J Mammal Evol (2014) 21:383–393
DOI 10.1007/s10914-014-9255-8

ORIGINAL PAPER

Avoiding Competition: the Ecological History of Late Cenozoic Metatherian Carnivores in South America

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Abstract The ecological interaction between small and medium sized South American metatherian carnivores, from the Miocene to Recent, has been analyzed with the objective to understand the ecological interactions between the Hathliacynidae (Sparassodonta) and some Didelphoidea (Didelphimorphia). The species richness through time for these two groups, along with the body mass, diet, and several morphofunctional variables has been analyzed here. The results show a double-wedge geometry of the diversity curve. The climax of the Hathliacynidae took place during the Santacrucian mammal-age with a subsequent decline, in the species richness of this family, followed by the extinction of the family at the Barrancalobian subage. Carnivorous Didelphoidea show a first maximum species richness during the Chapadmalalan followed by a decline and a new rise during Recent times. The coexistence of these mentioned groups took place from the Chasicoan to the Chapadmalalan mammal-ages covering a time span of around 6,000,000 years. The multivariate and univariate analyses of morphofunctional variables suggest a restriction of the Hathliacynidae to hypercarnivory while the Didelphoidea occupied the niche of meso- and hypocarnivory. The body mass analyses show some overlap in small sizes but it is not correlated with any superposition in the morphospace of functional variables. In summary, any passive replacement or active displacement between the Hathliacynidae and carnivorous Didelphoidea are supported by the fossil record. In turn, a partition of the metatherian carnivorous guild seems to have occurred through to the Neogene. The extinction of the Hathliacynidae seems to be a result of environmental change.

Keywords Hathliacynidae · Didelphoidea · South America · Competition · Replacement

Introduction

During the Paleogene and most of the Neogene, the guild of carnivorous mammals in South America was occupied by metatherians. Placental carnivores arrived later, by the late Miocene, to South American landscapes (Soibelzon and Prevosti 2007; Prevosti et al. 2013). By the early Paleogene, several metatherian lineages occupied the niche of carnivory. All of these were mesocarnivores (Zimicz 2012) with a diet composed of vertebrate meat complemented with invertebrates and fruits. Some members of the Peradectidae, Mayulestidae, and the first Sparassodonta (*Allqokirus australis*) composed this stock of early carnivores (Muizon 1991, 1998; Zimicz 2012). By the late Paleocene-early Eocene, sparassodonts developed the first hypercarnivore type, e.g., *Nemolestes spalacotherinus* (a medium-sized species; Zimicz 2012). By the late Eocene the Sparassodonta radiated successfully into the niches of medium- and large-sized hypercarnivores (Zimicz 2012). The first specialized proborhyaenids are well represented at this point in time (Forasiepi 2009).

The oldest hathliacynids are recorded in the early Oligocene (Goin et al. 2010) but the age predicted for the origin of the family is middle-late Eocene (Forasiepi 2009). As other sparassodonts, the main history of the group took place during the Neogene when they reached their acme and posteriorly declined and went extinct. From an ecological point, the Hathliacynidae have been considered as omnivores (Marshall 1978, 1981; Argot 2004) as well as hypercarnivores

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Electronic supplementary material The online version of this article (doi:10.1007/s10914-014-9255-8) contains supplementary material, which is available to authorized users.

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(Prevosti et al. 2012, 2013) of small and medium size forms (Prevosti et al. 2013). The hathliacynids were probably terrestrial and scansorial (Marshall 1977a; Muizon 1998; Argot 2003; Ercoli 2010; Ercoli et al. 2012; Prevosti et al. 2012).

Didelphimorphia developed different carnivorous types, especially from the middle Neogene until the Recent. All Neogene taxa are included in the Didelphoidea, and are actually considered a natural group including the Didelphidae, Sparassocynidae, and Caluromyidae (Goin 1991). The family Didelphidae includes the monophyletic group of large carnivorous-omnivorous opossums (Jansa and Voss 2005; Jansa et al. 2006; Flores 2009). The Sparassocynidae is an extinct family of carnivorous didelphimorphians known from the Miocene and Pliocene of Argentina (Reig and Simpson 1972; Simpson 1974; Forasiepi et al. 2009). Finally, the Caluromyidae include the more strictly frugivorous opossums represented in the fossil record since the early Miocene (Goin et al. 2007). Didelphoids carnivores filled the size range of small and medium sizes from 0 to 10 kg and they were adapted to a terrestrial and scansorial lifestyle (Szalay 1994; Muizon and Argot 2003; Viera and Astúa de Moraes 2003).

The late Cenozoic history of didelphoids is mostly known from fossil specimens recovered at numerous localities in the Pampean Region, central Argentina (Goin 1995). Carnivorous didelphoids are well represented since the Huayquerian SALMA (*Hyperdidelphys, Thylophorops, Didelphis, Sparassocynus, Hesperocynus*, and *Thylatheridium*), reaching their largest diversity by the Chapadmalalan SALMA (Goin and Pardiñas 1996; Goin and Montalvo 1988; Forasiepi et al. 2009; Goin et al. 2009).

