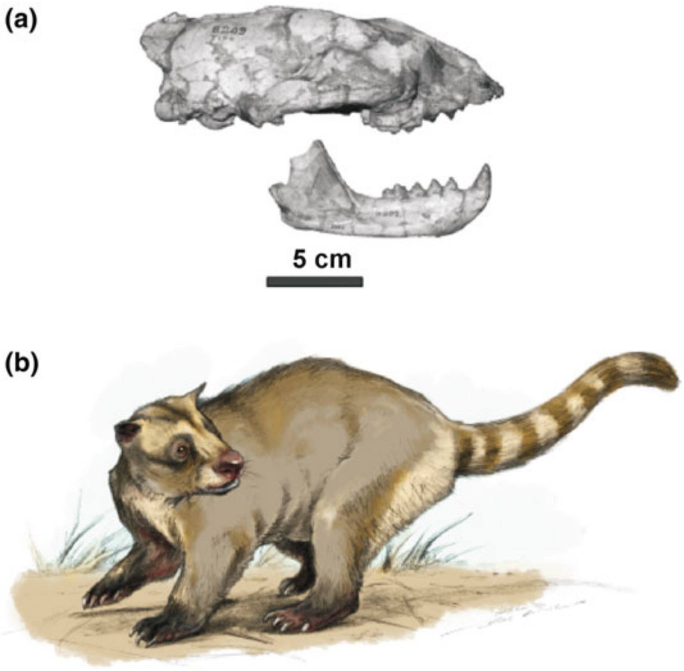


Fig. 4.11 Lateral view of the skull of *Cyonasua brevirostris* (MACN Pv 8209, Holotype of *Amphinasua longirostris*), and life reconstruction of *Cyonasua* (**b**). Scale = 5 cm

Pleistocene (Prevosti and Soibelzon 2012; Prevosti et al. 2013), as suggested by the unpublished *Procyon* specimens from the Middle Pleistocene of Venezuela. *Procyon cancrivorus* may have its origin in South America (Prevosti and Soibelzon 2012).

Cyonasua Ameghino 1885
(Fig. 4.11; Tables 4.1 and 4.2)

Species in South America: *Cyonasua argentina* Ameghino 1885, *Cyonasua brevirostris* (Moreno and Mercerat 1891), *Cyonasua clausa* (Ameghino 1904), *Cyonasua groeberi* JL Kraglievich and Reig 1955, *Cyonasua lutaria* (Cabrera 1936), *Cyonasua meranii* (C. Ameghino and Kraglievich 1925), and *Cyonasua pascuali* Linares 1982.

Temporal and geographic distribution: The fossil record of *Cyonasua* principally includes Argentina, and scarce material from Bolivia, and Venezuela from the late Miocene (Huayquerian) to the Middle Pleistocene (Ensenadan) (Soibelzon and Prevosti 2007, 2013; Prevosti and Soibelzon 2012; Forasiepi et al. 2014). The oldest specimen of this genus (*Cyonasua* sp.) is from Catamarca province, Argentina, and has an age of between 8.7 and 7.14 Ma (Esteban et al. 2014), while the youngest belongs to *Cy. meranii* and was collected in the Ensenadan of Buenos

Aires Province (ca. 1 Ma; Soibelzon and Prevosti 2007, 2013; Prevosti and Soibelzon 2012). Several species have been recorded in the Huayquerian: *Cy. argentina* in Entre Ríos and possibly Catamarca, *Cy. pascuali* in Mendoza, and *Cy. brevirostris* in Catamarca and La Pampa (Berta and Marshall 1978; Berman 1989). *Cyonasua lutaria* is present in the Chapadmalalan (ca. 3.3 Ma) of Buenos Aires and possibly in the Pliocene of Catamarca (Kraglievich and Reig 1954; Kraglievich and Olazábal 1959; Berta and Marshall 1978; Marshall et al. 1979; Berman 1989). *Cyonasua clausa* is only known from the Montehermosan (early Pliocene) of Buenos Aires, and *Cy. groeberi* from the late Miocene or Pliocene of Córdoba (Kraglievich and Reig 1954; Berta and Marshall 1978). *Cyonasua* is also recorded in the Huayquerian of Jujuy, in the late Pliocene of Venezuela, and in the late Miocene of Bolivia (Berman 1989; Forasiepi et al. 2014; Poiré et al. 2015). Procyonid postcranial remains that could belong to *Cyonasua* have been found in the late Miocene–early Pliocene of Peru (Soibelzon and Prevosti 2013).

