Chapter 3
South American Endemic Mammalian Predators (Order Sparassodonta)

Abstract The Sparassodonta was a clade of mammalian predators that evolved in South America from the early Paleocene (?Tiupampan–Peligran) or early Eocene (Itaboraian) to the early Pliocene (Chapadmalalan). They were a monophyletic group of metatherians closely related to living marsupials (e.g., opossums and kangaroos). Diverse ecological niches presented many opportunities for occupation by different morphotypes (principally defined by body mass and locomotion). The probable diet was hypercarnivorous for about 90% of the nearly 60 currently identified species. Here, we present a synthesis of the systematics, distribution, and paleoecology of the extinct Sparassodonta.

Keywords Borhyaenidae · Hathliacynidae · Hondadelphydae · Proborhyaenidae Thylacosmilidae

3.1 Introduction

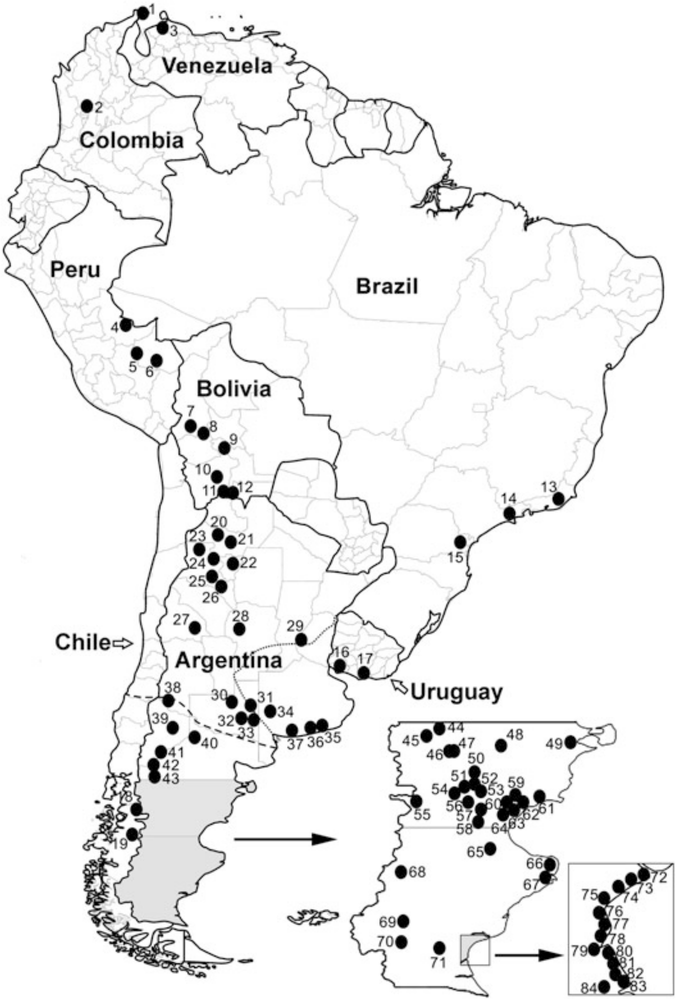
The Sparassodonta was a group of predaceous metatherians, now extinct. Their fossil record arguably extends from the early Paleocene (possibly ?Tiupampan–Peligran) or early Eocene (Itaboraian) up to the early Pliocene (Chapadmalalan) (Simpson 1950, 1980; Marshall 1977a, 1978, 1979, 1981; Goin and Pascual 1987; Marshall and de Muizon 1988; de Muizon 1994, 1998, 1999; Forasiepi 2009; Babot and Forasiepi 2016) (Table 3.1). Sparassodonta is an exclusively South American monophyletic group with most fossil evidence concentrated in the southern parts of the continent (Fig. 3.1).

The phylogenetic affinities of Sparassodonta within Metatheria have been a controversial issue in recent decades with a number of opposing positions proposed. Earlier views that Sparassodonta were directly related to one or more of thylacinids, dasyurids, and didelphids have been challenged by recent work showing that sparassodonts cannot be included in crown group Marsupialia (e.g., Szalay 1994; Rougier et al. 1998, 2004; Babot 2005; Ladevèze and de Muizon 2007, 2010; Forasiepi 2009; Engelman and Croft 2014; Forasiepi et al. 2015; Suarez et al. 2015;

F.J. Prevosti and A.M. Forasiepi, *Evolution of South American Mammalian Predators During the Cenozoic: Paleobiogeographic and Paleoenvironmental Contingencies*,
Springer Geology, https://doi.org/10.1007/978-3-319-03701-1_3

Table 3.1 Distribution of sparassodonts in the South American Stages/Ages

Taxa	Tiupampan	Peligran	Itaboraian	Riochican	Casamayoran	Mustersan	Tinguirirican	Deseadan	Colhuehuapian	Santacrucian	Friasian	Colloncuran	Laventan	Mayoan	Chasicoan	Huayquerian	Montehermosan	Chapadmalalan
Nemolestes spalacotherinus					■													
Patene campbelli						■												
Patene coluapiensis					■													
Patene simpsoni			■		■													
Stylocynus paranensis																■		
Hondadelphys fieldsi													■					
Acyon myctoderos													■					
Acyon tricuspidatus										■								
Acyon herrerae (nomen dubium)									■									
Borhyaenidium altiplanicus																■		
Borhyaenidium musteloides																■		
Borhyaenidium riggsi																		■
Chasicostylus castroi															■			
Cladosictis centralis									■									
Cladosictis patagonica										■	■							
Contrerascynus borhyaenoides															■			
Notictis ortizi																■		
Notocynus hermosicus																	■	
Notogale mitis								■										
Perathereutes pungens										■								
Pseudonotictis chubutensis												■						
Pseudonotictis pusillus										■								
Sallacyon hoffstetteri								■										
Sipalocyon externa									■									
Sipalocyon gracilis										■	■							
Sipalocyon obusta (nomen dubium)										■								
Procladosictis anomala						■												
Dukecynus magnus													■					
Lycopsis longirostrus													■					
Lycopsis padillai												■						
Lycopsis torresi										■								
Lycopsis viverensis															■			
Pharsophorus lacerans								■										
Pharsophorus tenax								■										
Plesiofelis schlosseri						■												
Prothylacynus patagonicus										■	■							
Pseudolycopsis cabrerai															■			
Pseudothylacynus rectus									■									
Arminiheringia auceta					■													
Arminiheringia contigua					■													
Arminiheringia cultrata					■													
Callistoe vincei					■													
Paraborhyaena boliviana								■										
Proborhyaena gigantea								■										
Anachlysictis gracilis													■					
Patagosmilus goini												■						
Thylacosmilus atrox																■	■	■
Acrocyon riggsi									■									
Acrocyon sectorius										■								
Arctodictis munizi										■								
Arctodictis sinclairi									■									
Australohyaena antiquua								■										
Borhyaena macrodonta									■									
Borhyaena tuberata										■	■							
Fredszalaya hunteri								■										
Angelocabrerus daptes (nomen dubium)					■													
Argyrolestes peralestinus (nomen dubium)					■													
Eutemnodus americanus (nomen dubium)																■		
? Sparassodonta																		
Allqokirus australis	■																	
Andinodelphys cohcabanbensis	■																	
Jaskhadelphys minutus	■																	
Mayulestes ferox	■																	
Pucadelphys andinus	■																	



Babot and Forasiepi 2016; Fig. 3.2). The discovery of the fine skeleton of *Mayulestes ferox* from the Paleocene of Bolivia (claimed to be the most basal sparassodont; de Muizon 1994, 1998; de Muizon et al. 2015) reignited interest in the phylogeny of the group. The phylogenetic position of *Mayulestes* within Sparassodonta, as well as other Tiupampan metatherians, is matter of discussion (see below).

The nearly 60 currently identified members of the clade cover many different shapes, sizes, and locomotor types (Table 3.2). All forms fit within carnivory, most of them consistent with hypercarnivory (Marshall 1977a, 1978, 1979, 1981; Prevosti et al. 2013; Wroe et al. 2013), and with bite forces higher than placental carnivorans (Wroe et al. 2004b; Blanco et al. 2011). Locomotor habits range from terrestrial to arboreal. As indicated by Argot and Babot (2011), terrestriality appears

◀**Fig. 3.1** Map of South America with the localities where sparassodont remains were found. COLOMBIA: 1, La Guajira; 2, La Venta. VENEZUELA: 3, Urumaco. PERU: 4, Santa Rosa; 5, Fitzcarrald; 6, Madre de Dios. BOLIVIA: 7, Achiri; 8, Salla-Lurivay; 9, Tiupampa; 10, Cerdas; 11, Nazareno; 12, Quebrada Honda. BRAZIL: 13, São Jasé de Itaboraí; 14, Tremembé; 15, Curitiba. URUGUAY: 16, Arazatí; 17, Paso del Cuello. CHILE: 18, Alto Río Cisnes; 19, Pampa Castillo. ARGENTINA: 20, Estrecho del Tronco; 21, Pampa Grande; 22, Tafí Viejo; 23, Antofagasta de la Sierra; 24, Chiquimil; 25, Puerta del Corral Quemado; 26, Andalgalá; 27, Loma de las Tapias; 28, Nono; 29, Paraná; 30, Telén; 31, El Guanaco; 32, Quehué; 33, Salinas Grandes de Hidalgo; 34, Arroyo Chasicó; 35, Barranca de los Lobos; 36, Chapadmalal; 37, Monte Hermoso; 38, Quebrada Fiera; 39, Cerro Bandera and Sierra del Portezuelo Norte; 40, Paso Córdova; 41, Cañadón del Tordillo; 42, Pilcaniyeu; 43, Río Chico; 44, El Petiso; 45, Cerro Zeballos; 46, Laguna Fría; 47, La Barda; 48, Sacanana; 49, Gaiman; 50, Laguna de la Bombilla; 51, Laguna Payahilé; 52, Gran Hondonada; 53, Rinconada de López; 54, La Curandera; 55, Río Senguer; 56, Cerro del Humo; 57, Barranca Norte (north slope of the Colhué-Huapi Lake); 58, Barranca Sur or Gran Barranca (south slope of the Colhué-Huapi Lake); 59, Cabeza Blanca; 60, Yacimiento Las Flores; 61, Cerro Redondo; 62, Punta Peligro; 63, Bajo de la Palangana; 64, Cañadón Hondo; 65, Pico Truncado; 66, Puerto Deseado; 67, La Flecha; 68, Lago Pueyrredón; 69, Sheuen; 70, Karaiken; 71, Río Santa Cruz; 72, Monte León; 73, La Cueva; 74, Yegua Quemada; 75, Monte Observación; 76, Jack Harvey; 77, Cañadón de las Vacas; 78, Wreck Hat; 79, Coy Inlet; 80, La Costa; 81, Corrigen Kaik; 82, Estancia Angelina; 83, Río Gallegos (locality); 84, Kallik Aike Norte (=Felton's Estancia)

to have been the primitive condition for the group (recorded in *Arctodictis sinclairi*, *Borhyaena tuberata*, *Callistoe vincei*, *Lycopsis longirostrus*, *Thylacosmilus atrox*, and in the stem marsupials from Tiupampa, with a gradient of increasing arboreality from *Pucadelphys andinus*, *Andinodelphys cochabambensis*, to *Mayulestes ferox*; de Muizon and Argot 2003; Argot and Babot 2011). The climbing abilities among sparassodonts apparently evolved independently in different lineages of medium- to small-sized hathliacynids (*Cladosictis patagonica*, *Sipalocyon gracilis*, *Pseudonotictis pusillus*) and some large-size borhyaenoids (*Prothylacynus patagonicus*). An incipient cursoriality has been suggested for *Borhyana tuberata* and *Thylacosmilus atrox* (Argot 2004a; Ercoli et al. 2012).

Both the total taxonomic diversity of Sparassodonta through the Cenozoic and their morphological disparity seem to be lower than in placental Carnivora, which fits with the general pattern of a more restricted morphospace occupied by marsupials compared to placentals (Sears 2004; Sánchez-Villagra 2013; Prevosti et al. 2012a; Echarri and Prevosti 2015; a contrary conclusion in Goswami et al. 2011). When analyzing the taxonomic composition of the most studied SA fossil association—Santa Cruz Formation, early Miocene (Santacrucian)—, it may be seen that the sparassodont diversity reached eleven (or at least nine) species, which roughly matches carnivoran taxonomic richness in some current environments (Prevosti et al. 2012b, but see Croft 2001, 2006; Wroe et al. 2004a). In addition, during most of the Cenozoic, the carnivorous adaptive zone of South America was shared between the Sparassodonta and nonmammalian taxa, such as Sebecidae (crocodiles), Phorusrhacidae ("terror birds"), Madtsoiidae (snakes), and, for about 3 Ma (from the late Miocene to the mid-Pliocene), with placental carnivores and didelphimorphian marsupials (Degrange et al. 2010; Prevosti et al. 2013; Scheyer et al.

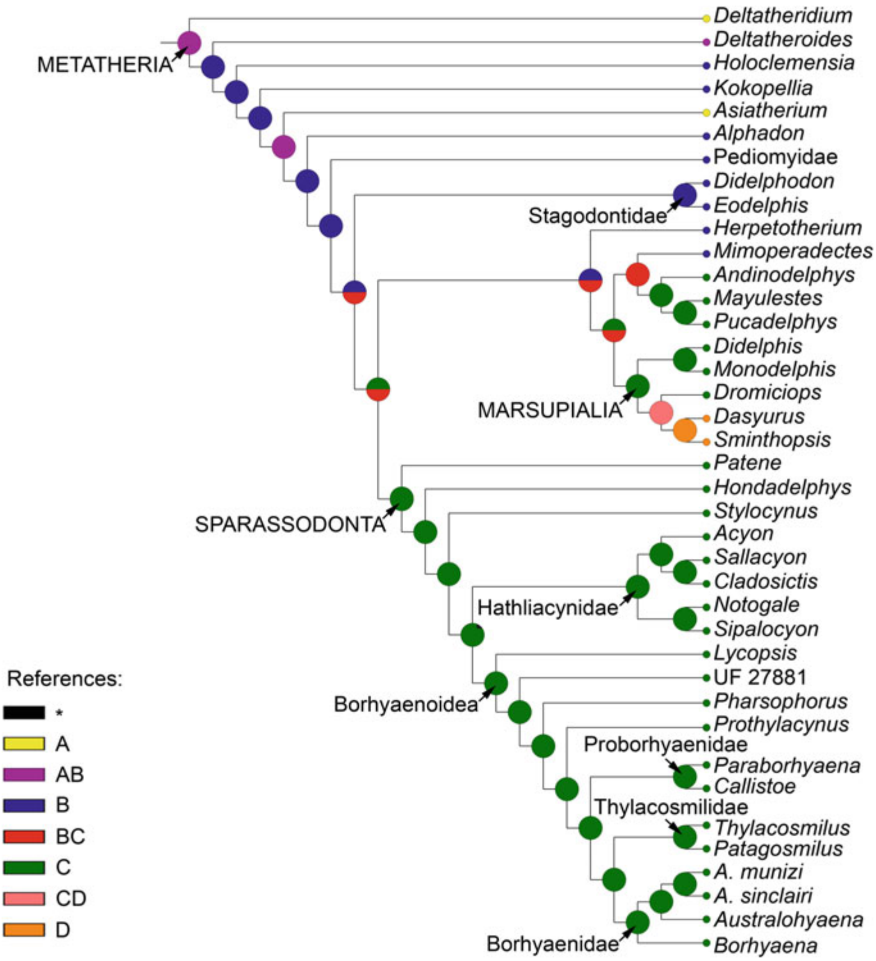


Fig. 3.2 Phylogenetic hypothesis of the Sparassodonta and their relationships with other metatherians. Cladogram obtained under implied weighting (Forasiepi et al. 2015) showing the reconstruction of the ancestral areas at each node obtained by S-DIVA (Statistical Dispersal–Vicariance Analysis) and exported from RASP (Reconstruct Ancestral State in Phylogenies). Color key represents possible ancestral ranges at different nodes: A, Asia; B, North America; C, South America; D, Australia; black with an asterisk represents other ancestral ranges

2013; Zimicz 2014). This would have favoured a partitioning of the carnivorous adaptive zone (Wroe et al. 2004a; Ercoli et al. 2013; Forasiepi and Sánchez-Villagra 2014) in which each taxonomic group would have occupied a particular role in the terrestrial ecosystems.