From the late Miocene to the early Pliocene, the Sparassodonta coexisted in South America with placental carnivores (Soibelzon and Prevosti 2007; Prevosti et al. 2013). Several authors have suggested that the arrival of placental carnivores was the cause of the extinction of the sparassodonts (Simpson 1950, 1969, 1971, 1980; Patterson and Pascual 1972; Savage 1977). Other authors question this idea (Marshall 1977b, 1978; Reig 1981; Bond 1986; Pascual and Bond 1986; Goin 1989, 1995; Ortiz Jaureguizar 1989, 2001; Marshall and Cifelli 1990; Alberdi et al. 1995; Forasiepi 2009; Forasiepi et al. 2009; Prevosti et al. 2009). A close examination of the diversity curve of both groups demonstrates that no active or passive replacement occurred (Prevosti et al. 2013). Sparassodonta coexisted also with Didelphoidea. The sparassodonts were more specialized in the predator niche than Didelphoidea. The temporal and the body size overlap, the terrestrial/scansorial habits, and the decided carnivorous trend of several extinct didelphoids led several authors to postulate a possible competitive interaction between the small- and medium-sized Sparassodonta (Hathliacynidae) and the carnivorous didelphoids (Marshall 1977b, 1978; Goin 1989; Goin and Pardiñas 1996; Goin et al. 2009; Forasiepi 2009). On the contrary, Prevosti et al. (2013) pointed out the existence of a potential niche separation between these two groups of South American metatherians.

Different models have been used to understand the evolution of two clades occupying the same adaptive zone at the same time in a given geographic area. The active displacement that implies competition (Benton 1983) or the passive replacement that implies the action of external factors on the species populations (Benton 1983) commonly shows “double-wedge” geometries on the diversity patterns (Van Valkenburgh 1999). In general, one clade begins to decline in diversity while a second begins to increase. When the rate of displacement is gradual, a competitive interaction is inferred but, when the rate of replacement is rapid and associated with environmental changes, an opportunistic process is suspected (Benton 1983). The simplest model to analyze the competitive interaction in the fossil record is that which verifies a linear decrease in the diversity of the first clade concomitantly with a linear increase in the diversity of the second clade (Benton 1983; Krause 1986; Van Valkenburgh 1999). Other models consider the joined action of biotic and physical factors (Rosenzweig and McCord 1991; Sepkoski 1996, 2001; Sepkoski et al. 2000).

The aim of the present review is to clarify the ecological relationships between Hathliacynidae and the carnivorous Didelphoidea in order to determine the potential existence of competitive interactions between them.

Methods

In order to understand the ecological interactions, the diversity of Sparassodonta and carnivorous Didelphoidea was calculated for each age, following current chronostratigraphic and biogeographic charts (Flynn and Swisher 1995; Cione and Tonni 2005, modified by Woodburne et al. 2006; Gelfo et al. 2009; Madden et al. 2010; Ré et al. 2010; see Prevosti et al. 2013: Fig. 1). The geographical and chronological information of the fossil taxa included here was drawn from the literature (Marshall 1978, 1979, 1981; Patterson and Marshall 1978; Marshall et al. 1983; Goin and Montalvo 1988; Pascual and Ortiz Jaureguizar 1990; Goin 1991; Goin and Pardiñas 1996; Goin et al. 2009; Forasiepi 2009; Forasiepi et al. 2009). The taxonomy of Hathliacynidae follows Forasiepi (2009). The taxonomy of Didelphoidea mainly follows Goin and Montalvo (1988), Goin (1991), Goin and Pardiñas (1996), Goin et al. (2009), and Forasiepi et al. (2009).

The diversity was measured as the number of species in each period considering South American Land Mammal Ages (SALMAs) as time unit. A taxon was included in counts of intermediate ages when it was found in an older and younger age. The diversity pattern of Hathliacynidae and the carnivorous Didelphoidea were compared in order to detect