Paleoecology: The estimated body mass of *Cyonasua* using the lower carnassial is about 6 kg (Prevosti et al. 2013); however, this value seems to be an underestimate because this taxon has a small lower m1 and skull measurements indicates a larger body size. We made new estimation using the condylobasal length of the skull (LCB), and the distance between the skull condyles and the anterior border of the orbits (LOO), using the formulae of Van Valkenbrugh (1990) based on a sample of living Carnivora. We obtained body mass estimates of 20.5 kg (SKL) and 23.4 kg (OOL) for the holotype of *Cyonasua brevirostris* (MLP 10-52), and 21.8 kg (OOL) for an incomplete skull of *Cy. lutaria* (MMP S 369). Using geometric similarity and the mean of these estimations, we inferred the body size of other species: *Cyonasua argentina*: 19.6 kg; *Cyonasua pascuali*: 17.04 kg, *Cyonasua groeberi*: 23.1 kg, *Cyonasua clausa*: 23.9 kg, *Cyonasua lutaria*: 21.8 kg; *Cyonasua meranii*: 20.6 kg. The estimates for some species (e.g., *Cy. lutaria* and *Cy. brevirostris*) accord better with the body masses of some living species (e.g., *Gulo gulo* (Linnaeus 1758) and *Neofelis nebulosa* (Griffith 1821), with a body mass of ca. 20 kg and 22 kg, respectively) that have similar cranial measurements, but not with others (e.g., *Mellivora capensis* (Schreber 1776)) and *Canis latrans* Say 1823, with a body mass of ca. 10 kg and 13 kg, respectively; see Van Valkenburgh 1990). The results obtained with geometric similarity are likely overestimates, because they are larger than the body mass of *Procyon lotor* (ca. 8 kg–10 kg) despite its having similar dental measurements. Thus, we consider that a mean between the dental and cranial estimators is the best way to reduce bias (Table 4.2). Using this procedure, the body mass of *Cyonasua* is between 15 kg (*Cy. clausa*) and 11 kg (*Cy. pascuali*). Using postcranial measurements of some species of *Cyonasua*, preliminary work by Tarquini et al. (2015; 2016) obtained body masses between 13 kg–25 kg, which overlap with the ones obtained here using cranial measurements and the "mean approach". Wroe et al. (2004) reported a body mass of 23.7 kg for *Cy. argentina* based on the Van Valkenburgh (1990) SKL equation. Unfortunately, there is no *Cyonasua* skull confidently assigned to *Cy. argentina*, and we cannot identify which specimen was used in this analysis. Dental morphology suggests a hypocarnivorous and omnivorous diet (Prevosti et al. 2013;

Soibelzon and Prevosti 2013). Soibelzon (2011) inferred that *Cyonasua* had a more predatory niche than living South American procyonids. However, shearing structures useful to process meat are reduced in the dentition of *Cyonasua* suggesting an omnivorous and generalist diet. A recent study of postcranial elements of *Cyonasua* (Tarquini et al. 2017) suggests that this taxon had generalized locomotor habits, with some degree of grasping ability, congruent with climbing capabilities.

Comments: The fossil record and phylogenetic position suggest that *Cyonasua* evolved in South America (Baskin 1989, 2004; Prevosti and Soibelzon 2012; Forasiepi et al. 2014). Recently, several rodent remains (i.e., *Actenomys* sp., *Microcavia* sp.,) and small notoungulates (i.e., *Paedotherium*) have been found in a paleocave, in the Chapadmalal "Formation" ("middle" Pliocene) near Miramar (Buenos Aires, Argentina). This association has been interpreted as the product of the depredation of *Cyonasua lutaria* or a carnivorous didelphimorphian (i.e., *Thylophorops chapadmalensis*) (Cenizo et al. 2016) and could indicate that *Cyonasua* preyed on these small mammals.

Chapalmalania Ameghino 1909
(Fig. 4.12; Tables 4.1 and 4.2)

Species in South America: *Chapalmalania altaefrontis* Kraglievich and Olazabal 1959 and *Ch. ortognatha* Ameghino 1908.