Table 3.2 Body mass (BM) and diet of sparassodonts

Taxa	BM (kg)	Mass category	RGA	Diet category	Comments
Nemolestes spalacotherinus	5.72	S	Unknown m4	hyp	BM from Zimicz (2012) and Prevosti et al. (2013). RGA of m3: 0.35. Diet from Prevosti et al. (2013)
Patene campbelli	1	S	Unknown m4	omn	BM from Zimicz (2012). Diet taken from *Patene simpsoni*, following Prevosti et al. (2013)
Patene coluapiensis	3.07	S	Unknown m4	omn	BM mean from Zimicz (2012) and Prevosti et al. (2013). Diet taken from *Patene simpsoni,* following Prevosti et al. (2013)
Patene simpsoni	1.35	S	Unknown m4	omn	BM mean from Zimicz (2012) and Prevosti et al. (2013). RGA of m3: 0.76. Diet from Prevosti et al. (2013)
Stylocynus paranensis	31.05	L	0.61	omn	BM from mean of tooth variables from Wroe et al. (2004a) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Hondadelphys fieldsi	3.7	S	0.63	omn	BM from tooth variables and diet from Prevosti et al. (2013)
Acyon myctoderos	13–17.5	M to L	0.27	hyp	BM from postcranial variables from Engelman et al. 2015. Diet from Prevosti et al. (2013)
Acyon tricuspidatus	6.51	S	0.30	hyp	BM mean from Wroe et al. (2004a), Zimicz (2012), and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Acyon herrerae (nomen dubium)	8.23	M	0.30	hyp	BM mean from Wroe et al. (2004a), Zimicz (2012), and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Borhyaenidium altiplanicus	1.16	S	Unknown m4	hyp	BM from Prevosti et al. (2013). Diet taken from *Borhyaenidium musteloides*, following Prevosti et al. (2013)

(continued)

Table 3.2 (continued)

Taxa	BM (kg)	Mass category	RGA	Diet category	Comments
Borhyaenidium musteloides	1.56	S	0.30	hyp	BM and diet from Prevosti et al. (2013)
Borhyaenidium riggsi	1.98	S	0.32	hyp	BM and diet from Prevosti et al. (2013)
Chasicostylus castroi	8.27	M	Unknown m4	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet taken from *B. musteloides,* following Prevosti et al. (2013)
Cladosictis centralis	3.9	S	Unknown m4	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet taken from *C. patagonica,* following Prevosti et al. (2013)
Cladosictis patagonica	6.6	S	0.17	hyp	BM from Ercoli and Prevosti (2011). Diet from Prevosti et al. (2013)
Contrerascynus borhyaenoides	12.6	M	0.27	hyp	This work. BM from equations from Gordon (2003), based on the lengh of m3. Diet from Prevosti et al. (2013)
Notictis ortizi	1.17	S	Unknown m4	hyp	BM from Prevosti et al. (2013). Diet taken from *Pseudonotictis pusillus,* following Prevosti et al. (2013)
Notocynus hermosicus	2.48	S	Unknown m4	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet taken from *S. gracilis*, following Prevosti et al. (2013)
Notogale mitis	3.06	S	0.37	hyp	BM mean from Wroe et al. (2004a), Zimicz (2012), and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Perathereutes pungens	1.75	S	0.34	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet from Prevosti et al. (2013).
Pseudonotictis chubutensis	0.89	S	Unknown m4	hyp	BM from Zimicz (2014). Diet taken from *Pseudonotictis pusillus*, following Prevosti et al. (2013)

(continued)

Table 3.2 (continued)

Taxa	BM (kg)	Mass category	RGA	Diet category	Comments
Pseudonotictis pusillus	1.17	S	0.30	hyp	BM from Ercoli and Prevosti (2011). Diet from Prevosti et al. (2013)
Sallacyon hoffstetteri	2.06	S	Unknown m4	hyp	BM mean from Zimicz (2012) and Prevosti et al. (2013). Diet taken from *Sipalocyon gracilis*, following Prevosti et al. (2013)
Sipalocyon externa	1.7	S	Unknown m4	hyp	BM mean from Prevosti et al. (2013) and Zimicz 2014. Diet taken from *Sipalocyon gracilis,* following Prevosti et al. (2013)
Sipalocyon gracilis	2.11	S	0.33	hyp	BM from Ercoli and Prevosti (2011). Diet from Prevosti et al. (2013)
Sipalocyon obusta (nomen dubium)	2.32	S	0.27	hyp	BM mean from Prevosti et al. (2013) and Zimicz (2014). Diet from Prevosti et al. (2013)
Procladosictis anomala	8.9	M	Unknown m4	hyp	BM from Zimicz (2012). Diet taken from *Cladosictis patagonica,* following Prevosti et al. (2013)
Dukecynus magnus	48.53	L	Unknown m4	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet taken from *Lycopsis torresi,* following Prevosti et al. (2013)
Lycopsis longirostrus	29.77	L	m4 in crypt	hyp	BM from Ercoli and Prevosti (2011). Diet taken from *Lycopsis torresi,* following Prevosti et al. (2013)
Lycopsis padillai	~22	L	Unknown m4	hyp	BM from Suarez et al. (2015). Diet taken from *Lycopsis torresi*
Lycopsis torresi	25.96	L	0.30	hyp	BM mean from Wroe et al. (2004a), Prevosti et al. (2013), and Suarez et al. (2015). Diet from Prevosti et al. (2013)
Lycopsis viverensis	14.5	M	0.26	hyp	BM mean from Prevosti et al. (2013) and Suarez et al. (2015). Diet from Prevosti et al. (2013)

(continued)

Table 3.2 (continued)

Taxa	BM (kg)	Mass category	RGA	Diet category	Comments
Pharsophorus lacerans	~27	L	0.17	hyp	BM mean from Zimicz (2012) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Pharsophorus tenax	16.8	L	0.53	meso	BM mean from Zimicz (2012) and Prevosti et al. (2013). Diet from Zimicz (2012)
Plesiofelis schlosseri	38.5	L	0.17	hyp	BM mean from Zimicz (2012) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Prothylacynus patagonicus	31.8	L	0.17	hyp	BM mean from Ercoli and Prevosti (2011). Diet from Prevosti et al. (2013)
Pseudolycopsis cabrerai	19.2	L	Unknown m4	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet taken from *L. viverensis,* following Prevosti et al. (2013)
Pseudothylacynus rectus	16.85	L	0.28	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Arminiheringia auceta	31.5	L	0	hyp	BM mean from Zimicz (2012) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Arminiheringia contigua	18.5	L	0	hyp	BM from Zimicz (2012). Diet from Prevosti et al. (2013)
Arminiheringia cultrata	24.85	L	0	hyp	BM mean from Zimicz (2012) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Callistoe vincei	~23	L	0	hyp	BM from Argot and Babot (2011). Diet from Prevosti et al. (2013)
Paraborhyaena boliviana	31.5	L	0	hyp	BM taken from *Arminiheringia auceta*. Diet from Prevosti et al. (2013)
Proborhyaena gigantea	~200	L	0	hyp	BM mean from Zimicz (2012), Prevosti et al. (2013), and Sorkin (2008). Diet from Prevosti et al. (2013)

(continued)

Table 3.2 (continued)

Taxa	BM (kg)	Mass category	RGA	Diet category	Comments
Anachlysictis gracilis	17	L	0	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Patagosmilus goini	~16	L	Unknown m4	hyp	This work. BM from equations of upper molars from Gordon (2003). Diet from *A. gracilis,* following Prevosti et al. (2013)
Thylacosmilus atrox	117.4	L	0	hyp	BM from Ercoli and Prevosti (2011). Diet from Prevosti et al. (2013)
Acrocyon riggsi	21.65	L	0	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Acrocyon sectorius	22.48	L	0	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Arctodictis munizi	43.87	L	0	hyp	BM mean from Wroe et al. (2004a), Vizcaíno et al. (2010), and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Arctodictis sinclairi	40	L	0	hyp	BM from Ercoli and Prevosti (2011). Diet from Prevosti et al. (2013)
Australohyaena antiquua	67	L	0	hyp	BM and diet from Forasiepi et al. (2015)
Borhyaena macrodonta	32.97	L	0	hyp	BM mean from Wroe et al. (2004a) and Prevosti et al. (2013). Diet from Prevosti et al. (2013)
Borhyaena tuberata	36.4	L	0	hyp	BM from Ercoli and Prevosti (2011). Diet from Prevosti et al. (2013)
Fredszalaya hunteri	31.8	L	Unknown m4	hyp	BM and diet taken from *Prothylacynus patagonicus,* following Prevosti et al. (2013)
Angelocabrerus daptes (nom. dub.)	~20.5	L	0	hyp	BM from Zimicz (2012). Diet from Prevosti et al. (2013)

(continued)

Table 3.2 (continued)

Taxa	BM (kg)	Mass category	RGA	Diet category	Comments
Argyrolestes peralestinus (nom. dub.)	4.95	S	Not found	hyp	BM and diet taken from *Nemolestes spalacotherinus,* following Prevosti et al. (2013)
Eutemnodus americanus (nom. dub.)	36.4	L	Unknown m4	hyp	BM and diet taken from *Borhyaena tuberata*, following Prevosti et al. (2013)

RGA: relative grinding area of lower carnassial (m4); nom. dub.: nomen dubium; L: large; M: medium; S: small; hyp: hypercarnivore; omn: omnivore; meso: mesocarnivore

3.2 Systematics, Distribution, and Paleoecology

We present a synthesis of the diversity, paleoecology, and temporal and geographic distribution of the Sparassodonta Detailed paleoecological studies are limited to those species best represented in the fossil record. Where there was insufficient evidence, closely related species are also used to supply paleoecological inferences. Body mass estimates are the most accurate when estimated on the basis of postcranial variables (e.g., Millien and Bovy 2010), but this evidence is mostly unavailable, so equations based on tooth measurements provide the only possible method (Myers 2001 in Wroe et al. 2004a; Gordon 2003 in Zimicz 2012, 2014; Prevosti et al. 2013). For the hypercarnivorous sparassodonts without grinding surfaces in the molars, the body mass predictions are usually underestimates (Prevosti et al. 2012b). Values in Table 3.2 were calculated on the basis of means derived from (1) postcranial data with correction for phylogeny, (2) postcranial data without correction for phylogeny, (3) combinations of skull and tooth variables, and (4) tooth variables alone. The diet was calculated with RGA tooth equations (modified from Van Valkenburgh 1991), and values were taken from Zimicz (2012) and Prevosti et al. (2013).

Mammalia Linnaeus 1758
Metatheria Huxley 1880
Sparassodonta Ameghino 1894

Sparassodonta includes hathliacynids, borhyaenoids, and all the taxa with a closer relationship to them than to living marsupials (Forasiepi 2009).

Nemolestes Ameghino 1902a
(Tables 3.1 and 3.2)

Included species. *Nemolestes spalacotherinus* Ameghino 1902a.

Temporal and geographic distribution. Middle to late Eocene (?Itaboraian and Casamayoran), Argentina and Brazil.

Paleoecology. Small-sized sparassodont (6.5 kg or ~5 kg; Zimicz 2012; Prevosti et al. 2013, respectively). Lower molars have reduced grinding areas; RGA tooth equations suggested hypercarnivorous diet (Zimicz 2012; Prevosti et al. 2013).

Comments. *Nemolestes spalacotherinus* is known by isolated teeth from Patagonia, Argentina. In addition, one lower molar from Itaboraí, Brazil, was referred to cf *Nemolestes* sp. (Marshall 1978; Bergqvist et al. 2006). Affinities with borhyaenoids have been suggested (e.g., Marshall 1978); however, its generalized tooth morphology likely indicates that *Nemolestes* does not belong to any major division within the group (Forasiepi 2009; Fig. 3.2).

Patene Simpson 1935
(Tables 3.1 and 3.2)

Included species. *Patene coluapiensis* Simpson 1935 (type species), *P. simpsoni* Paula Couto 1952, and *P. campbelli* Goin and Candela 2004.

Temporal and geographic distribution. *Patene simpsoni* comes from the early to middle Eocene (Itaboraian and Casamayoran), Argentina and Brazil; *P. coluapiensis* from the middle Eocene (Casamayoran), Argentina; *P. campbelli* from the latest middle–earliest late Eocene (Mustersan), Peru.

Paleoecology. *Patene* includes species of small body size (*P. simpsoni*: 1.3 kg or 1.4 kg; *P. coluapiensis*: 3.6 kg or 2.54 kg; *P. campbelli*: 1 kg or 5.37 kg in Zimicz 2012 and Prevosti et al. 2013, respectively). Estimations of *P. campbelli* in Zimicz (2012) better reflect the linear measurements for the smallest of the species of the genus (Goin and Candela 2004). Their broader molar grinding areas provide RGA values on the order of that of omnivorous/mesocarnivorous taxa (Zimicz 2012; Prevosti et al. 2013).

Comments. Material assigned to *Patene* species includes isolated teeth or tooth series associated with fragmentary maxillae and dentaries (Simpson 1935, 1948; Marshall 1981; Goin et al. 1986). *Patene* was considered a hathliacynid (e.g., Marshall 1981; Goin and Candela 2004); however, cladistic analyses recovered this taxon outside the major sparassodont groups (Forasiepi 2009; Engelman and Croft 2014; Forasiepi et al. 2015; Fig. 3.2).

Patene simpsoni and *P. campbelli* have been found in tropical latitudes of South America: the first from São José de Itaboraí (Brazil) and Estrecho del Tronco, Salta (Argentina), the latter from Santa Rosa (Peru) (Goin et al. 1986; Goin and Candela 2004), whereas *P. coluapiensis* comes from higher Patagonian latitudes (Marshall 1981).

The age of the Paleogene Santa Rosa fossil site in Peru, where *P. campbelli* comes from, has been controversial, with recent views in agreement that it is late middle Eocene or late Eocene (Bond et al. 2015).

Stylocynus Mercerat 1917
(Fig. 3.3a; Tables 3.1 and 3.2)

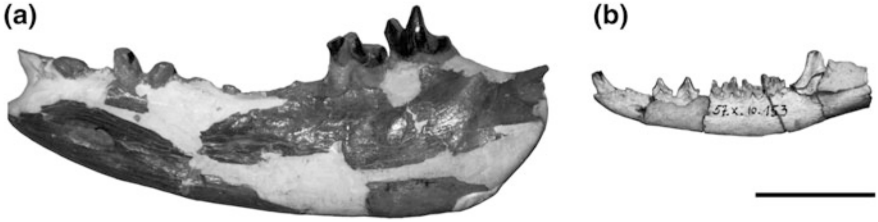


Fig. 3.3 *Stylocynus paranensis* (MLP 11-94, Holotype) from the late Miocene (Huayquerian Age), Paraná (Argentina), incomplete left dentary in lateral view (**a**); *Borhyaenidium musteloides* (MLP 57-X-10-153, Holotype) from the late Miocene (Huayquerian Age), Salinas Grandes de Hidalgo (Argentina), left dentary in lateral view (**b**). Scale bar = 3 cm

Included species. *Stylocynus paranensis* Mercerat 1917.

Temporal and geographic distribution. Late Miocene (Huayquerian) Argentina and possible Venezuela.

Paleoecology. *Stylocynus paranensis* was a large sparassodont (35.3 kg or 26.8 kg based on tooth equations; Wroe et al. 2004a; Prevosti et al. 2013, respectively), and probably with omnivorous/mesocarnivorous diet (Prevosti et al. 2013).

Comments. Material assigned to *S. paranensis* includes fragments of maxillae and dentaries with associated teeth from the Mesopotamian area in Argentina (e.g., Marshall 1979). Material tentatively assigned to *Stylocynus* has been recovered from northwestern Argentina (Babot and Ortiz 2008) and Urumaco in Venezuela (Linares 2004). The latter material appears to have been misplaced (Sánchez-Villagra per. com. 2015).

Marshall (1979) considered *S. paranensis* as a highly specialized borhyaenoid. Alternatively, cladistic analyses recovered *S. paranensis* outside major sparassodont groups (Forasiepi 2009; Engelman and Croft 2014; Forasiepi et al. 2015; Fig. 3.2), and in contrast, its tooth morphology could interpreted as plesiomorphic.

Hondadelphidae Marshall et al. 1990
Hondadelphys Marshall 1976a
(Tables 3.1 and 3.2)

Included species. *Hondadelphys fieldsi* Marshall 1976a.

Temporal and geographic distribution. Middle Miocene (Laventan), Colombia.

Paleoecology. Small size (3.7 kg estimated with tooth equations) and omnivorous (Prevosti et al. 2013).

Comments. *Hondadelphys fieldsi* has provoked different opinions regarding its affinities. Marshall (1976a) originally considered *H. fieldsi* to be a didelphid later placing it in Sparassodonta (Marshall et al. 1990; Goin 1997). Goin (1997) suggested that *H. fieldsi* was probably related to thylacosmilids, but cladistic analysis places outside of any major group (Forasiepi 2009; see also Marshall et al. 1990; Fig. 3.2). This hypothesis is in agreement with the "museum" model for the tropics, as a region in which old lineages have been able to persist for longer than in higher latitudes (see also Suarez et al. 2015).

Hathliacynidae Ameghino 1894

Hathliacynidae are small- to medium-sized sparassodonts, with long and slender skulls and dentaries that are fox- or weasel-like in appearance (Figs. 3.4, 3.5 and 3.6). All hathliacynids may have had a hypercarnivorous diet as suggested by the RGA dental index; however, the molars have very reduced crushing surfaces, which suggest the possibility of some dietary flexibility.

Hathliacynidae is a monophyletic group and includes the common ancestor of *Sipalocyon* and *Cladosictis* and all the taxa with a closer relationship to them than to borhyaenoids (Forasiepi 2009; Fig. 3.2). The oldest hathliacynid is from the late Oligocene (Deseadan) and the youngest, *Borhyaenidium riggsi*, is from the mid-Pliocene (Chapadmalalan). Putative hathliacynids have been claimed for the middle Eocene (Casamayoran; Marshall 1981) or late Oligocene (La Cancha association; Goin et al. 2010), which may considerably extend the stratigraphic range of the group. However, systematic interpretation of these putative hathliacynids requires the support of a phylogenetic analysis.