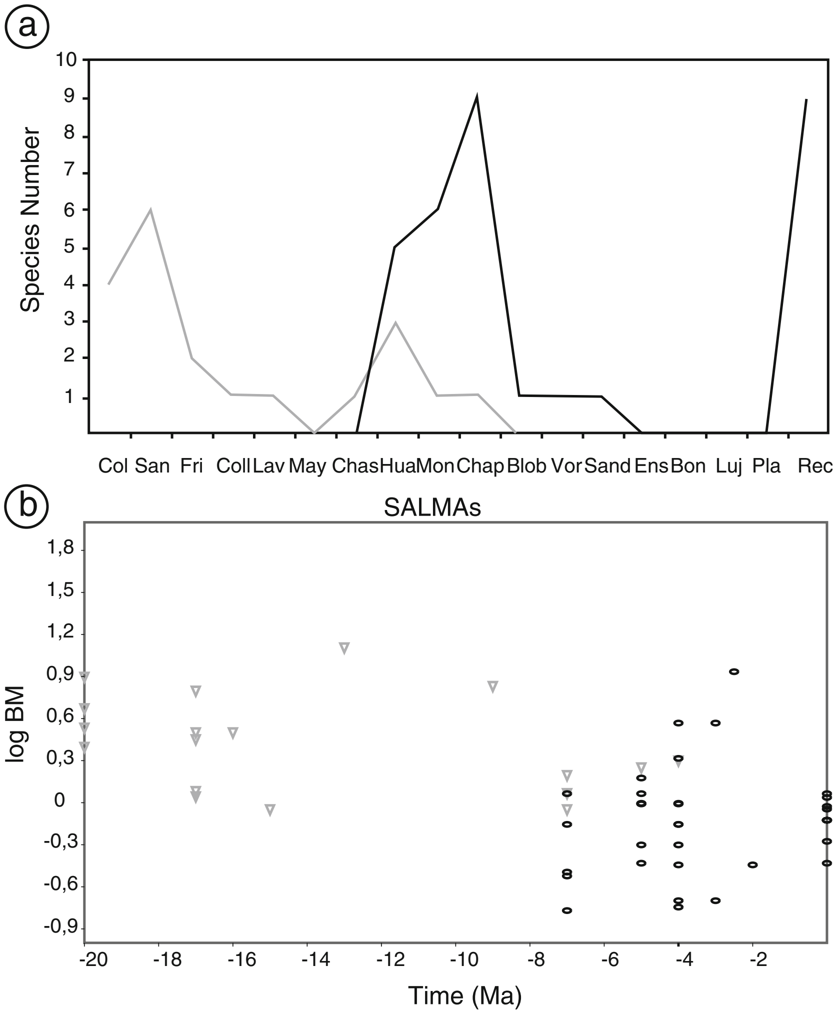

Fig. 1 **a**, Diversity through time for Hathliacynidae (*gray line*) and Didelphoidea (*black line*); **b**, Bivariate plot of body mass versus time for Hathliacynidae (*triangle*) and Didelphoidea (*oval*). Refs: *SALMAs* South American Land Mammal Ages; *Col* Colhuehuapian; *San* Santacrucian; *Fri* Friasian; *Coll* Colloncuran; *Lav* Laventan; *May* Mayoan; *Chas* Chasicoan; *Hua* Huayquerian; *Mon* Montehermosan; *Chap* Chapadmalalan; *Blob* Barrancalobian; *Vor* Vorohuean; *Sand* Sanandresian; *Ens* Ensenadan; *Bon* Bonaerian; *Luj* Lujanian; *Pla* Platan; *Rec* Recent

ecological interactions. The terms "competitive displacement" and "opportunistic replacement" as well as the condition to infer each process in the fossil record follows Benton (1983) and Krause (1986).

To evaluate the ecological overlap, body mass data of Hathliacynidae were compiled from Prevosti et al. (2013) and the body mass of extinct Didelphoidea was then estimated. Data of body mass of living didelphids were taken from Smith et al. (2003). The least square regressions used to estimate the weight of extinct species are based on dental measurements (Gordon 2003). Size categories mentioned in the text are mostly based in Carbone et al. (2007): small (< 2 kg); medium (2–10 kg); and large (> 10 kg).

Following Van Valkenburgh (1991) and Friscia et al. (2007), a set of morphometric variables were analyzed to evaluate the potential superposition in the trophic habits. These variables are: relative grinding area (RGA); relative blade length (RBL); relative size (RPS) and shape (PS) of the biggest lower premolar. Additionally, the relative length of the premolar blade with respect to the carnassials (LP/LM) was taken following Palmqvist et al. (2011). The lower fourth molar was considered as a carnassial tooth following Werdelin (1987). The RGA was used to discriminate between hypercarnivores (with RGA<0.5), mesocarnivores (with 0.5 <RGA<0.8), and hypocarnivores (RGA>0.8). A principal component analysis (PCA) on the variance-covariance matrix was performed with all morphometric variables in order to visualize the distribution of species in the morphospace. The potential overlap in the feeding requirements of Hathliacynidae and Didelphoidea was evaluated through the superposition in the multivariate space.

Results

Diversity During most of their record, the Hathliacynidae had a low diversity of six taxa or less. The diversity rose to a maximum in the Santacrucian SALMA (Fig. 1a). The Colhuehuapian SALMA provided four taxa and two in the Friasian. The Colloncuran and the Laventan SALMAs were represented by one and two taxa respectively. During the Chasicoan there was one species and four in the

Huayquerian (Fig. 1a). The number of species fell to one in the Montehermosan and the Chapadmalalan SALMAs. By the Barrancalobian the Hathliacynidae seem definitely extinct. The carnivorous Didelphoidea appear in the fossil record by the Huayquerian with five taxa (Fig. 1a). During the Montehermosan there were six species present and nine in the Chapadmalalan. After that, a strong decrease in the species richness was recorded with two species in the Barrancalobian, one in the Vorohuean and the Sanandresian. From the Ensenadan to the Platan, non-carnivorous didelphoids were recorded. In the Recent, a new rise in the species richness is recorded with nine taxa (Fig. 1a).