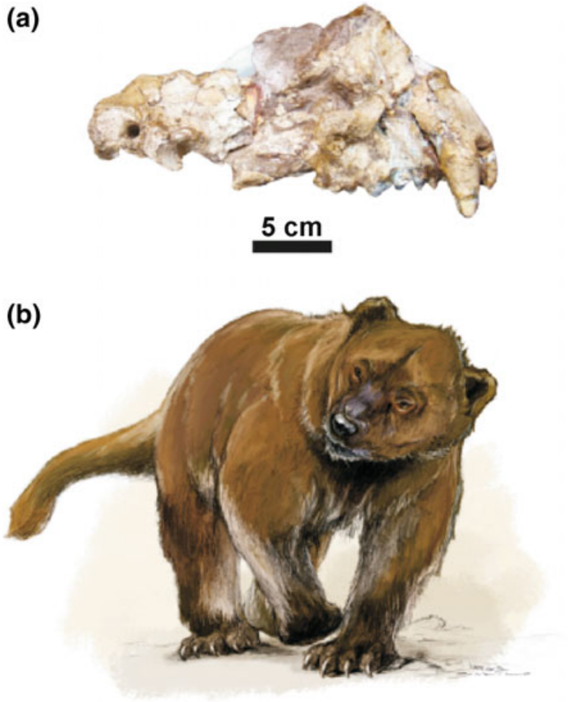


Fig. 4.12 Lateral view of the skull of *Chapalmalania altaefrontis* (MLP 54-V-17-1, Holotype) (**a**) and life reconstruction of *Chapalmalania* (**b**). Scale = 5 cm

Temporal and geographic distribution: *Chapalmalania altaefrontis* comes from the Pliocene of Mendoza, probably from Chapadmalalan levels, and *Ch. ortognatha* was found in the Chapadmalalan of Buenos Aires (ca. 3.3 Ma; Ameghino 1908; Kraglievich and Olazabal 1959; Berman 1994; Soibelzon and Prevosti 2007, 2013). One specimen of *Chapalmalania* cf. *Ch. altaefrontis* was discovered in the Pliocene of Catamarca and one assigned to *Ch. altaefrontis* in the Vorohuean (late Pliocene) of Buenos Aires (Kraglievich and Olazabal 1959; Marshall et al. 1979; Berman 1994). An isolated upper M1 of *Chapalmalania* sp. was recently found in the late Pliocene of Colombia (Forasiepi et al. 2014).

Paleoecology: The body mass of *Chapalmalania* species was estimated to have been about 22 kg using lower carnassial length (Prevosti et al. 2013). As in the case of *Cyonasua*, this value seems to be an underestimate. However considering the size of the cranial remains and the specimen MMP 1121 M, new estimations using the SKL and OOL equations (Van Valkenburgh 1990), we obtained a body mass of 125 kg–181 kg (mean: 153.76 kg), comparable to small/medium-sized bears (e.g., *Ursus americanus* Pallas 1780). The mean of the dental and cranial estimates (ca. 90 kg), gives a lower value comparable to females of small-sized bears (e.g., *Tremarctos ornatus*; Wilson and Mittermeier 2009). Wroe et al. (2004) reported a body mass of 93.1 kg for *Ch. altaefrontis* based on the Van Valkenburgh (1990) SKL equation, but there is no a complete skull for taking this measurement. An omnivorous scavenger diet was inferred for *Chapalmalania* (Kraglievich and Olazábal 1959; Berman 1994; Soibelzon and Prevosti 2007, 2013). Recently, de los Reyes et al. (2013) interpreted some bite marks found in a caudal vertebra of a Pliocene glyptodont as produced by *Chapalmalania*.

Comments: Species determination is a difficult task. The holotype of *Ch. ortognatha* is an anterior portion of palate with the premaxillary region, incisors, and canines, while the holotype of *Ch. altaefrontis* is a rostrum with complete dentition and a portion of the basicranium. Consequently, the determination of isolated mandibles is subjective. A skull, MMP 1121 M from the Chapadmalalan of Buenos Aires could belong to *Ch. ortognatha* (Prevosti et al. 2013), or to a third species, with the rostrum being clearly longer than in *Ch. altaefrontis*. Following the interpretation for *Cyonasua*, *Chapalmalania* could have originated in SA (Prevosti and Soibelzon 2012).

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