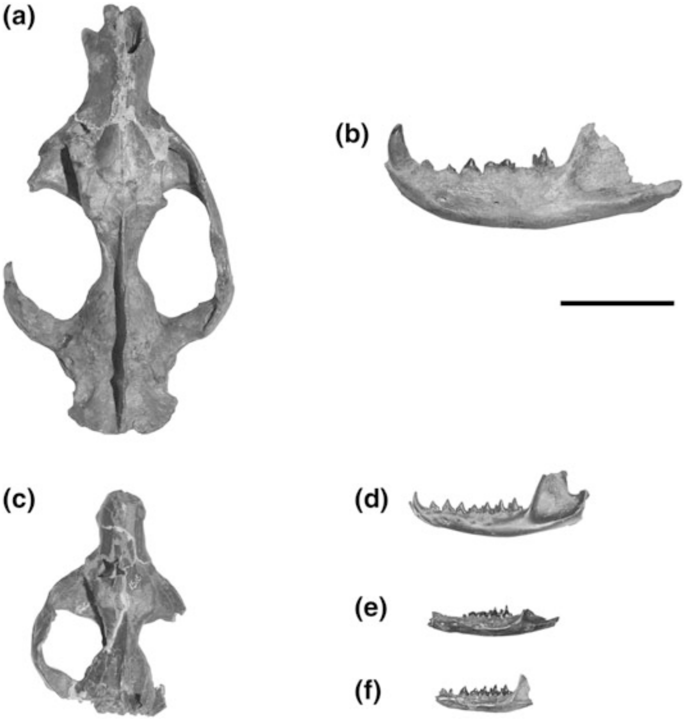


Fig. 3.4 Hathliacynidae from the early Miocene (Santacrucian Age), Santa Cruz Formation, Patagonia. *Cladosictis patagonica* (MACN-A 5927–5929, single specimen) cranium in dorsal view (**a**) and left dentary in lateral view (**b**); *Sipalocyon gracilis* (YPM PU 15154) nearly complete skull in dorsal view (**c**) and (YPM PU 15373) left dentary in lateral view (**d**); *Pseudonotictis pusillus* (MLP 11–26) left dentary in lateral view; *Perathereutes pungens* (MACN-A 684, Holotype) left dentary in lateral view (**e**). Scale bar = 5 cm

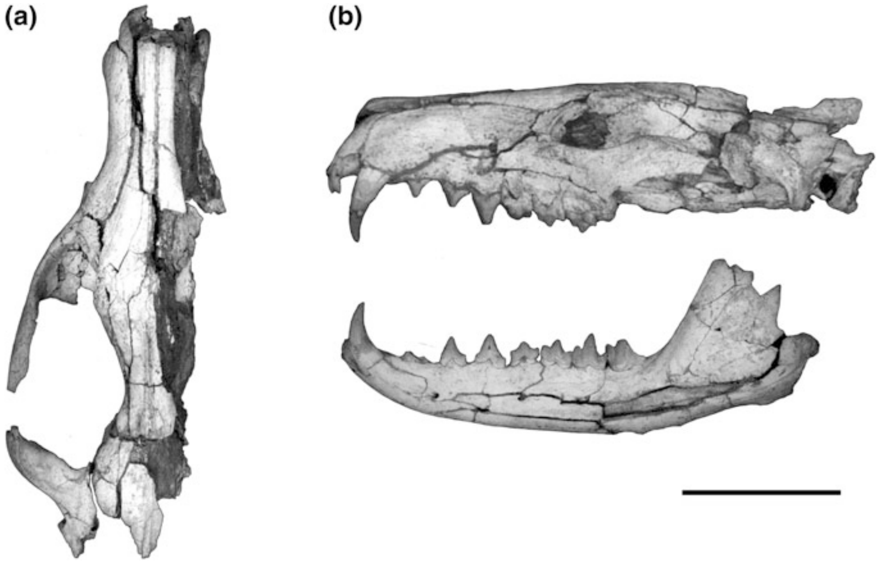


Fig. 3.5 *Acyon myctoderos* (MNHN-Bol-V-003668, Holotype), from the middle Miocene (Laventan Age), Quebrada Honda (Bolivia), cranium in dorsal view (**a**) and cranium with left dentary in lateral view (**b**). Scale bar = 5 cm

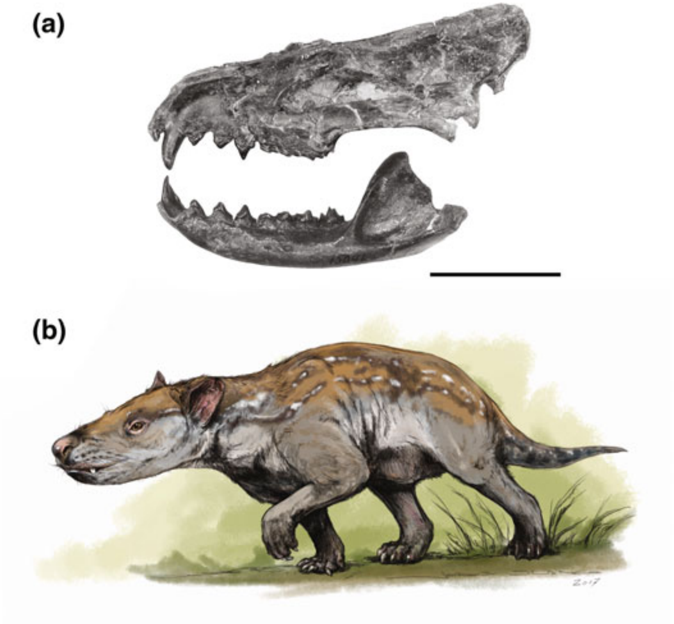


Fig. 3.6 *Cladosictis patagonica* (YPM PU 15046) from the early Miocene (Santacrucian Age), 15 km south of Coy Inlet, Patagonia (Argentina), cranium and left dentary in lateral view (**a**); artistic reconstruction by Jorge Blanco (**b**). Scale bar = 5 cm

Published phylogenies are in conflict with regard to the internal arrangement of the group (e.g., de Muizon 1999; Babot et al. 2002; Babot 2005; Forasiepi et al. 2006, 2015; Forasiepi 2009; Engelman and Croft 2014; Suarez et al. 2015), which suggests that the hathliacynid relationships deserve further and detailed analysis.

Acyon Ameghino 1887
(Fig. 3.5; Tables 3.1 and 3.2)

Included species. *Acyon tricuspidatus* Ameghino 1887 (type species), *A. herrerae* (Marshall 1981) (nomen dubium), and *A. myctoderos* Forasiepi, Sánchez-Villagra, Goin, Takai, Kay, and Shigehara 2006.

Temporal and geographic distribution. *Acyon herrerae* comes from the early Miocene (Colhuehuapian), Chubut, Argentina; *A. tricuspidatus* from the early Miocene (Santacrucian), Argentina; *A. myctoderos* from the middle Miocene (Laventan), Bolivia (Forasiepi et al. 2006; Engelman et al. 2015).

Paleoecology. On the basis of long bones, the body mass of the largest species, *A. myctoderos,* was estimated to lay between 13 kg and 17.5 kg (Engelman et al. 2015). Similar values resulted from predictions based on tooth equations (12 kg and 12.7 kg; Prevosti et al. 2013; Zimicz 2014, respectively). For *A. tricuspidatus* and on the basis of tooth equations, a body mass of 8 kg (Wroe et al. 2004a), 5.3 kg (Prevosti et al. 2013), or 6.24 kg (Zimicz 2014) was obtained, while *A. herrerae* was predicted to lay between 9.7 kg (Wroe et al. 2004a), ~7 kg (Prevosti et al. 2013), and ~8 kg (Zimicz 2014). The RGA tooth equation suggested hypercarnivorous diet (Prevosti et al. 2013; Zimicz 2014).

Comments. Species of the genus *Acyon* have wolf-shaped skulls, similar to *Cladosictis*, to whom it may be close phylogenetically (Forasiepi et al. 2006; Engelman and Croft 2014; but see Suarez et al. 2015). Out of the three species, *Acyon* (=*Anatherium*) *herrerae* may represent a junior synonym of *A. tricuspidatus* (Forasiepi et al. 2006).

Borhyaenidium Pascual and Bocchino 1963
(Fig. 3.3b; Tables 3.1 and 3.2)

Included species. *Borhyaenidium musteloides* Pascual and Bocchino 1963 (type species), *B. altiplanicus* Villarroel and Marshall 1983, and *B. riggsi* Marshall 1981.

Temporal and geographic distribution. *Borhyaenidium musteloides* and *B. altiplanicus* come from the late Miocene (Huayquerian), Argentina and Bolivia; *Borhyaenidium riggsi* from the latest early Pliocene (Chapadmalalan), Argentina.

Paleoecology. The genus *Borhyaenidium* includes small hathliacynids (*B. altiplanicus*: 1.16 kg; *B. musteloides:* 1.56 kg; *B. riggsi*: 1.98 kg estimated with tooth equations) with hypercarnivorous diet (Prevosti et al. 2013; Zimicz 2014).

Comments. The holotype of *Borhyaenidium riggsi* comes from unit 32 from the stratigraphic profile from Stahlecker at Puerta del Corral Quemado (Marshall and Patterson 1981: 70), above a tuff—level 29—with radiometric dating of 3.54 Ma (see also Esteban et al. 2014). This agrees with a Chapadmalalan Age based on the same-age fauna from the Atlantic coast (Table 1.1; see also Prevosti et al. 2013; contra Reguero and Candela 2011, who suggested Montehermosan Age). *Borhyaenidium riggsi* and *Thylacosmilus atrox* are the most recent sparassodonts.

Little material has been recovered for *Borhyaenidium*. Currently, the three species are known only by their holotypes. Marshall (1981) and Villarroel and Marshall (1983) suggested that *Borhyaenidium* was closely related to the Santacrucian genus *Perathereuthes*. This hypothesis remains to be tested.

Chasicostylus Reig 1957
(Tables 3.1 and 3.2)

Included species. *Chasicostylus castroi* Reig 1957.

Temporal and geographic distribution. Late Miocene (Chasicoan), Argentina.

Paleoecology. *Chasicostylus castroi* was in the range of *Cladosictis* species with 6.74 kg or 9.8 kg body mass estimations based on tooth equations (Prevosti et al. 2013; Wroe et al. 2004a, respectively) and characterized by hypercarnivorous diet (Prevosti et al. 2013; Zimicz 2014).

Comments. Marshall (1981) suggested that *Chasicostylus castroi* was closely related to *Cladosictis* species. However, no cladistic analysis has yet tested the phylogenetic position of this taxon.

Cladosictis Ameghino 1887
(Figs. 3.4a, b, 3.6; Tables 3.1 and 3.2)

Included species. *Cladosictis patagonica* Ameghino 1887 (type species) and *C. centralis* Ameghino 1902b.

Temporal and geographic distribution. *Cladosictis centralis* comes from the early Miocene (Colhuehuapian), Argentina; *C. patagonica* from the early to middle Miocene (Santacrucian and Friasian), Argentina and Chile.

Paleoecology. *Cladosictis* includes species of size and shape similar to the South American marten (*Eira barbara*). The body mass estimations for *C. patagonica*, based on the centroid size of the ulna and tibia, suggested 6.6 kg (Ercoli and Prevosti 2011). Other predictions based on postcranial variables suggested between 4 kg and 8 kg (Argot 2003a, 2004a) and 4 kg (Wroe et al. 2004a), while based on tooth variables: 3.7 kg (Vizcaíno et al. 2010) and 4.68 kg (Prevosti et al. 2013; Zimicz 2014). *C. centralis* is in the range of *C. patagonica* (tooth variables predicted 4.4 kg or 3.4 kg; Wroe et al. 2004a; Prevosti et al. 2013, respectively).

Based on postcranial availability, the locomotion has been studied only in *C. patagonica*. Originally, Sinclair (1906) suggested arboreal habits; however, recent studies considered *C. patagonica* to have been scansorial (Marshall 1978; Argot 2003a, 2004a; Ercoli et al. 2012). The limbs were short and plantigrade or semiplantigrade (Sinclair 1906), with manipulative capacities (Argot 2003a) and some digging capability (Ercoli et al. 2012). *Cladosictis patagonica* was possibly an ambusher and active predator (Argot 2003a, 2004a). A hypercarnivorous diet was inferred for *Cladoscitis* species on the basis of the RGA tooth equations (Prevosti et al. 2013; Zimicz 2014).

Comments. *Cladosictis patagonica* is the most abundant sparassodont recovered from the Santa Cruz Formation, and together with *Borhyaena tuberata* and *Prothylacynus patagonicus* is one of the best represented Santacrucian sparassodonts. There is notable variation among the specimens, which is interpreted as intraspecific variability. Some specimens are larger and more robust, with taller cranial crests, deeper dentaries, and more crowded dentition than others.

The phylogenetic analyses are not conclusive on the affinities of *Cladosictis*. Some cladistic hypotheses recovered *Cladosictis* and *Acyon* as sister taxa (Forasiepi et al. 2006; Engelman and Croft 2014), or alternatively *Sallacyon hoffstetteri* (Engelman and Croft 2014), *Notogale miti*s (de Muizon 1999; Babot et al. 2002), or these taxa plus *Sipalocyon* (Suarez et al. 2015) as sister taxa.

Contrerascynus Mones 2014
(Tables 3.1 and 3.2)

Included species. *Contrerascynus borhyaenoides* (Contreras 1990).

Temporal and geographic distribution. Late Miocene (Chasicoan), Argentina.

Paleoecology. Based on the length of m3 (Gordon 2003, using dasyurids), estimations suggested a body mass of 12.6 kg. The calculation of the RGA suggested hypercarnivorous diet.

Comments. *Contrerascynus borhyaenoides* is known only by a fragmentary dentary with a dental morphology that resembles *Acyon* (=*Anatherium* in Contreras 1990); however, it is larger and comparable to *Lycopsis viverensis* from the Chasicoan of Pampean area.

The finding of the material in the Quebrada de Ullúm, San Juan (Argentina), provides a new area for prospecting in the central-western part of Argentina.

*Noticti*s Ameghino 1889
(Tables 3.1 and 3.2)

Included species. *Notictis ortizi* Ameghino 1889.

Temporal and geographic distribution. Late Miocene (Huayquerian), Argentina.

Paleoecology. The body mass of *N. ortizi* was estimated at 0.9 kg, and the diet was considered hypercarnivorous (Prevosti et al. 2013; Zimicz 2014).

Comments. *Notictis ortizi* is represented only by the holotype, a fragment of dentary with partial dentition. This taxon is the smallest Huayquerian sparassodont, similar in size to the Santacrucian *Pseudonotictis pusillus*. Phylogenetic affinities between these taxa were suggested by Marshall (1981). This hypothesis awaits testing.

Notocynus Mercerat 1891
(Tables 3.1 and 3.2)

Included species. *Notocynus hermosicus* Mercerat 1891.

Temporal and geographic distribution. Early Pliocene (Montehermosan), Argentina.

Paleoecology. *Notocynus hermosicus* was a small hathliacynid with a body mass estimation of 1.77 kg or 3.2 kg (Prevosti et al. 2013; Wroe et al. 2004a, respectively). The diet was considered hypercarnivorous (Prevosti et al. 2013; Zimicz 2014).

Comments. *Notocynus hermosicus* is known only by its holotype, a single fragmentary dentary, collected from Monte Hermoso type locality (Cabrera 1927; Marshall 1981). *Notocynus hermosicus* and *Thylacosmilus atrox* are currently the only two Montehermosan sparassodonts known.

Notogale Loomis 1914
(Tables 3.1 and 3.2)

Included species. *Notogale mitis* (Ameghino 1897).

Temporal and geographic distribution. Late Oligocene (Deseadan), Argentina and Bolivia.

Paleoecology. *Notogale mitis* was similar in size to *Cladosictis* according to linear measurements of the dentition (e.g., Marshall 1981). However, tooth equations considerably understimated its probable body size (2.72 kg Prevosti et al. 2013; 3.4 kg in Zimicz 2012 vs. 6.6 kg for *Cladosictis patagonica* in Ercoli and Prevosti 2011). A hypercarnivorous diet was suggested on the basis of RGA tooth equations (Zimicz 2012; Prevosti et al. 2013).

Comments. *Notogale mitis* has a broad distribution in South America, from Patagonia in the south to the Bolivian locality of Salla in the north, where it is the most abundant sparassodont (sensu Marshall 1981). Marshall (1981) suggested that *Notogale* was closely related to *Cladosictis*. This hypothesis was supported by de Muizon (1999) and Babot et al. (2002) with a cladistic approach placing them as sister taxa. Other studies have recovered *Notogale* and *Sipalocyon* or *Sallacyon* as sister taxa (Forasiepi 2009; Engelman and Croft 2014; Suarez et al. 2015).

Perathereutes Ameghino 1891
(Fig. 3.4e; Tables 3.1 and 3.2)

Included species. *Perathereutes pungens* Ameghino 1891.

Temporal and geographic distribution. Early Miocene (Santacrucian), Argentina.

Paleoecology. *Perathereutes pungens* was intermediate in size between *Sipalocyon gracilis* and *Pseudonotictis pusillus*. On the basis of tooth equations, Wroe et al. (2004a) provided values of 2.5 kg, whereas Prevosti et al. (2013) and Zimicz (2014) suggested ~1 kg. The diet was suggested as hypercarnivorous (Prevosti et al. 2013).

Comments. This taxon is known from scarce material from Patagonia. Marshall (1981) suggested phylogenetic affinities between *P. pungens* and the late Miocene *Borhyaenidium musteloides*. This hypothesis awaits testing.