In general, the species of the Hathliacynidae were of medium size and ranged between 2 kg and 10 kg in body mass (Fig. 1b). On the contrary, the majority of the Didelphoidea weighed below 2 kg in body weight (see Electronic Supplementary Information). However, during the period of coexistence, both groups overlaped in the small size range (Fig. 1b). The hathliacynids involved in that overlap are *Borhyaenidium musteloides*, *B. altiplanicus*, *B. riggsi*, *Notyctis ortizi,* and *Notocynus hermosicus* (Table 1). The didelphoids are *Thylophorops perplanus*, *Hyperdidelphys pattersoni,* and *Hyperdidelphys dimartinoi* (Table 1).

Geographic Distribution The geographic distribution of the coeval species is sympatric in few taxa (see Elecronic Supplementary Information). *Borhyaenidium musteloides* is known from Huayquerian levels of the Epecuén Formation in La Pampa Province, Argentina (Marshall 1981), while *B. riggsi* comes from the Montehermosan levels of the Corral Quemado Formation, Catamarca Province (Marshall 1981). The specimens of *B. altiplanicus* were exhumed from the Huayquerian levels of the Mauri VI Formation, La Paz, Bolivia (Villarroel and Marshall 1983). *Notocynus hermosicus* is known from Monte Hermoso locality in Buenos Aires Province, while *Noticitis ortizi* come from the Ituzaingó Formation (Entre Ríos Province). Regarding the geographic distribution of didelphoids, *Hyperdidelphys pattersoni* is known from the Huayquerian and the Montehermosan beds of Catamarca and La Pampa provinces (Goin and Pardiñas 1996). *Hyperdidelphys dimartinoi* comes from Chapadmalalan beds of Buenos Aires Province. *Thylophorops perplanus* is known from the Montehermosan levels of Buenos Aires Province. In summary, only in Buenos Aires Province were sympatric species recorded for the Huayquerian (*B. musteloides* and *H. pattersonii*) and the Montehermosan (*N. hermosicus* and *T. perplanus*) stages.

Diet A PCA were performed using the variance-covariance matrix of all ratios (Table 1). Three components was extracted that explain 98.71 % of the variance among all taxa (Table 2). PC1 accounts for the size effect. Most of the size-independent morphological variation is explained by PC2 and to a lesser degree by PC3. The variable loadings show a strong correlation between the RPS and the PC1, which is expected because it is a size dependent ratio. The RGA is highly correlated with the PC2 (Table 2) as well as RBL. These variables are opposite in sign and explain the major variance along the PC2 (Fig. 2). The PS and the LP/LM are slightly correlated with the PC2; however, they are strongly correlated with the PC3 (Table 2). The morphospaces defined by PC1-2 and PC2-3 show a clear segregation of the hathliacynids from the didelphoids (Fig. 2a–b). In the former, the Hathliacynidae are confined to the left lower corner of the graph. An exception is *Acyon myctoderos,* which is located in the right lower corner. This fact reflects the high body mass of this species, which is the largest hathliacynid (Table 1). The Didelphoidea occupy the left and right upper corners of the graph (Fig. 2). On the space defined by PC2-3, the hathliacynids occupy the left part of the graph while didelphoids are located on the right side with the exception of *Lutreolina crassicaudata* (Fig. 2b). PC2 again separates the two groups while PC3 accounts for much of the within group variance. In relation to the contribution of ratios to the variance, RGA and RBL clearly define the taxonomic groups. Hathliacynids are characterized by large relative blades and small grinding areas in their carnassials teeth while the didelphoids are characterized by short relative blades and moderate to large grinding areas (Fig. 2a–b). The morphological variation within Hathliacynidae is low and only *A. myctoderos* constitutes an outlier in the morphospace. Contrary to this, the variation within the Didelphoidea is large. The species of *Thylophorops* are distanced from the remaining didelphoids by their large relative grinding areas, short relative blades lengths, and short and massive lower premolars. The species of *Didelphis* and *Philander* are characterized by the presence of moderate grinding areas, short relative blades lengths, and large premolars. The species of *Hyperdidelphys*, *Thylatheridium*, *Sparassocynus,* and *Hesperocynus* are characterized by having moderate grinding areas, short relative blades, and short lower premolars.

The dietary classification based on the RGA ratio allowed identifying the Hathliacynidae as hypercarnivores (Table 1). The Didelphoidea result in being mainly classified as mesocarnivorous with the exception of the genus *Thylophorops*, a hypocarnivorous taxon (Table 1). These results are interesting in light of the PCA because the hathliacynids are well segregated from didelphoids and, the species of *Thylophorops* are clearly separated from the remaining didelphoids. The mesocarnivorous didelphoids are a group highly variable in the PCA with at least two subcategories.