Pseudonotictis Marshall 1981
(Fig. 3.4f; Tables 3.1 and 3.2)

Included species. *Pseudonotictis pusillus* (Ameghino 1891) (type species) and *P. chubutensis* Martin and Tejedor 2007.

Temporal and geographic distribution. *Pseudonotictis pusillus* comes from the early Miocene (Santacrucian), Argentina; *P. chubutensis* from the middle Miocene (Colloncuran), Argentina.

Paleoecology. *Pseudonotictis pusillus* and *P. chubutensis* are the smallest sparassodonts from the Santacrucian and Colloncuran outcrops, respectively. They would have had a size similar to the extant weasel (*Mustela frenata*). The body mass of *P. pusillus* was estimated at 1.17 kg based on the centroid size of the humerus (Ercoli and Prevosti 2011), roughly similar to the values obtained with tooth variables (0.93 kg in Prevosti et al. 2013). The body mass of *P. chubutensis* provided smaller values (0.89 kg in Zimicz 2014).

Study of locomotion in *P. pusillus* suggested scansorial habits with evident arboreal capabilities (Argot 2003a; Ercoli et al. 2012). A hypercarnivorous diet was suggested for *P. pusillus* on the basis of RGA tooth equations (Prevosti et al. 2013).

Comments. The genus was erected by Marshall (1981) to include *P. pusillus*, which closely resembles the late Miocene (Huayquerian) *Notictis ortizi*.

Sallacyon Villarroel and Marshall 1982
(Tables 3.1 and 3.2)

Included species. *Sallacyon hoffstetteri* Villarroel and Marshall 1982.

Temporal and geographic distribution. Late Oligocene (Deseadan), Bolivia.

Paleoecology. *Sallacyon hoffstetteri* was slightly smaller than *Sipalocyon gracilis* according to Villarroel and Marshall (1982). Body mass estimations provided values similar to or sligthly larger than *Sipalocyon gracilis* (1.13 kg in Prevosti et al. 2013; 3 kg in Zimicz 2012). The diet was considered hypercarnivorous (Prevosti et al. 2013; Zimicz 2012).

Comments. *Sallacyon hoffstetteri* is a Neotropical sparassodont hitherto known only from the Deseadan outcrops of Bolivia (Villarroel and Marshall 1982; Petter and Hoffstetter 1983; de Muizon 1999). Its dental morphology and dentary resemble the early Miocene (Santacrucian) *Perathereutes pungens* and *Sipalocyon gracilis*, to whom it may be phylogenetically close (Villarroel and Marshall 1982; Petter and Hoffstetter 1983). Alternatively, cladistic studies positioned this taxon together with *Notogale* (Forasiepi 2009; Suarez et al. 2015), or in a basal branch among hathliacynids (de Muizon 1999; Babot 2005; Forasiepi et al. 2006).

Sipalocyon Ameghino 1887
(Fig. 3.4c, d; Tables 3.1 and 3.2)

Included species. *Sipalocyon gracilis* Ameghino 1887 (type species), *S. externa* Ameghino 1902b, and *S. obusta* (Ameghino 1891) (nomen dubium).

Temporal and geographic distribution. *Sipalocyon externa* comes from the early Miocene (Colhuehuapian), Argentina; *S. obusta* from the early Miocene (Santacrucian), Argentina; *S. gracilis* from the early to middle Miocene (Santacrucian and Friasian), Argentina and Chile.

Paleoecology. On the basis of the centroid size of the ulna, the body mass of *S. gracilis* was estimated to be 2.11 kg (Ercoli and Prevosti 2011). This value is in the range of the predictions of Argot (2003a) (between 1 kg and 5 kg according to different specimens) based on postcranial equations, and the estimations of Vizcaíno et al. (2010; 1.93 kg), Prevosti et al. (2013; 1.96 kg), and Zimicz (2014; 3.15 kg) based on tooth equations. The other two species are in the same range of size (*S. externa*: 0.93 kg or 2.48 kg; *S. obusta*: 1.83 kg or 2.81 kg based on tooth equations; Prevosti et al. 2013; Zimicz 2014, respectively).

Originally, Sinclair (1906) suggested arboreal habits for *S. gracilis*; however, recent studies suggested scansorial locomotion (Marshall 1978; Argot 2003a, 2004a; Ercoli et al. 2012). The limbs would have had skillful manipulative capabilities (Argot 2003a, 2004a). A hypercarnivorous diet was suggested for *S. gracilis* and *S. obusta* on the basis of RGA tooth equations (Prevosti et al. 2013; Zimicz 2014).

Comments. *Sipalocyon gracilis* is a common taxon in the Santacrucian levels of Patagonia. On the contrary, the second Santacrucian species, *S. obusta,* is extremely scarce and is "virtually identical to …*S. gracilis*" (Marshall 1981: 60), but with shallower and more slender dentary and m4 with more reduced talonid. These differences could represent intraspecific variability in *S. gracilis*. Consequently, *S. obusta* is only tentatively recognized and considered nomen dubium.

Marshall (1981) suggested that *Sipalocyon* was phylogenetically close to *Perathereutes*. Alternatively, cladistic analyses recovered *Sipalocyon* as the sister taxon of *Notogale* plus *Cladosictis* (de Muizon 1999; Babot et al. 2002); sister taxon of *Notogale* (Forasiepi et al. 2006; Engelman and Croft 2014), or *Notogale* plus *Sallacyon* (Forasiepi 2009; Engelman and Croft 2014; Forasiepi et al 2015; Suarez et al. 2015).

?Hathliacynidae
Procladosictis Ameghino 1902a
(Tables 3.1 and 3.2)

Included species. *Procladosictis anomala* Ameghino 1902a.

Temporal and geographic distribution. Latest middle–earliest late Eocene (Mustersan), Argentina.

Paleoecology. The body mass of *P. anomala* was estimated at 8.9 kg (Zimicz 2012) with a possible hypercarnivorous diet (Prevosti et al. 2013).

Comments. *Procladosictis anomala* is known only by its type specimen, a fragment of maxilla with dentition. The molars have broad stylar shelves and deep ectoflexus, which are unusual features among sparassodonts. Marshall (1981) considered *P. anomala* a hathliacynid; however, new material is needed to illuminate its relationships (Forasiepi 2009).

Borhyaenoidea Simpson 1930

Borhyaenoidea includes medium- to large-sized sparassodonts, recorded from the middle Eocene (Casamayoran) to the latest early Pliocene (Chapadmalalan) (Figs. 3.7, 3.8, 3.9, 3.10, 3.11, 3.12 and 3.13). It includes the common ancestor of *Prothylacynus* and *Borhyaena* and all the taxa that are more closely related to them than to hathliacynids (Forasiepi 2009). There is significant morphological disparity in the cranium, dentition, and postcranial skeleton. Some taxa were slender and light, such as the fox-like *Lycopsis viverensis,* others were massive and robust, exhibiting deep dentaries sometimes fused at symphysis, such as the bear-like *Arctodictis munizi*, while others had hypertrophied sabertooth canines, such as *Thylacosmilus*. The diet as indicated by the RGA dental index was hypercarnivorous for most of the group; however, some borhyaenoids with larger protocones and broader talonids may have had a more flexible diet than proborhyaenids, thylacosmilids, and borhyaenids, whose molars lack crushing surfaces.

Dukecynus Goin 1997
(Tables 3.1 and 3.2)

Included species. *Dukecynus magnus* Goin 1997.

Temporal and geographic distribution. Middle Miocene (Laventan), Colombia.

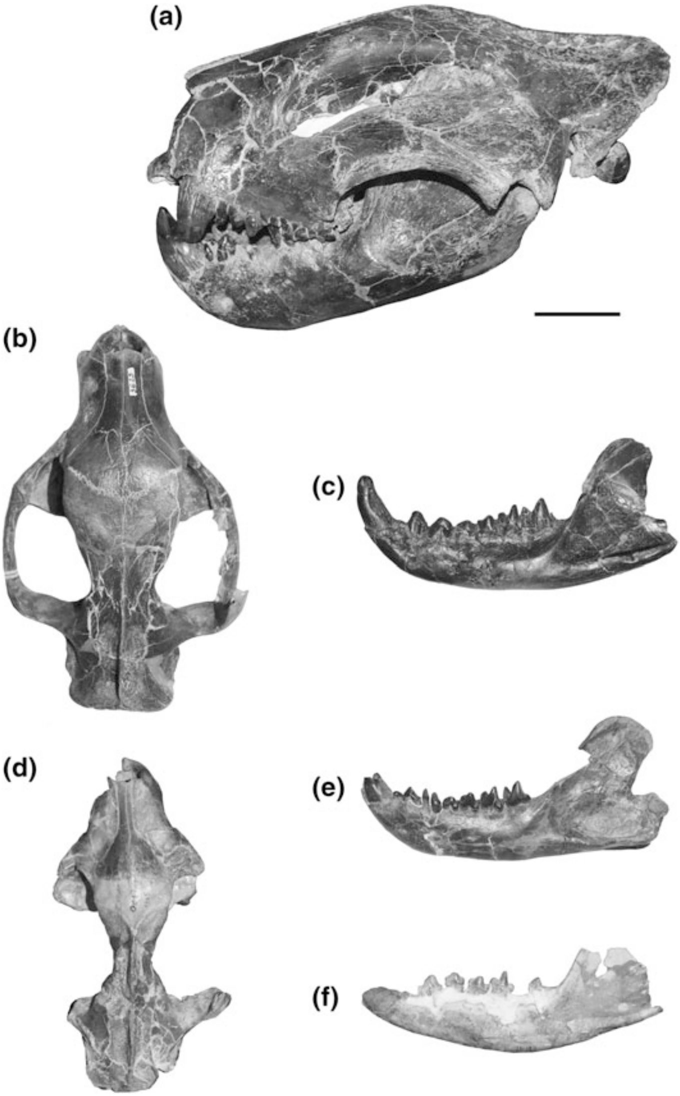


Fig. 3.7 Borhyaenoidea from the early Miocene (Santacrucian Age), Santa Cruz Formation, Patagonia, Argentina. *Arctodictis munizi* (CORD-PZ 1210) cranium and left dentary in lateral view (**a**); *Borhyaena tuberata* (MPM-PV 3625) cranium in dorsal view (**b**) and (MACN-A 12700) inverted right dentary in lateral view (**c**); *Prothylacynus patagonicus* (MACN-A 5931–5937, single specimen) cranium of juvenile specimen (**d**), (MACN-A 706–720, Holotype) left dentary in lateral view (**e**); *Lycopsis torresi* (MLP 11-113, Holotype), left dentary in lateral view (**f**). Scale bar = 5 cm

Paleoecology. The body mass of *D. magnus* was estimated at 68.4 kg or 52.6 kg (Wroe et al. 2004a; see also comment below) or 24.6 kg (Prevosti et al. 2013) on the basis of dental variables. The hypercarnivorous diet was inferred the same as for *Lycopsis torresi* (Prevosti et al. 2013).

Comments. *Dukecynus magnus* was originally considered a member of the paraphyletic "prothylacynines" and related to the Chasicoan *Pseudolycopsis* (Goin 1997). Cladistic reconstructions position most of the "prothylacynines" (i.e., *Prothylacynus*, *Lycopsis*) among basal clades of Borhyaenoidea, a likely position also for *D. magnus*.

In his monograph about borhyaenoids, Marshall (1978) mentioned a putative *Arctodictis* specimen (UCMP 39250). This material was later assigned to *Dukecynus magnus* (Goin 1997; Forasiepi et al. 2004). For this specimen, Wroe et al. (2004a) obtained a body mass of 51.6 kg.

Lycopsis Cabrera 1927
(Figs. 3.7f, 3.8; Tables 3.1 and 3.2)

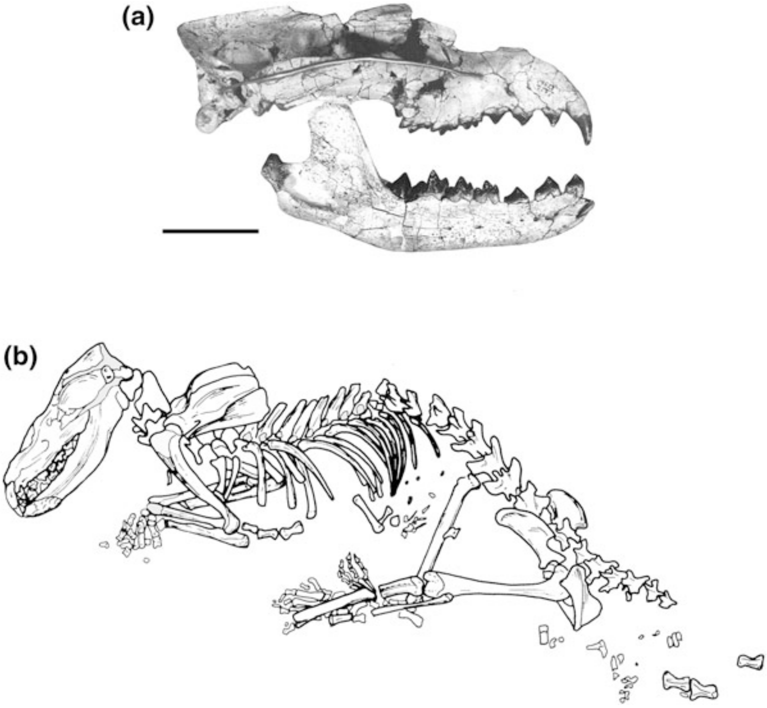


Fig. 3.8 *Lycopsis longirostrus* (UCMP 38061, Holotype), from the middle Miocene (Laventan Age), La Venta (Colombia), cranium and right dentary in lateral view (**a**) and line drawing of the skeleton (taken from Marshall 1977b) (**b**). Scale bar = 5 cm

Included species. *Lycopsis torresi* Cabrera 1927 (type species), *L. longirostrus* Marshall 1977b, *L. viverensis* Forasiepi et al. 2003, *L. padillai* Suarez, Forasiepi, Goin, Jaramillo 2015.

Temporal and geographic distribution. *Lycopsis torresi* was found in the early Miocene (Santacrucian), Argentina; *L. padillai* and *L. longirostrus* from middle Miocene (Colloncuran and Laventan, respectively), Colombia; *L. viverensis* from late Miocene (Chasicoan), Argentina.

Paleoecology. The four species are clearly differentiated by size. A recent study (Suarez et al. 2015) on the basis of the upper molar occlusal row length predicted a body mass for *Lycopsis torresi* at ~27 kg, and in the range of *L. padillai* with ~22 kg. The smallest species *L. viverensis* was estimated at ~18 kg while the largest *L. longirostrus* at ~44 kg. These results are roughly consistent with Prevosti et al. (2013) based on tooth measurements (*L. torresi*: 31.5 kg; *L. viverensis*, 11 kg; *L. longirostrus*: 42.5 kg), but are overestimated compared with the values obtained using postcranial variables. On the basis of the centroid size of the ulna and humerus, Ercoli and Prevosti (2011) provided values of 29.77 kg for *L. longirostrus*, while on the basis of postcranial variables Argot (2004b) suggested 17.1 kg and Wroe et al. (2004a) calculated 12.8 kg for the same taxon. For *L. torresi* and on the basis of tooth variables, Wroe et al. (2004a) obtained 19.4 kg.

The only species of *Lycopsis* with a known postcranium is *L. longirostrus*. For this taxon, Argot (2004a, b) and Ercoli et al. (2012) concurred in viewing this taxon as possessing terrestrial progression and reduced running capabilities. The limbs were plantigrade with grasping abilities in the forelimb.

The diet was hypercarnivorous, as suggested by the RGA dental equations (Prevosti et al. 2013). In the abdominal area of *L. longirostrus,* "between the ribs and right tibia were broken rodent bones and an upper molar of *Scleromys colombianus*" (Caviomorpha), (Marshall 1977b: 641)—evidently, the predator's last meal.

Comments. The holotype of *L. longirostrus* consists of an almost complete skeleton, still articulated (Marshall 1977b; Fig. 3.8). The last molar is not completely erupted (Forasiepi and Sánchez-Villagra 2014), which suggests the specimen was a subadult.

The monophyly of the genus *Lycopsis* has been recently supported (Suarez et al. 2015), with the Laventan *L. longirostrus* recorded as the most basal member of the genus. The results of Suarez et al. (2015) implied a diversification within (or before) the early Miocene and that *Lycopsis* had at least two migration events between the Neotropical and the temperate regions, with divergence into new species in the temperate region. The persistence of a basal taxon (*L. longirostrus*) in Neotropical areas in younger (middle Miocene) ages was interpreted under the "museum" evolutionary model (Suarez et al. 2015).

Lycopsis is the genus of Sparassodonta with the broadest distribution, ranging from La Guajira (Colombia) to Patagonia (Argentina) (Suarez et al. 2015).

Pharsophorus Ameghino 1897
(Tables 3.1 and 3.2)

Included species. *Pharsophorus lacerans* Ameghino 1897 (type species) and *P. tenax* Ameghino 1897.

Temporal and geographic distribution. *Pharsophorus lacerans* and *P. tenax* come from the late Oligocene (Deseadan), Argentina (both species) and Bolivia (the former only).

Paleoecology. The two *Pharsophorus* species differ clearly by size. Estimations for *P. lacerans* are ~27 kg, with hypercarnivorous diet (Zimicz 2012; Prevosti et al. 2013). Estimations for *P. tenax* have suggested 18.7 kg (Zimicz 2012) and mesocarnivorous diet (Zimicz 2012).