In short, the PCA and the RGA suggest that the Hathliacynidae and the Didelphoidea constitute two clearly

Table 1 Raw data used in the morphospace analysis

Taxon	Age	BM	RGA	RPS	PS	LP/LM	RBL	DIET
Didelphidae								
Didelphis albiventris	Rec	0.90	0.61	1.30	0.21	1.10	0.61	Meso
Didelphis marsupialis	Rec	1.10	0.65	1.45	0.26	0.93	0.53	Meso
Didelphis aurita	Rec	1.16	0.63	1.42	0.22	1.10	0.60	Meso
Didelphis imperfecta	Rec	0.90	———	———	———	———	———	Meso
Philander frenatus	Rec	0.39	———	———	———	———	———	Meso
Philander mcilhenyii	Rec	0.29	———	———	———	———	———	Meso
Philander opossum	Rec	0.75	0.55	1.25	0.31	0.88	0.62	Meso
Chironectes minimus	Rec	0.94	0.72	2.29	0.65	0.76	0.65	Meso
Lutreolina crassicaudata	Rec	0.40	0.57	3.28	0.48	0.87	0.75	Meso
Didelphis crucialis	Chap	0.62	0.63	1.63	0.43	0.97	0.58	Meso
Didelphis reigi	Chap	0.62	0.63	1.54	0.30	1.15	0.60	Meso
Didelphis solimoensis	Huay	0.40	0.63	1.79	0.40	1.04	0.56	Meso
Lutreolina tracheia	Mont-Chap	0.30	0.67	3.07	0.38	0.89	0.61	Meso
Thylatheridium hudsoni	Huay	0.17	0.61	2.74	0.70	0.54	0.63	Meso
Thylatheridium pascuali	Chap	0.25	0.55	2.16	0.69	0.54	0.66	Meso
Thylatheridium cristatum	Chap	0.20	0.55	3.31	0.71	0.54	0.68	Meso
Thylophorops chapadmalensis	Chap-BaLob	3.70	0.89	2.07	0.49	0.83	0.57	Hypo
Thylophorops perplanus	Huay	1.50	0.95	2.69	0.61	0.73	0.53	Hypo
Thylophorops lorenzinii	SanAnd	8.60	1.15	2.00	0.52	0.60	0.44	Hypo
Hyperdidelphys inexpectata	Mont-Chap	0.99	0.53	2.37	0.64	0.56	0.69	Meso
Hyperdidelphys parvula	Mont-Chap	0.98	0.67	2.25	0.46	0.58	0.60	Meso
Hyperdidelphys pattersoni	Huay-Mont	1.16	0.55	1.57	0.52	0.62	0.68	Meso
Hyperdidelphys dimartinoi	Huay	2.07	———	———	———	———	———	Meso
Sparassocynidae								
Sparassocynus derivatus	Chap-Vor	0.36	0.62	3.02	0.87	0.58	0.54	Meso
Sparassocynus bahiai	Mont	0.37	0.54	2.19	0.59	0.54	0.63	Meso
Sparassocynus heterotropicus	Huay	0.32	0.56	2.61	0.73	0.56	0.75	Meso
Hesperocynus dolgopolae	Huay	0.30	0.61	2.12	0.63	0.62	0.57	Meso
Hathliacynidae								
Acyon myctoderos	Lave	12.70	0.27	4.24	0.39	0.79	0.80	Hyper
Acyon tricuspidatus	San	6.24	0.30	1.52	0.35	0.77	0.81	Hyper
Acyon herrerae	Col	7.84	0.30	1.18	0.28	0.93	0.78	Hyper
Borhyaenidium musteloides	Huay	1.56	0.30	2.00	0.41	0.91	0.83	Hyper
Borhyaenidium altiplanicus	Huay	1.16	0.30	1.90	0.41	0.96	0.71	Hyper
Borhyaenidium riggsi	Chap	1.98	———	———	———	———	———	Hyper
Chasicostylus castroi	Chas	6.74	———	———	———	———	———	Hyper
Cladosictis centralis	Col	3.40	0.17	1.90	0.43	0.83	0.75	Hyper
Cladosictis patagonica	Col-Fri	4.68	0.17	1.88	0.42	0.85	0.78	Hyper
Notictis ortizi	Huay	0.89	0.30	2.08	0.50	0.69	0.90	Hyper
Notocynus hermosicus	Mont	1.77	0.33	1.66	0.40	0.80	0.90	Hyper
Perathereutes pungens	San	1.10	0.34	1.75	0.33	0.97	0.77	Hyper
Pseudonotictis pusillus	San	1.20	0.30	1.55	0.38	0.86	0.90	Hyper
Pseudonotictis chubutensis	Coll	0.89	———	———	———	———	———	Hyper
Sipalocyon gracilis	San-Fri	3.15	0.33	1.60	0.39	0.88	0.85	Hyper
Sipalocyon externa	Col	2.48	———	———	———	———	———	Hyper
Sipalocyon obusta	San	2.81	———	———	———	———	———	Hyper