Comments. Of the two species, *P. lacerans* is the largest and the best represented. *Pharsophorus tenax* was named by Ameghino (1897) on the basis of an isolated m1. The holotype was missing, and at the time of Marshall's revision of the group (1978), a neotype was designated. Simultaneously, Patterson and Marshall (1978) synonymized *P. tenax* with *P. lacerans*. In 1997, the material used by Ameghino to define the species was found by A. Ramos in MACN collections and given the number MACN-A 11113. A new revision of this species is required to restore the original holotype and to evaluate the validity of the taxon. Provisionally, we consider here *P. tenax* as a valid species, as Marshall (1978) had concluded.

Originally, Ameghino (1897) and later Marshall (1978) suggested affinities between *Pharsophorus* and *Borhyaena*, while Patterson and Marshall (1978) suggested possible phylogenetic relationships with thylacosmilids. In agreement with both views, cladistic analyses recovered *P. lacerans* as the sister taxon of thylacosmilids, proborhyaenids, and borhyaenids (Forasiepi 2009; Engelman and Croft 2014; Forasiepi et al. 2015; Suarez et al. 2015).

Plesiofelis Roth 1903
(Tables 3.1 and 3.2)

Included species. *Plesiofelis schlosseri* Roth 1903.

Temporal and geographic distribution. Latest middle–earliest late Eocene (Mustersan), Argentina.

Paleoecology. *Plesiofelis schlosseri* was slightly larger than *Pharsophorus lacerans*. Body mass estimations suggested ~45 kg and ~ 32 kg (Zimicz 2012 and Prevosti et al. 2013, respectively) with hypercarnivorous diet.

Comments. Cabrera (1927) and Simpson (1948) considered *Plesiofelis* to be synonym of *Pharsophorus*. Later, Marshall (1978) recognized *Plesiofelis* as a valid taxon. As suggested by their close phylogenetic affinity, the two taxa have similar tooth morphology (Marshall 1978; Forasiepi et al. 2015; an alternative interpretation was presented by Goin et al. 2007).

Prothylacynus Ameghino 1891
(Fig. 3.7d, e; Tables 3.1 and 3.2)

Included species. *Prothylacynus patagonicus* Ameghino 1891.

Temporal and geographic distribution. Early to middle Miocene (Santacrucian, Friasian, and Colloncuran), Argentina and Chile.

Paleoecology. For *P. patagonicus*, estimations on the basis of the centroid size of the ulna and tibia suggested a body mass of 31.8 kg (Ercoli and Prevosti 2011), similar to ~30 kg of Argot (2003b) on the basis of postcranial variables, and comparable to a wolverine (*Gulo gulo*). Other predictions are somewhat different (e.g., 26.8 kg using variables from the femur in Wroe et al. 2004a; 13.83 kg and 20.6 kg using dental measurements in Vizcaíno et al. 2010; Prevosti et al. 2013, respectively).

Originally, Sinclair (1906) and Marshall (1978) indicated terrestrial locomotion for *P. patagonicus*; however, more recent analysis has suggested scansorial adaptations (Argot 2003b, 2004a; Ercoli et al. 2012). The limb architecture suggested plantigrade (Sinclair 1906) or semiplantigrade posture (Argot 2003b, 2004a), with skillful manipulative behavior. *Prothylacynus patagonicus* was possibly a more active predator than contemporaneous *Borhyaena tuberata*, with a flexible vertebral column that allowed powerful jumps from a crouched position (Argot 2003b, 2004a). A hypercarnivorous diet was estimated based on the RGA dental index (Prevosti et al. 2013).

Comments. *Prothylacynus patagonicus* is a species frequently found in Santacrucian outcrops, which have yielded both cranial and postcranial material (Sinclair 1906).

Traditionally, *Prothylacynus* was grouped with *Lycopsis*, *Pseudolycopsis*, *Pseudothylacynus*, *Stylocynus*, and *Dukecynus* in the subfamily Prothylacyninae (Marshall 1979; Marshall et al. 1990; Goin 1997). Later analyses considered Prothylacyninae paraphyletic with *Prothylacynus* placed among basal borhyaenoids (Babot 2005; Forasiepi et al. 2006, 2015; Forasiepi 2009; Engelman and Croft 2014; Suarez et al. 2015).

Pseudolycopsis Marshall 1976b
(Tables 3.1 and 3.2)

Included species. *Pseudolycopsis cabrerai* Marshall 1976b.

Temporal and geographic distribution. Late Miocene (Chasicoan), Argentina.

Paleoecology. Using dental variables, the body mass of *P. cabrerai* was suggested to be 24 kg or 14.4 kg (Wroe et al. 2004a; Prevosti et al. 2013, respectively). Diet similar to *Lycopsis* species (Prevosti et al. 2013).

Comments. *Pseudolycopsis cabrerai* is known by a fragment of palate (Marshall 1976b).

Marshall suggested that *Pseudolycopsis* was likely related to the genus *Lycopsis* (Marshall 1976b, 1979).

Pseudothylacynus Ameghino 1902b
(Tables 3.1 and 3.2)

Included species. *Pseudothylacynus rectus* Ameghino 1902b.

Temporal and geographic distribution. Early Miocene (Colhuehuapian), Argentina.

Paleoecology. Body mass estimates using dental variables are 14 kg and 19.7 kg (Wroe et al. 2004a; Prevosti et al. 2013, respectively). Diet was hypercarnivorous.

Comments. Little material is identified from this species. The anatomy of the dentition closely resembles that to *Prothylacynus*, suggesting close phylogenetic affinities (Marshall 1979).

Proborhyaenidae Ameghino 1897

Traditionally, Proborhyaenidae was considered the group that includes the largest hypercarnivorous mammalian predators from the middle Eocene (Casamayoran) to the late Oligocene (Deseadan) of South America (Marshall 1978; Bond and Pascual 1983; Petter and Hoffstetter 1983; Babot et al. 2002; Fig. 3.9). However, recent cladistic analyses are not congruent regarding their monophyly. Some studies have concluded that they are monophyletic (e.g., Babot et al. 2002; Engelman and Croft 2014), although the most exhaustive analysis that included several species of this group recorded them as paraphyletic (Babot 2005; Argot and Babot 2011).

Arminiheringia Ameghino 1902a
(Tables 3.1 and 3.2)

Included species. *Arminiheringia auceta* Ameghino 1902a (type species), *A. cultrata* Ameghino 1902a, and *A. contigua* Ameghino 1904.

Temporal and geographic distribution. Middle Eocene (Casamayoran), Argentina.

Paleoecology. *Arminiheringia* included large-size sparassodonts: *A. auceta*, 31.3 kg and 31.7 kg (Prevosti et al. 2013; Zimicz 2012, respectively); *A. cultrata,* 24 kg and 25.7 kg (Prevosti et al. 2013; Zimicz 2012, respectively), and *A. contigua*, 18.5 kg (Zimicz 2012). The diet was hypercanivorous, with capacity to break bones (Zimicz 2012).

Comments. Three valid species of *Arminiheringia* are considered following Babot (2005). However, the validity of some of these taxa has been questioned, because of a lack of diagnostic features. Simpson (1948) considered *A. cultrata* to be a synonym of *A. contigua,* but Marshall (1978) concluded *A. cultrata* was a synonym of *A. auceta.*

Classically, *Arminiheringia* was considered phylogenetically close to *Thylacosmilus* (Scott 1937), but a later diagnosis did not confirm that their morphological resemblances indicated close ancestry (Simpson 1948; Marshall 1976c, 1978). Recent cladistic analysis recovered *A. auceta* and *Callistoe vincei* as sister taxa (Babot 2005).

Callistoe Babot et al. 2002
(Tables 3.1 and 3.2)

Included species. *Callistoe vincei* Babot et al. 2002.

Temporal and geographic distribution. Middle Eocene (Vacan subage of the Casamayoran), Argentina.

Paleoecology. The body mass of *C. vincei* was estimated using postcranial variables, producing a value of ~23 kg (Argot and Babot 2011), in the range of *Thylacinus cynocephalus*. Estimations using tooth variables instead indicated body masses of 32.6 kg and 27.75 kg (Argot and Babot 2011; Prevosti et al. 2013, respectively).

Terrestrial locomotion was suggested for *C. vincei* with limbs that favored flexion/extension parasagittal movements, rather than pronation/supination (Argot and Babot 2011). The long claws in the forelimb suggested the capacity to dig for small prey in burrows, while the mobile thumb suggested that it could grab and manipulate objects (Argot and Babot 2011).

Comments. *Callistoe vincei* is known by exceptional material, represented by a cranium and complete postcranial elements (Babot et al. 2002; Babot 2005; Argot and Babot 2011). The holotype of *C. vincei* is the best preserved Paleogene sparassodont recovered to date (2016).

Callistoe vincei has been found in Pampa Grande, Salta, northern Argentina (Babot et al. 2002). Paleoenvironmental reconstructions suggested it lived in a temperate humid forest biome (Powell et al. 2011). *Callistoe vincei* is large and slender compared to other proborhyaenids. Cladistic reconstructions recovered *C. vincei* the sister taxon of *Arminiheringia* (Babot 2005) or alternatively, as sister taxon of *Paraborhyaena boliviana* (Babot et al. 2002; Engelman and Croft 2014).

Paraborhyaena Hoffstetter and Petter 1983
(Tables 3.1 and 3.2)

Included species. *Paraborhyaena boliviana* Hoffstetter and Petter 1983.

Temporal and geographic distribution. Late Oligocene (Deseadan), Bolivia.

Paleoecology. The body mass should be in the range of *A, auceta*, considering the similarity of its measurements. Diet was hypercarnivorous (Prevosti et al. 2013).

Comments. *Paraborhyaena boliviana* is a Neotropical sparassodont known by a single specimen (Hoffstetter and Petter 1983). Originally, Petter and Hoffstetter (1983) considered close affinities between *P. boliviana* and *Arminiheringia* and *Proborhyaena* species. Later, cladistic analysis alternatively grouped *P. boliviana* and *C. vincei* (Babot et al. 2002; Engelman and Croft 2014), *P. boliviana* and *Proborhyaena gigantea* plus thylacosmilids (Babot 2005), or *P. boliviana* and thylacosmilids (Suarez et al. 2015).

Proborhyaena Ameghino 1897
(Fig. 3.9; Tables 3.1 and 3.2)

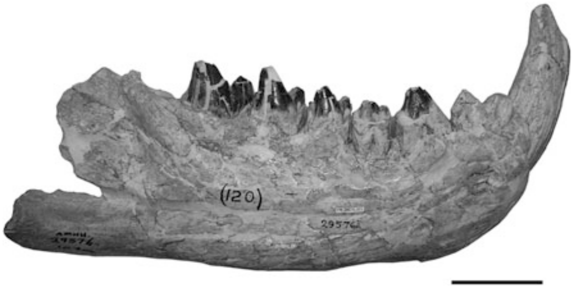


Fig. 3.9 *Proborhyaena gigantea* (AMNH 29576), from the late Oligocene (Deseadan), Rinconada de López, Patagonia (Argentina), right dentary in lateral view. Scale bar = 5 cm

Included species. *Proborhyaena gigantea* Ameghino 1897.

Temporal and geographic distribution. Late Oligocene (Deseadan), Argentina and Uruguay.

Paleoecology. *Proborhyaena gigantea* is the largest known sparassodont, with a size similar to the South American spectacled bear (*Tremarctos ornatus*). Body mass estimations are disparate. Zimicz (2012) and Prevosti et al. (2013) provided values between 93 kg and 153.6 kg, respectively. Sorkin (2008) based on the lower canine–last molar length suggested 600 kg, a value that is surely overestimated. *Proborhyaena gigantea* was a hypercarnivorous bone-cracker, and likely able to actively predate in the fashion of living hyenas (*Crocuta crocuta*) (Zimicz 2012).

Proborhyaena gigantea may have had a powerful canine bite as suggested by mandibular force profiles (Blanco et al. 2011), with unpredictable direction of forces and capabilities to break bones at the level of the last molar.

Comments. *Proborhyaena gigantea* had a large distribution through the southern cone of South American with findings in Patagonia, Mendoza, and Uruguay (Mones and Ubilla 1978; Patterson and Marshall 1978; Bond and Pascual 1983).

Originally, Marshall (1978) suggested close affinities between *P. gigantea* and *Arminiheringia.* Alternatively, cladistic analysis recovered *P. gigantea* as the sister taxon of thylacosmilids (Babot 2005).

Thylacosmilidae Riggs 1933

Thylacosmilidae includes taxa with the most unusual morphology among South American native predators. The overall cranial morphology resembles sabertooth felids (Chap. 4) in that both acquired large hypertrophied upper canines (Figs. 3.10 and 3.11). This is renowned as a classic example of convergent evolution (e.g., Riggs 1933, 1934; Simpson 1971; Marshall 1976c, 1977a; Turnbull 1978; Turnbull and Segall 1984; Churcher 1985). Other features include short cranium with massive snout, and presence of bony auditory bulla; mandibles with a subvertical symphyseal flange, shallow ramus with the alveolar and ventral edges subparallel and straight; small but deep masseteric fossa, poorly inflected angle, low condyle in relation to the alveolar plane; cheekteeth bowed and simplified molar structures favoring shearing and suggesting a highly specialized hypercarnivorous diet (Marshall 1976c; Goin and Pascual 1987; Goin 1997; Mones and Rinderknecht 2004; Forasiepi and Carlini 2010).

Thylacosmilidae is a monophyletic group and includes three species: *Anachlysictis gracilis, Patagosmilus goini,* and *Thylacosmilus atrox*. Its stratigraphic range dates from the middle Miocene (Colloncuran) to the latest early Pliocene (Chapadmalalan). In addition, a putative thylacosmilid represented by an isolated upper molar has been collected from the early Miocene (Colhuehuapian) of Patagonia (Goin et al. 2007). If the assignation of the Patagonian specimen is correct, the stratigraphic range of the group dates back 5 Ma more than currently accepted (Goin et al. 2007). Another putative thylacosmilid is represented by a middle Miocene (Laventan) specimen (Goin 1997). It has a much more generalized morphology than other thylacosmilids, with the symphyseal area of the dentary, the morphology of the maxilla, and the general structure of the dentition recalling thylacosmilids. This Laventan taxon could either represent a stem or basal thylacosmilid, or alternatively a different sparassodont lineage with incipient and convergent sabertooth architecture (Goin 1997).

Anachlysictis Goin 1997

(Fig. 3.10a; Tables 3.1 and 3.2)

Included species. *Anachlysictis gracilis* Goin 1997.

Temporal and geographic distribution. Middle Miocene (Laventan), Colombia.

Paleoecology. The body mass was estimated with tooth equations in ~18 and 16 kg (Wroe et al. 2004a; Prevosti et al. 2013, respectively).

Comments. *Anachlysictis gracilis* is known only by its holotype, a mandible with dentition and associated postcranium, which exhibit several plesiomorphies compared to *Thylacosmilus atrox* (Goin 1997; Forasiepi and Carlini 2010).

Patagosmilus Forasiepi and Carlini 2010

(Fig. 3.10b, c; Tables 3.1 and 3.2)

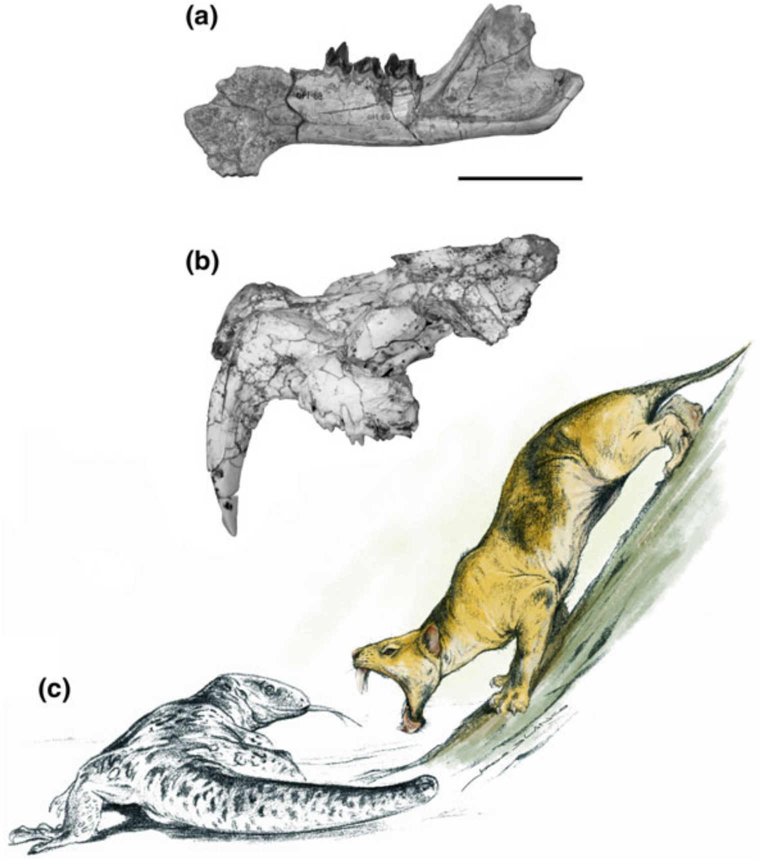


Fig. 3.10 *Anachlysictis gracilis* (IGM 184247, Holotype) from the middle Miocene (Laventan Age), La Venta (Colombia), inverted right dentary in lateral view. *Patagosmilus goini* (MLP 07-VII-1-1), partial cranium in lateral view (**b**); artistic reconstruction by Jorge Blanco (**c**). Scale bar = 5 cm

Included species. *Patagosmilus goini* Forasiepi and Carlini 2010.

Temporal and geographic distribution. Middle Miocene (Colloncuran) Argentina.

Paleoecology. In view of its linear measurements, *P. goini* probably had a body mass similar to that of *Anachlysictis gracilis* (Prevosti et al. 2013). Diet was hypercarnivorous.

Comments. *Patagosmilus goini* is represented by a partial skull and a few postcranial elements. From the middle Miocene (Colloncuran) of Patagonia, this is to date the oldest definite thylacosmilid. Cladistic analyses recovered *P. goini* and *Thylacosmilus atrox* as sister taxa (Engelman and Croft 2014; Forasiepi et al. 2015; Suarez et al. 2015).

Thylacosmilus Riggs 1933
(Fig. 3.11; Tables 3.1 and 3.2)

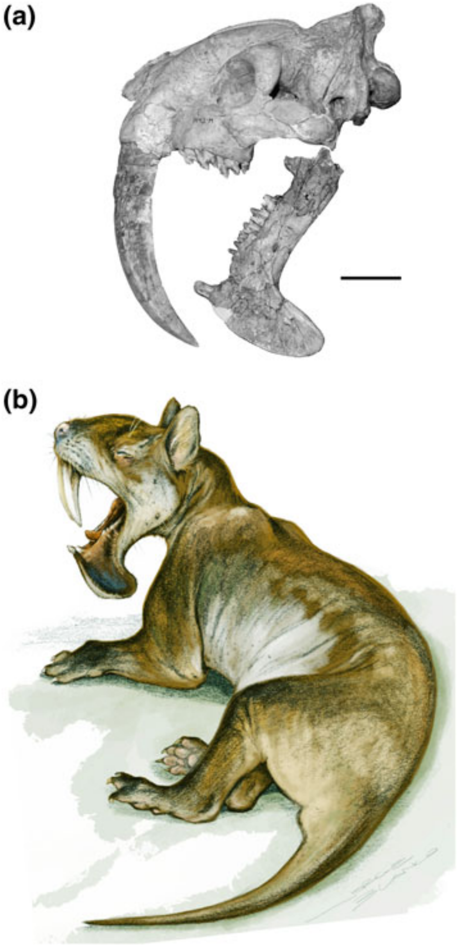


Fig. 3.11 *Thylacosmilus atrox* (MMP 1443), from the late early Pliocene (Chapadmalalan Age), Chapadmalal (Argentina), complete cranium and dentary in lateral view (**a**); artistic reconstruction by Jorge Blanco (**b**). Scale bar = 5 cm

Included species. *Thylacosmilus atrox* Riggs 1933.

Temporal and geographic distribution. Late Miocene to latest early Pliocene (Huayquerian, Montehermosan, and Chapadmalalan), Argentina and Uruguay.

Paleoecology. The efforts to calculate the body mass of *T. atrox* have yielded substantialy different values, which could be either a response to marked intraspecific variability, different methodologies for the estimations, or both. Based on the centroid size of the tibia and ulna, Ercoli and Prevosti (2011) obtained 117.4 kg, which is similar to the 116 kg calculated by Wroe et al (1999) on the basis of femoral variables (but not 58 kg on the basis of the circumference of the femur; Wroe et al. 2004a). Using other postcranial equations Argot (2004c) obtained somewhat different values (47.5 kg–49.5 kg, 82 kg–86.7 kg, and 108 kg for the holotype). Larger values were obtained using condylobasal skull length (150 kg; Sorkin 2008), while highly unlikely lower estimates were predicted from endocranial volume (26 kg; Wroe et al. 2003) and tooth variables (30.2 kg; Prevosti et al. 2013).

The study of the postcranial skeleton indicated terrestrial progression with incipient cursoriality (Riggs 1934; Ercoli et al. 2012), possibly an ambush predator, attacking by surprise rather than the chase (Goin and Pascual 1987; Argot 2004a, c). Riggs (1934) and Argot (2004c) concluded that the forelimbs were digitigrade or semidigitigrade, while the hindlimbs were plantigrade. The forelimbs would have had manipulative capabilities to capture and secure prey (Argot 2004a, b). The neck was longer than in other sparassodonts, more flexible and strongly muscled (Argot 2004a, c).

Thylacosmilus atrox was hypercarnivorous but with a bite force extremely low compared to other sparassodonts (Wroe et al. 2004b; Blanco et al. 2011). Geometric morphometric studies suggested that the cranium shared a morphospace similar to *Barbourofelis* (Prevosti et al. 2010), another eutherian sabertooth.

Several functional studies have discussed the predation behaviour of *T. atrox* compared to eutherian saber-toothed cats. Most studies have adopted the stabbing model, in which the primarily force applied to the canines was neck driven (e.g., Marshall 1976c; Turnbull 1978; Churcher 1985; Argot 2004a, c; Wroe et al. 2004b, 2013), rather than the primary force coming from jaw adductors, as in saber-toothed cats (i.e., the canine-sharing bite model following Wroe et al. 2004b, 2013) (e.g., Goin and Pascual 1987; Therrien 2005). A recent 3D finite element analysis has demonstrated that the jaw adductors played an insignificant role in the killing bite (Wroe et al. 2013). A maximal gape of 105.8° was inferred for *T. atrox*, which is much larger than for any saber-toothed cat (Wroe et al. 2013). Goin and Pascual (1987) considered the high ratio between length and width of the upper canines and were in favor of long and shallow wounds on vital, bone-free body surfaces of the prey, such as abdomen and throat with canines fuctioning as guides during molar occlusion.

Comments. *Thylacosmilus atrox* had a morphology that departs from other sparassodonts. It had a short and massive skull with complete postorbital bar, and very small nasals as seen in dorsal view, partially covered by the maxilla. The large saber-like upper canine was ever-growing and deeply anchored in the maxilla

(Riggs 1934; Marshall 1976c; Turnbull and Segall 1984; Goin and Pascual 1987). There has been discussion of the dental formula. One specimen clearly possessed at least one pair of lower incisors—possibly more than one—(Goin and Pascual 1987). Wear facets on the lower incisors suggested that uppers were also present (Churcher 1985). *Thylacosmilus atrox* had two premolars in each jaw; the last upper premolar has been interpreted as a retained deciduous element (Goin and Pascual 1987; Forasiepi and Sánchez-Villagra 2014).

Goin and Pascual (1987) suggested that all known late Miocene–Pliocene thylacosmilid remains belong to a single species. Citing Article 23a of the International Code of Zoological Nomenclature, the authors suggested maintaining the broadly known name of the junior synonym *Thylacosmilus atrox* Riggs 1933, instead of *Achlysictis lelongi* Ameghino 1891.

Borhyaenidae Ameghino 1894

Borhyaenidae are large-sized sparassodonts with massive skulls and dentaries strongly attached or fused at symphysis, resembling the cranial architecture of the Tasmanian devil (*Sarcophilus harrisi*). All taxa may have had hypercarnivorous diet (Prevosti et al. 2013). Borhyaenidae includes the common ancestor of *Borhyaena*, *Arctodictis,* and all its descendants (e.g., Forasiepi 2009; Forasiepi et al. 2015). The oldest borhyaenid, *Australohyaena antiquua*, comes from the late Oligocene (Deseadan) while the youngest from the middle Miocene (Colloncuran) (Table 3.1). Classically, several Paleogene sparassodonts were included within the Borhyaenidae; however, we use here a more restricted definition. A putative *Borhyaena* sp. has been identified for the late Miocene (Huayquerian) (Marshall 1978). If correct, the stratigraphic range of the group should be extended another ~10 Ma over the range indicated here.

Acrocyon Ameghino 1887
(Tables 3.1 and 3.2)

Included species. *Acrocyon sectorius* Ameghino 1887 (type species) and *A. riggsi* (Sinclair 1930).

Temporal and geographic distribution. *Acrocyon riggsi* and *A. sectorius* come from the early Miocene (Colhuehuapian and Santacrucian, respectively), Argentina.

Paleoecology. The two *Acrocyon* species overlapped in size. Body mass estimations for *A. sectorius* on the basis of tooth variables provided 28.7 kg and 16.26 kg (Wroe et al. 2004a; Prevosti et al. 2013, respectively), while *A. riggsi* resulted in 26.3 kg and 17 kg (Wroe et al. 2004a; Prevosti et al. 2013, respectively).

Comments. Oiso (1991) questionably referred one poorly preserved specimen from the middle Miocene (Colloncuran) of Nazareno (Bolivia) to *Acrocyon* sp. Alternatively, Croft et al. (in press) suggested that the specimen possibly belongs to a new species also present in Cerdas (Bolivia) in outcrops of comparable age.

Acrocyon species are very similar in size and morphology to the contemporaneous species of *Borhyaena*. The likely possibility that *Acrocyon* represents part of the intraspecific variability of *Borhyaena* should be explored (Forasiepi 2009).

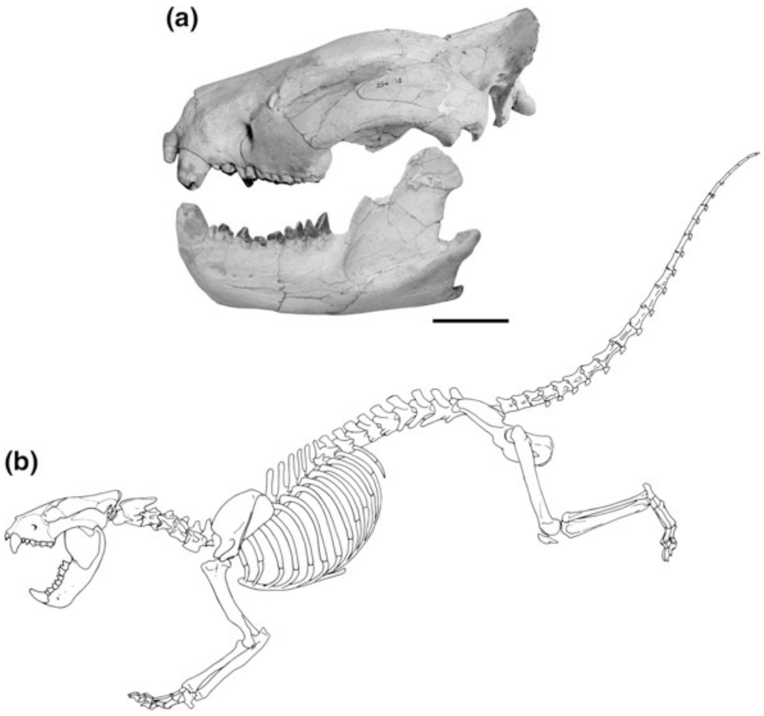


Fig. 3.12 *Arctodictis sinclairi* (MLP 85-VII-3-1), from the early Miocene (Colhuehuapian Age), Gran Barranca, Patagonia (Argentina), cranium and left dentary in lateral view (**a**); restoration of the skeleton (modified from Forasiepi 2009) (**b**). Scale bar = 5 cm

Arctodictis Mercerat 1891
(Figs. 3.7a and 3.12; Tables 3.1 and 3.2)

Included species. *Arctodictis munizi* Mercerat 1891 (type species) and *A. sinclairi* Marshall 1978.

Temporal and geographic distribution. *Arctodictis sinclairi* and *A. munizi* come from the early Miocene (Colhuehuapian and Santacrucian, respectively), Argentina.

Paleoecology. *Arctodictis munizi* was the largest post-Deseadan sparassodont with linear skull measurements similar to a lion. Based on the available material, the body mass of *A. munizi* seems to be underestimated (e.g., 51.6 kg in Wroe et al. 2004a; 37 kg in Vizcaíno et al. 2010; 43 kg in Prevosti et al. 2013, based on tooth equations). The older *A. sinclairi* is about 20% smaller (in linear cranial measurements) than the Santacrucian taxon, and its body mass was estimated at ~40 kg using the centroid size of the humerus and ulna (Ercoli and Prevosti 2011). Estimations for *A. sinclairi* using tooth variables appear to be underestimated (e.g., 23.3 kg in Wroe et al. 2004a; 18.34 kg in Prevosti et al. 2013).

Arctodictis sinclairi was considered a generalized terrestrial sparassodont with plantigrade posture (Forasiepi 2009; Ercoli et al. 2012). Both *Arctodictis* species have dentitions that suggested a hypercarnivorous diet (Prevosti et al. 2013). In particular, *A. munizi* was considered a bone-cracker (Forasiepi et al. 2004).

Comments. *Arctodictis sinclairi* is known by an almost complete skeleton (Fig. 3.12; Forasiepi 2009). *Arctodictis* species have a similar skull, dentition, and postcranium to *Australohyaena antiquua* and *Borhyaena* species. Cladistic analyses suggested that those taxa shared a close common ancestor (Forasiepi et al. 2004, 2006, 2015; Forasiepi 2009; Engelman and Croft 2014; Suarez et al. 2015).

Australohyaena Forasiepi et al. 2015
(Tables 3.1 and 3.2)

Included species. *Australohyaena antiquua* (Ameghino 1894).

Temporal and geographic distribution. Late Oligocene (Deseadan), Argentina.

Paleoecology. *Australohyaena antiquua* was large (~70 kg of body mass) and robust (Forasiepi et al. 2015). The tooth morphology indicated a hypercarnivorous diet. The tooth equations together with the robustness of p3, vaulted skull, robustness of the jaws, and strong development of the temporal musculature (inferred from skull bony landmarks) suggested that *A. antiquua* was a bone-cracker and thus a hyena-like ecomorph (Forasiepi et al. 2015).

Comments. *Australohyaena antiquua* is represented by an almost complete skull and dentition. Phylogenetic reconstructions placed it close to the Miocene genus *Arctodictis* (Forasiepi et al. 2015).

Originally, the species was recognized as ?*Borhyaena antiqua* Ameghino 1894, then changed to *Proborhyaena antiqua* by Ameghino (1897), *Pharsophorus*? *antiquus* by Marshall (1978) and *Australohyaena antiqua* by Forasiepi et al. (2015). However, the spelling in Latin fem. sing. adj. is “antiquua.” Under the provisions of ICZN art. 33.2, the name was suggested to correct *Australohyaena antiquua* (Babot and Forasiepi 2016).

Borhyaena Ameghino 1887
(Figs. 3.7b, c and 3.13; Tables 3.1 and 3.2)

Included species. *Borhyaena tuberata* Ameghino 1887 (type species) and *B. macrodonta* (Ameghino 1902b).

Temporal and geographic distribution. *Borhyaena macrodonta* comes from the early Miocene (Colhuehuapian), Argentina; *B. tuberata* from the early to middle Miocene (Santacrucian and Friasian), Argentina and Chile.

Paleoecology. The body mass of *B. tuberata* was estimated on 36.4 kg on the basis of the centroid size of the ulna and tibia (Ercoli and Prevosti 2011). Slightly lower results were obtained by using equations based on the postcranium (e.g., ~23 kg in Argot 2003b; 21.4 kg in Wroe et al. 2004a) and the dentition (e.g., 23.31 kg or 28.5 kg, in Vizcaíno et al. 2010 and Prevosti et al. 2013, respectively). The body mass of *B. macrodonta* was estimated at 34.7 kg or 31.25 kg (Wroe et al. 2004a and Prevosti et al. 2013, respectively) using dental variables.

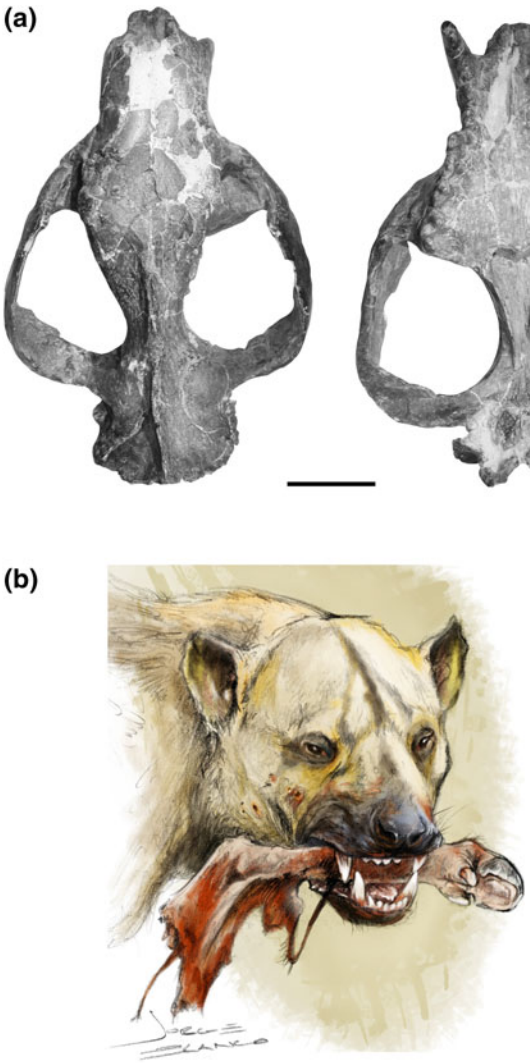


Fig. 3.13 *Borhyaena tuberata* (FMNH P 13252), from the early Miocene (Santacrucian Age), Patagonia (Argentina), cranium in dorsal and ventral views (**a**); artistic reconstruction by Jorge Blanco (**b**). Scale bar = 5 cm

The study of the postcranium of *B. tuberata* indicated that it was a terrestrial predator (Sinclair 1906; Marshall 1978; Argot 2003b, 2004a; Forasiepi 2009) with some cursorial capabilities (Argot 2003b; Ercoli et al. 2012). The limb architecture indicated parasagittal and more restricted pronation/supination movements, and semi- or fully digitigrade posture in the forelimb (Argot 2003b, 2004a).