AGE South American Land Mammal Age of the measured specimen; *BM* body mass (kg); *RGA* relative grinding area; *RPS* relative premolar size; *PS* premolar shape; *LP/LM* relative premolar length; *RBL* relative blade length. Diet abbreviation correspond to hypercarnivore, mesocarnivore, and hypocarnivore. The empty cells indicate the species that were only used in the diversity count and body mass analysis

Table 2 Variable loadings for principal components analysis (PCA). Under the heading for each component, in parentheses, is the percentage of the total variance it explains. For explanation of abbreviations, see Table 1

	PC1 (82,42)	PC2(10,363)	PC3(5,9387)	PC4(0,75915)	PC5(0,51043)
RGA	0.0467	0.843	0.279	−0.213	0.403
RBL	−0.010	−0.416	−0.182	−0.292	0.841
RPS	0.979	−0.109	0.165	−0.025	−0.014
PS	0.140	0.235	−0.534	0.754	0.263
LP/LM	−0.135	−0.222	0.758	0.546	0.243

different morphotypes. These differences in the morphofunctional traits probably represent different dietary specializations.

Despite the overlap in the range of small sizes recorded in the Huayquerian and the Montehermosan (Fig. 1a), any dietary superposition was evident between sympatric species. The results of PCA with all morphofunctional variables show a complete separation in the hathliacynid and the didelphoid morphospaces (Fig. 2a–b). All Hathliacynidae showed the morphological characteristics of the hypercarnivores, while Didelphoidea showed those of the meso- and hypocarnivores.

Discussion

There is a positive correlation between the number of taxa and the number of localities per age that affects the sample size in

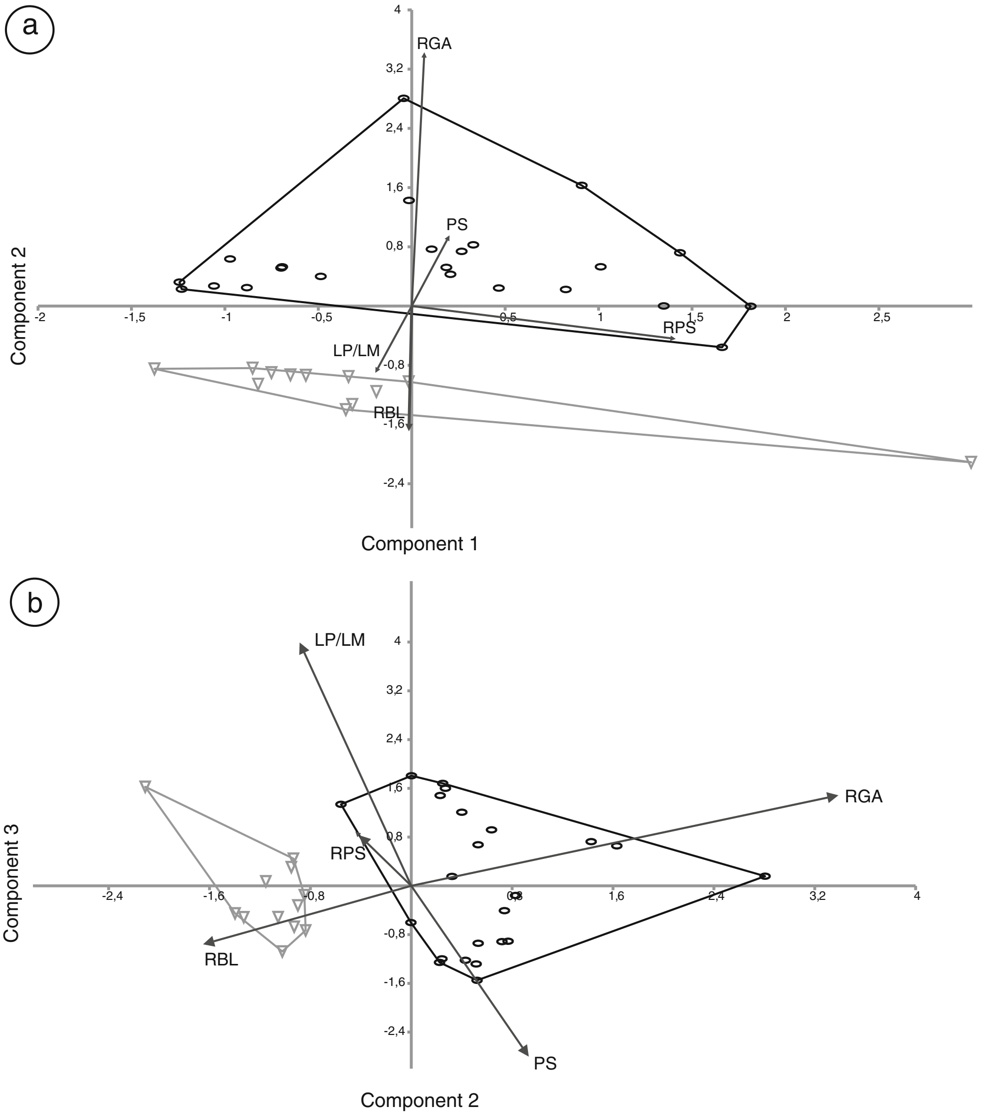

Fig. 2 Plot of principal component 1 versus principal component 2 (**a**) and principal component 2 versus principal component 3 (**b**) for the principal components analysis performed using all ratios, with taxa distinguished by taxonomic group. Ref: Hathliacynidae (*triangle*) and Didelphoidea (*oval*)