Borhyaena species were hypercarnivorous (Prevosti et al. 2013). Analysis of mandibular force profiles, studied in *B. tuberata,* indicated a powerful canine bite with unpredictable direction of forces and bone breaking capabilities at the level of the last molar (Blanco et al. 2011).

Comments. *Borhyaena tuberata* is an iconic sparassodont. It is the first sparassodont described (Ameghino 1887) and the archetype for the group. *Borhyaena tuberata* is represented by several specimens including cranial and postcranial remains (Sinclair 1906).

A fragmentary dentary with the m2 (MACN-PV 13207) has been collected from the late Miocene (Huayquerian) beds of Entre Ríos (Argentina), which closely resembles *Borhyaena* (Marshall 1978). If the assignation to the genus is proved to be correct, the stratigraphic range of the taxon would notably increase.

Fredszalaya Shockey and Anaya 2008
(Tables 3.1 and 3.2)

Included species. *Fredszalaya hunteri* Shockey and Anaya 2008.

Temporal and geographic distribution. Late Oligocene (Deseadan), Bolivia.

Paleoecology. Large-sized taxon, possible hypercarnivorous.

Comments. *Fredszalaya hunteri* is a Neotropical sparassodont, hitherto found only in the late Oligocene (Deseadan) of Bolivia. Shockey and Anaya (2008) suggested affinities between *F. hunteri* and *Borhyaena*. This hypothesis awaits testing with cladistic analysis.

3.2.1 Problematic Taxa

Some sparassodont species are based on scarce and fragmentary material, and consequently the diagnoses are indeterminate. In other cases, the holotypes are missing from collections. As a result, the following taxa are regarded as nomina dubia.

Angelocabrerus Simpson 1970
(Tables 3.1 and 3.2)

Included species. *Angelocabrerus daptes* Simpson 1970 (nomen dubium).

Temporal and geographic distribution. Middle Eocene (Casamayoran), Argentina.

Comments. *Angelocabrerus daptes* is based on a single, much worn specimen in the MMP collections, which was described and illustrated by Simpson (1970: Figs. 1–3). Because of the condition of the specimen, no diagnostic features can be recognized. The specimen can no longer be located (Dondas 2015 com. pers.). *Angelocabrerus daptes* was about the size of *Borhyaena* and *Arminiheringia* (∼20.5 kg; Zimicz 2012). According to Simpson, this taxon is closer in morphology to the geologically younger *Borhyaena* than the contemporaneous *Arminiheringia* (Simpson 1970). It was likely hypercarnivorous (Zimicz 2012). Because the holotype is lost, we consider this taxon as nomen dubium.

Argyrolestes Ameghino 1902a
(Tables 3.1 and 3.2)

Included species. *Argyrolestes peralestinus* Ameghino 1902a (nomen dubium).

Temporal and geographic distribution. Middle Eocene (Casamayoran), Argentina.

Comments. The species is known only by its holotype, a broken upper molar (Ameghino 1902a; Simpson 1948; Marshall 1978) collected from Patagonia. Currently, the material is lost from the MACN collections (Alvarez 2013, com. pers.). According to Marshall (1978), the specimen might correspond to one of the upper molars in the dentition of the contemporaneous *Nemolestes spalacotherinus*. Because of these uncertainties and loss of the holotype, we consider the taxon as nomen dubium.

Eutemnodus Burmeister 1885
(Tables 3.1 and 3.2)

Included species. *Eutemnodus americanus* Bravard 1858 (nomen dubium).

Temporal and geographic distribution. Late Miocene (Huayquerian), Argentina.

Comments. Only one species, *Eutemnodus americanus*, based on isolated upper molars is currently recognized (Forasiepi et al. 2007). In the revision of the borhyaenids, Marshall (1978) tentatively recognized the species *E. acutidens* and *E. propampinus*. In a later revision, the specimens included in these species were identified in different taxonomic groups (Forasiepi et al. 2007). The diagnosis of *Eutemnodus* is almost indeterminate (Marshall 1978), and for this reason we consider the taxon as nomen dubium. *Eutemnodus americanus* is interesting in that, if valid, it records the presence of a borhyaenid-like sparassodont in the late Miocene (Marshall 1978; Forasiepi et al. 2007).

3.2.2 Tiupampan Taxa

The finding of metatherians from the early Paleocene in Tiupampa, Bolivia, including exquisite cranial and postcranial material, provided new data on the early radiation of the group in South America. *Mayulestes ferox* and *Allqokirus australis* were claimed to be the earliest sparassodonts (e.g., de Muizon 1994, 1998; de Muizon et al. 1997; de Muizon 1998), or these two taxa in combination with *Pucadelphys andinus*, *Andinodelphys cochabambensis* and *Jaskhadelphys minutus* as recently suggested by Muizon et al. (2015). This hypothesis requires support from cladistic analyses. The “key” synapomorphy used to define the Sparassodonta (including *Mayulestes*) was the presence of a medial process of the squamosal projecting medially, nearly reaching the foramen ovale (de Muizon et al. 1997; de Muizon 1998). This process is clearly seen in *Mayulestes* (de Muizon 1998: Fig. 8), but its presence and universality among sparassodonts is ambiguous (Forasiepi 2009).

According to Goin (2003), the molar structure of *Mayulestes* is primitive and reminiscent of the Peradectoidea.

Phylogenetic hypotheses have recovered the Tiupampan taxa (i.e., *Mayulestes, Pucadelphys*, and *Andinodelphys*) as a monophyletic group, placed among stem Marsupialia (e.g., Rougier et al. 1998; Babot 2005; Forasiepi 2009 and derived matrixes: Engelman and Croft 2014; Forasiepi et al 2015; Suarez et al. in press). This hypothesis (Fig. 3.2) implies another parallel corollary: The South American metatherians are represented by lineages of diverse origin that invaded South America more than once and whose ancestral forms were Holarctic (Forasiepi 2009; see also Case et al. 2005; Goin et al. 2016). In turn, the crown group Marsupialia diverged in South America and represents a relict of one of these metatherian lineages that radiated in the continent, later invading Antarctica and Australia. By contrast, Metatheria is Holarctic in origin, with North America (Simpson 1950; Lillegraven 1969; Patterson and Pascual 1968, 1972; Tedford 1974; Keast 1977) or Asia (Luo et al. 2003) the probable area where the basal cladogenesis of the group took place (Fig. 3.2).

In summary, currently the accepted earliest sparassodonts are recorded in the early Eocene (Itaboraian), with a radiation of the group during the middle Eocene (Casamayoran) (Babot 2005; Forasiepi 2009; Babot and Forasiepi 2016). A large revision would required if the putative sparassodonts from Tiupampa were certainly members of Sparassodonta: The stratigraphic time span involved more than 10 Ma as currently understood, beginning with the start of the Cenozoic, and a much primitive metatherian morphology would have to define the group.

References

Ameghino F (1887) Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia Austral y depositados en el Museo de La Plata. Bol Mus La Plata 1:1–26

Ameghino F (1889) Contribución al conocimiento de los mamíferos de fósiles de la República Argentina, obra escrita bajo los auspicios de la Academia Nacional de Ciencias de la República Argentina para presentarla Exposición Universal de París de 1889. Acad Nac Cien Córdoba Actas 6:1–1027

Ameghino F (1891) Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno Inferior de la Patagonia austral. Especies nuevas, adiciones y correcciones. Rev Arg Hist Nat 1:289–328

Ameghino F (1894) Enumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. Acad Nac Cien Córdoba Bol 13:259–452

Ameghino F (1897) Mammifères Crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des conches à *Pyrotherium*. Bol Inst Geogr Arg 18:406–521

Ameghino F (1902a) Notice preliminaires sur les mammifères nouveaux des terraines Crétacés de Patagonie. Acad Nac Cien Córdoba Bol 17:5–70

Ameghino F (1902b) Première contribution à la connaissance de la faune Mammalogique des couches à *Colpodon*. Acad Nac Cien Córdoba Bol 17:71–141

Ameghino F (1904) Nuevas especies de mamíferos Cretáceos y Terciarios de la República Argentina. Anales Soc Ci Argent 56:193–208; 57:162–175, 327–341; 58:35–41, 57–71, 182–192, 225–291

Argot C (2003a) Postcranial functional adaptations in the South American Miocene borhyaenoids (Mammalia, Metatheria): *Cladosictis*, *Pseudonotictis*, and *Sipalocyon*. Alcheringa 27:303–356

Argot C (2003b) Functional adaptations of the postcranial skeleton of two Miocene borhyaenoids (Mammalia, Metatheria) *Borhyaena* and *Prothylacynus*, from South America. Palaeontology 46:1213–1267

Argot C (2004a) Evolution of South American mammalian predators (Borhyaenoidea): anatomical and palaeobiological implications. Zool J Linn Soc 140:487–521

Argot C (2004b) Functional-adaptative analysis of the postcranial skeleton of a Laventan borhyaenoid, *Lycopsis longirostris* (Marsupialia, Mammalia). J Vertebr Paleontol 24:689–708

Argot C (2004c) Functional-adaptive features and paleobiologic implications of the postcranial skeleton of the late Miocene sabretooth borhyaenoid, *Thylacosmilus atrox* (Metatheria). Alcheringa 28:229–266

Argot C, Babot MJ (2011) Postcranial morphology, functional adaptations and palaeobiology of *Callistoe vincei*, a predaceous metatherian from the Eocene of Salta, north-western Argentina. Palaeontology 54:447–480

Babot MJ (2005) Los Borhyaenoidea (Mammalia, Metatheria) del Terciario inferior del noroeste argentino. Aspectos filogenéticos, paleobiolólogicos y bioestratigráficos. Unpublished PhD. thesis, Universidad Nacional de Tucumán

Babot J, Forasiepi AM (2016) Mamíferos predadores nativos del Cenozoico sudamericano: evidencias filogenéticas y paleoecológicas. In: Agnolin FA, Lio GL, Brissón Egli F, Chimento NR, Novas FE (eds) Historia Evolutiva y Paleobiogeográfica de los Vertebrados de América del Sur.Contribuciones MACN, vol 6. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, pp 219–230

Babot MJ, Ortiz PE (2008) Primer registro de Borhyaenoidea (Mammalia, Metatheria, Sparassodonta) en la provincia de Tucumán (Formación India Muerta, Grupo Choromoro; Mioceno tardío). Acta Geol Lillo 21:34–48

Babot MJ, Powell JE, de Muizon C (2002) *Callistoe vincei*, a new Proborhyaenidae (Borhyaenoidea, Metatheria, Mammalia) from the early Eocene of Argentina. Geobios 35:615–629

Bergqvist LP, Lima Moreira A, Ribeiro Pinto D (2006) Bacia de São José de Itaboraí. 75 Anos de História e Ciência. Serviço Geológico do Brasil, Rio de Janeiro

Blanco E, Jones WW, Grinspan GA (2011) Fossil marsupial predators of South America (Marsupialia, Borhyaenoidea): bite mechanics and palaeobiological implications. Alcheringa 31:377–387

Bond M, Pascual R (1983) Nuevos y elocuentes restos craneanos de *Proborhyaena gigantea* Ameghino 1897 (Marsupialia, Borhyanidae, Proborhyaeninae) de la edad Deseadense. Un ejemplo de coevolución. Ameghiniana 20:47–60

Bond M, Tejedor MF, Campbell KE, Chornogubsky L, Novo N, Goin FJ (2015) Eocene primates of South America and the African origins of New World monkeys. Nature 520:538–541

Bravard A (1858) Monografía de los Terrenos Terciarios de las Cercanías del Paraná. Imprenta del Registro Oficial, Paraná. Reimpresión 1995, Imprenta del Congreso de la Nación, Buenos Aires

Burmeister G (1885) Examen crítico de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precedente. Anales Mus Nac Hist Nat Buenos Aires 3:95–174

Cabrera A (1927) Datos para el conocimiento de los dasyuroideos fósiles argentinos. Rev Mus La Plata 30:271–315

Case JA, Goin FJ, Woodburne MO (2005) "South American" marsupials from the late Cretaceous of North America and the origin of marsupial cohorts. J Mammal Evol 12:461–494

Churcher CS (1985) Dental functional morphology in the marsupial sabre-tooth *Thylacosmilus atrox* (Thylacosmilidae) compared to that of felid sabre-tooths. Aust Mammal 8:201–220

Contreras VH (1990) Un Nuevo Hathlyacyninae (Mammalia: Borhyaenidae) del Chasiquense (Mioceno Superior) de la provincial de San Juan, Argentina. V Congreso Argentino de Paleontología y Bioestratigrafía. Actas, Tucumán, pp 163–168

Croft DA (2001) Cenozoic environmental change in South America as indicated by mammalian body size distributions (cenograms). Divers Distrib 7:271–287

Croft DA (2006) Do marsupials make good predators? Insights from predator–prey diversity ratios. Evol Ecol Res 8:1192–1214

Croft DA, Carlini AA, Ciancio MR, Brandoni D, Drew NE, Engelman RK, Anaya F (in press) New mammal faunal data from Cerdas, Bolivia, a middle-latitude Neotropical site that chronicles the end of the middle Miocene Climatic Optimum in South America. J Vertebr Paleontol

de Muizon C (1994) A new carnivorous marsupial from the Paleocene of Bolivia and the problem of the marsupial monophyly. Nature 370:208–211

de Muizon C (1998) *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. Geodiversitas 20:19–142

de Muizon C (1999) Marsupial skulls from the Deseadan (late Oligocene) of Bolivia and phylogenetic analysis of the Borhyaenoidea (Marsupialia, Mammalia). Geobios 32:483–509

de Muizon C, Argot C (2003) Comparative anatomy of the Tiupampa didelphimorphs; an approach to locomotory habits of early marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria, pp 43–62

de Muizon C, Cifelli RL, Céspedes Paz R (1997) The origin of the dog-like borhyaenoid marsupials of South America. Nature 389:486–489

de Muizon C, Billet G, Argot C, Ladevèze S, Goussard F (2015) *Alcidedorbignya inopinata*, a basal pantodont (Placentalia, Mammalia) from the early Palaeocene of Bolivia: anatomy, phylogeny and palaeobiology. Geodiversitas 37:397–634

de Paula Couto C (1952) Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Polydolopidae and Borhyaenidae. Am Mus Novit 1559:1–27

Degrange FJ, Tambussi CP, Moreno K, Witmer LW, Wroe S (2010) Mechanical analysis of feeding behavior in the extinct "terror bird" *Andalgalornis steulleti* (Gruiformes: Phorusrhacidae). PLoS One 5:e1 1856

Echarri S, Prevosti FJ (2015) Differences in mandibular disparity between extant and extinct species of metatherian and placental carnivore clades. Lethaia 48:196–204

Engelman RK, Croft DA (2014) A new species of small-bodied sparassodont (Mammalia: Metatheria) from the middle Miocene locality of Quebrada Honda, Bolivia. J Vert Paleontol 34:672–688

Engelman RK, Anaya F, Croft DA (2015) New specimens of *Acyonmyctoderos* (Metatheria, Sparassodonta) from Quebrada Honda, Bolivia. Ameghiniana 52:204–225

Ercoli MD, Prevosti FJ (2011) Estimación de masa de las especies de Sparassodonta (Metatheria, Mammalia) de la Edad Santacrucense (Mioceno Temprano) a partir de tamaños de centroide de elementos apendiculares: inferencias paleoecológicas. Ameghiniana 48:462–479

Ercoli MD, Prevosti FJ, Álvarez A (2012) Form and function within a phylogenetic framework: locomotory habits of extant predators and some Miocene Sparassodonta (Metatheria). Zool J Linn Soc 165:224–251

Ercoli MD, Prevosti FJ, Forasiepi AM (2014) The structure of the mammalian predator guild in the Santa Cruz Formation (late early Miocene), Patagonia, Argentina. J Mammal Evol 21:369–381

Esteban G, Nasif N, Georgieff SM (2014) Cronobioestratigrafía del Mioceno tardío-Plioceno temprano, Puerta de Corral Quemado y Villavil, provincia de Catamarca, Argentina. Acta Geol Lillo 26:165–192

Forasiepi AM (2009) Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. Monografías Mus Arg Sci Nat "Bernardino Rivadavia" [ns] 6:1–174

Forasiepi AM, Carlini AA (2010) New thylacosmilid (Mammalia, Metatheria, Sparassodonta) from the Miocene of Patagonia, Argentina. Zootaxa 2552:55–68

Forasiepi AM, Sánchez-Villagra MR (2014) Heterochrony, dental ontogenetic diversity and the circumvention of constraints in marsupial mammals and extinct relatives. Paleobiology 40:222–237

Forasiepi AM, Goin FJ, di Martino V (2003) Una nueva especie de *Lycopsis* (Metatheria, Prothylacyninae) de la Formación Arroyo Chasicó (Mioceno Tardío), de la Provincia de Buenos Aires. Ameghiniana 40:249–253

Forasiepi AM, Goin FJ, Tauber AA (2004) Las especies de *Arctodictis* Mercerat 1891 (Metatheria, Borhyaenidae), grandes carnívoros del Mioceno de América del Sur. Rev Esp Paleontol 19:1–22

Forasiepi AM, Sánchez-Villagra MR, Goin FJ, Takai M, Kay RF, Shigehara N (2006) A new Hathliacynidae (Metatheria, Sparassodonta) from the middle Miocene of Quebrada Honda, Bolivia. J Vert Paleontol 26:670–684

Forasiepi AM, Martinelli AG, Goin FJ (2007) Revisión taxonómica de Parahyaenodon argentinus Ameghino y sus implicancias en el conocimiento de los grandes mamíferos carnívoros del Mio-Plioceno de América del Sur. Ameghiniana 44:143–159

Forasiepi AM, Babot MJ, Zimicz N (2015) *Australohyaena antiqua* (Mammalia, Metatheria, Sparassodonta), a large predator from the late Oligocene of Patagonia, Argentina. J Syst Palaeontol 13:503–525

Goin FJ (1997) New clues for understanding Neogene marsupial radiations. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) A history of the neotropical fauna. Vertebrate paleobiology of the Miocene in Colombia. Smithsonian Institution Press, Washington, pp 185–204

Goin FJ (2003) Early marsupial radiations in South America. In: Jones M, Dickman C, Archer M (eds) Predators with pouches. The biology of carnivorous marsupials. CSIRO Publishing, Victoria, pp 30–42

Goin FJ, Candela A (2004) New Paleogene marsupials from the Amazon Basin of Eastern Perú. In: Campbell KE Jr (ed) The Paleogene mammalian fauna of Santa Rosa, Amazonian Perú. Nat Hist Mus Los Angeles County, Science Series, vol 40, pp 15–60

Goin FJ, Pascual R (1987) News on the biology and taxonomy of the marsupials Thylacosmilidae (late Tertiary of Argentina). Anales de la Academia Nacional de Ciencias Exactas Físicas y Naturales de Buenos Aires 39:219–246

Goin FJ, Palma RM, Pascual R, Powell JE (1986) Persistencia de un primitivo Borhyaenidae (Mammalia, Marsupialia) en el Eoceno Temprano de Salta (Fm. Lumbrera, Argentina), aspectos geológicos y paleoambientales relacionados. Ameghiniana 23:47–56

Goin FJ, Abello MA, Bellosi E, Kay R, Madden R, Carlini AA (2007) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno Temprano, edad-mamífero Colhuehuapense). Parte I: Introducción, Didelphimorphia y Sparassodonta. Ameghiniana 44:29–71

Goin FJ, Abello MA, Chornogubsky L (2010) Middle tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America's Grande Coupure. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The paleontology of Gran Barranca: evolution and environmental change through the middle Cenozoic of Patagonia. Cambridge University Press, New York, pp 71–107

Goin FJ, Woodburne MO, Zimicz AN, Martin GM, Chornogubsky L (2016) A brief history of South American metatherians, evolutionary contexts and intercontinental dispersals. Springer, Dordrecht

Gordon CL (2003) A first look at estimating body size in dentally conservative marsupials. J Mammal Evol 10:1–21

Goswami A, Milne N, Wroe S (2011) Biting through constraints: cranial morphology, disparity, and convergence across living and fossil carnivorous mammals. Proc R Soc Lond [B] 278:1831–1839

Hoffstetter R, Petter G (1983) *Paraborhyaena boliviana* et *Andinogale sallensis,* deux marsupiaux (Borhyaenidae) nouveaux du Déséadien (Oligocène Inférieur) de Salla (Bolivie). C R Acad Sci 296:205–208

Keast A (1977) Historical biogeography of the marsupials. In: Stonehouse B, Gilnore D (eds) The biology of the marsupials. University Park Press, Baltimore, pp 69–95

Ladevèze S, de Muizon C (2007) The auditory region of Paleocene Pucadelphydae (Mammalia, Metatheria) from Tiupampa, Bolivia with phylogenetic implications. Palaeontology 50:1123–1154

Ladevèze S, de Muizon C (2010) Evidence of early evolution of Australidelphia (Mammalia, Metatheria) in South America: phylogenetic relationships of the metatherian from the late Paleocene of Itaboraí (Brazil) based on teeth and petrosal bones. Zool J Linn Soc 159:746–784

Lillegraven JA (1969) Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. Univ Kans Paleontol Contrib Pap 50:1–122

Linares OJ (2004) Bioestratigrafía de la fauna de mamíferos de las formaciones Socorro, Urumaco y Codore (Mioceno medio–Plioceno temprano) de la región de Urumaco, Falcón, Venezuela. Paleobiología Neotropical 1:1–23

Loomis FB (1914) The Deseado Formation of Patagonia. Amherst College, New Haven

Luo Z-X, Ji Q, Wible JR, Yuan CX (2003) An early Cretaceous tribosphenic mammal and metatherian evolution. Science 302:1934–1940

Marshall LG (1976a) New didelphine marsupials from the La Venta fauna (Miocene) of Colombia, South America. J Paleo 50:402–418

Marshall LG (1976b) A new borhyaenid (Marsupialia, Borhyaeninae) from the Arroyo Chasicó Formation (lower Pliocene), Buenos Aires Province, Argentina. Ameghiniana 13:289–299

Marshall LG (1976c) Evolution of the Thylacosmilidae, extinct saber-tooth marsupials of South America. PaleoBios 23:1–30

Marshall LG (1977a) Evolution of the carnivorous adaptative zone in South America. In: Hecht MK, Goody PC, Hecht BM (eds) Major patters in vertebrate evolution. Plenum Press, New York, pp 709–721

Marshall LG (1977b) A new species of *Lycopsis* (Borhyaenidae, Marsupialia) from the La Venta Fauna (Miocene) of Colombia, South America. J Paleontol 51:633–642

Marshall LG (1978) Evolution of the Borhyaenidae, extinct South American predaceous marsupials. Univ Calif Publ Geol Sci 117:1–89

Marshall LG (1979) Review of the Prothylacyninae, an extinct subfamily of South American “dog–like” marsupials. Fieldiana. Geol [ns] 3:1–50

Marshall LG (1981) Review of the Hathlyacyninae, an extinct subfamily of South American “dog–like” marsupials. Fieldiana. Geol [ns] 7:1–120

Marshall LG, de Muizon C (1988) The dawn of the age of mammals in South America. Natl Geogr Res 4:23–55

Marshall LG, Patterson B (1981) Geology and geochronology of the mammal-bearing tertiary of the Valle de Santa Maria and Rio Corral Quemado, Catamarca Province, Argentina. Fieldiana. Geol [ns] 9:1–80

Marshall LG, Case JA, Woodburne MO (1990) Phylogenetic relationships of the families of marsupials. Curr Mammal 2:433–502

Martin GM, Tejedor MF (2007) Nueva especie de *Pseudonotictis* (Metatheria, Sparassodonta, Hathliacynidae). Ameghiniana 44:747–750

Mercerat A (1891) Caracteres diagnósticos de algunas especies de Creodonta conservadas en el Museo de La Plata. Revista Mus. La Plata 2:51–56

Mercerat A (1917) Notas sobre algunos carnívoros fósiles y actuales de la América del Sud. H. Errado y Cia. Impresores, Buenos Aires

Millien V, Bovy H (2010) When teeth and bones disagree: body mass estimation of a giant extinct rodent. J Mammal 91:11–18

Mones A (2014) *Contrerascynus,* new name for *Simpsonia* Contreras, 1990 (Mammalia, Sparassodonta, Hathlyacynidae), *non* Rochebrune, 1904 (Bivalvia, Unionidae), *non* Baker, 1911 (Gastropoda, Lymnaeidae). Rev Bras Paleontol 17:435–436

Mones A, Rinderknecht A (2004) Primer registro de Thylacosmilidae en el Uruguay (Mammalia: Marsupialia: Sparassodonta). Comunicaciones Paleontológicas del Museo Nacional de Historia Natural y Antropología 34:193–200

Mones A, Ubilla M (1978) La edad Deseadense (Oligoceno Inferior) de la Formación Fray Bentos y su contenido paleontológico, con especial referencia a la presencia de *Proborhyaena cf. gigantea* Ameghino (Marsupialia, Borhyaenidae) en el Uruguay -nota preliminar. Comunicaciones Paleontológicas MHNM 7:151–157

Myers TJ (2001) Marsupial body mass prediction. Austral J Zool 49:99–118

Oiso Y (1991) New land mammal locality of middle Miocene (Colloncuran) age from Nazareno, Southern Bolivia. In: Suarez-Soruco R (ed) Fósiles y facies de Bolivia—vol 1 Vertebrados. Revista Técnica de YPF 12: 653–672

Pascual R, Bocchino A (1963) Un nuevo Borhyaninae (Marsupialia) del Plioceno Medio de Hidalgo (La Pampa). Ameghiniana 3:97–107

Patterson B, Marshall LG (1978) The Deseadan, early Oligocene, Marsupialia of South America. Fieldiana. Geol [ns] 41:37–100

Patterson B, Pascual R (1968) Evolution of mammals in southern continents. V. Fossil mammal fauna of South America. Quart Rev Biol 43:409–451

Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast A, Erk FC, Glass B (eds) Evolution of mammals and Southern continents. State Univesity of New York Press, Albany

Petter G, Hoffstetter R (1983) Les marsupiaux du Déséadien (Oligocène Inférieur) de Salla (Bolivie). Annls Paléont (Vert–Invert) 69:175–234

Powell JE, Babot MJ, García-López DA, Deraco MV, Herrera CM (2011) Eocene vertebrates of northwestern Argentina: annotated list. In: Salfity JA, Marquillas RA (eds) Cenozoic geology of the Central Andes of Argentina. SCS Publisher, Salta, pp 349–370

Prevosti FJ, Turazzini GF, Chemisquy MA (2010) Morfología craneana en tigres dientes de sable: alometría, función y filogenia. Ameghiniana 47:239–256

Prevosti FJ, Turazzini GF, Ercoli MD, Hingst-Zaher E (2012a) Mandible shape in marsupial and placental carnivorous mammals: a morphological comparative study using geometric morphometrics. Zool J Linn Soc 164:836–855

Prevosti FJ, Forasiepi AM, Ercoli MD, Turazzini GF (2012b) Paleoecology of the mammalian carnivores (Metatheria, Sparassodonta) of the Santa Cruz Formation (late early Miocene). In: Vizcaíno SF, Kay RF, Bargo MS (eds) early Miocene paleobiology in Patagonia. Cambridge University Press, Cambridge, pp 173–193

Prevosti FJ, Forasiepi AM, Zimicz N (2013) The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? J Mammal Evol 20:3–21

Reguero M, Candela AM (2011) Late Cenozoic mammals from Northwest of Argentina. In: Salfity JA, Marquillas RA (eds) Cenozoic geology of Central Andes of Argentina. Instituto del Cenozoico, Salta, pp 411–426

Reig OA (1957) Nota previa sobre los mamíferos de la Formación Chasicó. Ameghiniana 1:27–31

Riggs ES (1933) Preliminary description of a new marsupial saber-tooth from the Pliocene of Argentina. Field Mus Nat Hist Geol ser 6:61–66

Riggs ES (1934) A new marsupial saber-tooth from the Pliocene of Argentina and its relationships to other South American predaceous marsupials. T Am Philos Soc [ns] 24:1–31

Roth S (1903) Noticias sobre nuevos mamíferos fósiles del Cretáceo superior y Terciario de la Patagonia. Revista Mus. La Plata 11:133–158

Rougier GW, Wible JR, Novacek MJ (1998) Implications of *Deltatheridium* specimens for early marsupial history. Nature 396:459–463

Rougier GW, Wible JR, Novacek MJ (2004) New specimen of *Deltatheroides cretacicus* (Metatheria, Deltatheroidea) from the late Cretaceous of Mongolia. Bull Carnegie Mus Nat Hist 36:245–266

Sánchez-Villagra MR (2013) Why are there fewer marsupials than placentals? On the relevance of geography and physiology to evolutionary patterns of mammalian diversity and disparity. J Mammal Evol 20:279–290

Scheyer TM, Aguilera OA, Delfino M, Fortier DC, Carlini AA, Sánchez R et al (2013) Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. Nat. Commun 4:1907. doi:10.1038/ncomms2940

Scott WB (1937) A history of land mammals in the Western Hemisphere (revised edition). The MacMillan Company, New York

Sears K (2004) Constraints on the morphological evolution of marsupial shoulder girdles. Evolution 58:2353–2370

Shockey BJ, Anaya F (2008) Postcranial osteology of mammals from Salla, Bolivia (late Oligocene): form, function, and phylogenetic implications. In: Sargis EJ, Dagosto M (eds) Mammalian evolutionary morphology. A tribute to Frederick S. Szalayc. Springer, Netherlands, pp 135–157

Simpson GG (1930) Post-Mesozoic marsupialia. In: Junk W (ed) Fossilium catalogus. I: Animalia. W. Junk, Berlin, pp 1–87

Simpson GG (1935) Descriptions of the oldest known South American mammals from the Río Chico Formation. Amer Mus Novit 793:1–25

Simpson GG (1948) The beginning of the age of mammals in South America, Part 1. Bull Amer Mus Nat Hist 91:1–232

Simpson GG (1950) History of the fauna of Latin America. Am Sci 38:361–389

Simpson GG (1970) Mammals from the early Cenozoic of Chubut, Argentina. Breviora 360:1–13

Simpson GG (1971) The evolution of marsupials in South America. An Acad Bras Cien 43:103–118

Simpson GG (1980) Splendid isolation: the curious history of South American mammals. Yale Univesity Press, New Haven

Sinclair WJ (1906) Mammalia of the Santa Cruz beds: Marsupialia. Rep Princeton Univ Exped Patagonia, 1896–1899, 4 (Paleontology). Princeton

Sinclair WJ (1930) New carnivorous marsupials from the Deseado Formation of Patagonia. Field Mus Nat Hist Geol Ser 1:35–39

Sorkin B (2008) A biomechanical constraint on body mass in terrestrial mammalian predators. Lethaia 41:333–347

Suarez C, Forasiepi AM, Goin FJ, Jaramillo C (2015) Insights into the Neotropics prior to the Great American Biotic Interchange: new evidence of mammalian predators from the Miocene of Northern Colombia. J Vert Paleontol. doi:10.1080/02724634.2015.1029581

Szalay FS (1994) Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge University Press, New York

Tedford RH (1974) Marsupials and the new paleogeography. In: Ross CA (ed) Paleogeographic provinces and provinciality. Society of Economic Paleontologists and Mineralogists, Special Publication 21:109–126

Therrien F (2005) Feeding behaviour and bite force of sabretoothed predators. Zool J Linn Soc 145:393–426

Turnbull WD (1978) Another look at dental specialization in the extinct saber-toothed marsupial, *Thylacosmilus*, compared with its placental counterparts. In: Butler PM, Joysey KA (eds) Development, function and evolution of teeth. Academic Press, London, pp 399–414

Turnbull WD, Segall W (1984) The ear region of the marsupial sabertooth, *Thylacosmilus*: influence of the sabertooth lifestyle upon it, and convergence with placental sabertooths. J Morphol 181:239–270

Van Valkenburgh B (1991) Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. Paleobiology 17:340–362

Villarroel C, Marshall LG (1982) Geology of the Deseadan (early Oligocene) age estratos Salla in the Salla-Luribay Basin, Bolivia with description of new Marsupialia. Geobios Mem Spec 6:201–211

Villarroel C, Marshall LG (1983) Two new late Tertiary marsupials (Hathlyacyninae and Sparassocyninae) from the Bolivian Altiplano. J Paleo 57:1061–1066

Vizcaíno SF, Bargo MS, Kay RF, Fariña RA, GiacomoM Di, Perry JMG, Prevosti FJ, Toledo N, Cassini GH, Fernicola JC (2010) A baseline paleoecological study for the Santa Cruz

Formation (late–early Miocene) at the Atlantic coast of Patagonia, Argentina. Palaeogeogr Palaeoclimatol Palaeoecol 292:507–519

Wroe S, Myers TJ, Wells RT, Gillespie A (1999) Estimating the weight of the Pleistocene marsupial lion, *Thylacoleo carnifex* (Thylacoleonidae: Marsupialia): implications for the ecomorphology of a marsupial super-predator and hypotheses of impoverishment of Australian marsupial carnivore faunas. Aust J Zool 47:489–498

Wroe S, Myers TJ, Seebacher F, Kear B, Gillespie A, Crowther Salisbury S (2003) An alternative method for predicting body mass: the case of the Pleistocene marsupial lion. Paleobiology 29:403–411

Wroe S, Argot C, Dickman C (2004a) On the rarity of big fierce carnivores and primacy of isolation and area: tracking large mammalian carnivore diversity on two isolated continents. Proc R Soc Lond [B] 271:1203–1211

Wroe S, McHenry C, Thomason C (2004b) Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. Proc R Soc Lond [B] 272:619–625

Wroe S, Chamoli U, Parr WCH, Clausen P, Ridgely R et al (2013) Comparative biomechanical modeling of metatherian and placental saber-tooths: A different kind of bite for an extreme pouched predator. PLoS ONE 8(6):e66888

Zimicz AN (2012) Ecomorfología de los marsupiales paleógenos de América del Sur. Unpublished PhD. thesis, Universidad Nacional La Plata

Zimicz AN (2014) Avoiding competition: the ecological history of late Cenozoic metatherian carnivores in South America. J Mammal Evol 21:383–393