the diversity analysis of the Cenozoic South American fossil record (Prevosti et al. 2013). Several mammalian assemblages are only partially known (e.g., Mayoan Age) and others have mostly regional distributions (Patagonian assemblages of the Miocene). Such biases contribute to the incompleteness of the South American fossil record and obviously affect the interpretation of the diversity patterns.

Taken into account the biases in the fossil record, the origin of Hathliacynidae can be traced back to the middle-late Eocene (Forasiepi 2009). The species richness of the family was low (less than two species per age: Zimicz 2012) until the early-middle Miocene (Santacrucian) when the Hathliacynidae rose to their acme. The low diversity of the family recorded from the Colloncuran to the Chasicoan is probably due to biases in the fossil record. The number of sites of the Santacrucian and the Huayquerian is twice or more than that of any age of the mentioned span (Prevosti et al. 2013: Table 1). Based on this, the definite decline of Hathliacynidae is considered to begin after the Huayquerian. Although the last record of the family is in the Chapadmalalan (early Pliocene; Fig. 1a), a well-sampled land mammal-bearing age, the span from Barrancalobian to Sanandresian is represented by few localities, so the diversity of hathliacynids could increase with new collections (expeditions or prospections) from this time interval. The first carnivorous didelphoids were recorded in the Huayquerian SALMA. However, the high initial diversity (five species and five genera) is suggestive of a bias in the previous record of the group. The group increases their diversity until the Chapadmalalan SALMA (Fig. 1a). Between the Barrancalobian and the Platan, the diversity of carnivorous didelphoids falls drastically from nine species to less than two. As it occurs with the hathliacynids, this drop could well be exaggerated by a biases in the fossil record. A new rise in the Recent is recorded with nine species of carnivorous didelphoids. Despite the bias recorded for the Barrancalobian to Sanandresian span, the low diversity of both metatherian groups could be related to a strong environmental change promoted by the onset of the Northern Hemisphere Glaciation (see below). The joined diversity curves of the hathliacynids and didelphoids shows double wedge geometry. Such a pattern could be the result of negative interactions between clades (competitive displacement or predation) or the result of chance or environmental changes (Van Valkenburgh 1999).

From a methodological point of view, the results of PCA corroborate previous studies that emphasize the utility of simple linear measures on the dietary inference of small- to medium-sized carnivores (Van Valkenburgh 1991; Friscia et al. 2007). This study shows that the relative grinding areas and the relative blade lengths are well discriminant ratios in extinct taxa as suggested by Friscia et al. (2007) and can be used to determine the diet of extinct carnivores. Other variables such as premolar shape and relative premolar length are less correlated with dietary preferences but also contribute to the total morphological variance (Fig. 2a). The analysis of RGA shows that the Hathliacynidae were restricted to hypercarnivore niches while the didelphoids occupied the niches of meso- and hypocarnivores. Although the PCA does not discriminate between all dietary categories, it shows a clear separation between hathliacynids and didelphoids (Fig. 2a–b). Additionally, a clear separation is evident between the species of *Thylophorops* (the only hypocarnivores from the RGA analysis) and the remaining didelphoids. Some didelphoids fall in the intermediate zone between the two taxonomic groups. *Lutreolina crassicaudata* is closer to the hathliacynids zone (Fig. 2b). The RGA value for *Lutreolina* is in the boundary between meso- and hypercarnivory (Table 1), so probably their classification as mesocarnivores responds to a inability of RGA to discriminate in the boundaries of the categories. Despite the dietary consideration of the species, the multivariate analysis shows that the two metatherian groups clearly diverged in their morphologies and any overlap is recorded in their morphofunctional traits.

Previous studies on the decline and extinction of Hathliacynidae conferred a major role to the ecological interplay with medium-sized didelphids, mustelids, and canids (Marshall 1978; Goin 1989; Goin and Pardiñas 1996). Recently, Prevosti et al. (2013) demonstrated that probably none ecological displacement did take place between Sparassodonta and Carnivora. In regard to the interaction between the hathliacynids and the didelphoids, the results of PCA do not support any competitive displacement or passive replacement. Diet and body mass played a crucial role in the niche differentiation of sympatric species of carnivorous metatherians in South America. The same pattern was observed in the case of the interaction between the placental carnivores and the sparassodonts (Prevosti et al. 2013). Contrary to what occurred with the placental carnivores, the didelphoids never occupied the niche of hypercarnivores even after the Chapadmalalan SALMA when the last hathliacynid was recorded. Probably the didelphoids were poor competitors with the successful placental carnivores that occupied the hypercarnivore niche after the extinction of the sparassodonts (Prevosti et al. 2013). This fact probably reflects a metabolic constraint of the metatherians to survive in cold environments (see below). With respect to the potential intra-guild predation mentioned earlier, although the body mass of hathliacynids allows them to prey on didelphoids of similar and lower weight, a closer examination of the craniodental variables of both groups (Van Valkenburgh and Koepfli 1993; Meachen-Samuels and Van Valkenburgh 2009) is needed to clarify this aspect.

The hathliacynids originated in the Paleogene (probably middle Eocene: Forasiepi 2009) when greenhouse condition prevailed in the global climates. A minor component of the carnivoran mammalian fauna persisted (Forasiepi 2009; Zimicz 2012; Prevosti et al. 2013) and survived the global climatic crash of the Eocene-Oligocene boundary that caused several extinction and turnovers events around the world (Stehlin 1909; Prothero 1994; Meng and McKenna 1998; Goin et al. 2010). The Neogene climate represents the transition from the greenhouse climate of the Paleogene to the icehouse climate of the Quaternary (Bruch et al. 2007). After the Mi1 glaciation, the Miocene climates were distinguished by the extreme climatic optima (Middle Miocene Climatic Optimum) alternating with major long-term climatic cooling (Middle Miocene Transition). Both events determine the evolution of hathliacynid diversity promoting the acme of the clade and probably the gradual decrease in the species richness, respectively. The final step in the evolution of the hathliacynids occurred in the Mio-Pliocene Transition. The cooling trend established with the Middle Miocene Transition was sustained throughout the remaining of the Miocene until the early Pliocene (Flower and Kennett 1994; Lewis et al. 2008; Filippelli and Flores 2009). The onset of the Northern Hemisphere Glaciation at the middle-late Pliocene imposed a new and strong fall in global temperatures (Filippelli and Flores 2009). Such freezing conditions probably caused the final extinction of Hathliacynidae; their last record occurs during the Chapadmalalan SALMA with *Borhyaenidium riggsi.* Suggestively, the extinction of the hathliacynids was coeval with a local faunal turnover that took place at the mid-Pliocene. Thirty-seven percent of all genera and 53 % of all species became extinct between the older Chapadmalalan and the younger Barrancalobian chronostratigraphic units (Vizcaíno et al. 2004). One of the most striking features of the Barrancalobian fauna is the absence of medium and large carnivores (Vizcaíno et al. 2004). With the exception of *Sparassocynus derivatus,* a small mesocarnivorous didelphoid, no other vertebrate carnivore is recorded. The virtual absence of carnivorous taxa and especially the absence of the hypercarnivores shows the strong influence that climatic deterioration would cause on the guild of the highly specialized carnivores (Van Valkenburgh 2007). In this sense, it is important to note that carnivory is a food strategy related with high metabolism in eutherians. Marsupials have low basal metabolic rates (McNab 2005); consequently, the high cost of thermoregulation has important consequences on their overall biology including their resistance to cold environments and the potential food resources that can be exploited by them (McNab 2005, 2008). If all metatherians have a similar energetic metabolism compared to living marsupials, then the extinction of the Hathliacynidae seems to have occurred as the result of the sustained drop in ambient temperatures during most of the 10 Ma, from the middle Miocene to middle Pliocene (Zachos et al. 2001). The climatic changes involved in the mid-Pliocene faunal turnover probably accelerated an extinction process that was triggered by the Middle Miocene Transition. The impact of cold climates on the carnivorous metatherian is evident looking at the Paleogene faunas. In South American landscapes, where metatherians coexisted with placentals at least since the early Cenozoic (Bond et al. 1995; Gelfo et al. 2009; Woodburne et al. 2014), hypercarnivory was successfully exploited during the greenhouse period (Zimicz 2012). After the Middle Miocene Transition, when temperatures decline progressively, hypercarnivorous metatherian were no longer present and the only carnivorous marsupials recorded were the meso- and hypocarnivorous didelphoids.

The carnivorous Didelphoidea appeared in the Huayquerian stage with a diversity of five species that represent five genera. This high initial diversity suggests a bias in the fossil record probably related to the scarce number of sites between the Colloncuran and Chasicoan ages. Considering that the origin of the Didelphoidea has been estimated as a late Eocene event (Steiner et al. 2005), it is probable that new paleontological prospecting in the early-middle Miocene beds of South America will result in an increase in the diversity of carnivorous didelphoids. Taking into account the known record of carnivorous didelphoids, the success of this group is strongly evident being represented by nine species and five genera. As mentioned above, the didelphoids had meso- and hypocarnivorous diets even after the extinction of Hathliacynidae. The generalist nature of their feeding requirements probably allows them to survive in the changing world of the Pliocene-Pleistocene Transition, characterized by a glacial-interglacial cyclic event (Tiedemann et al. 1994). The onset of the Northern Hemisphere Glaciation and the Chapadmalalan-Barrancalobian extinction event (Vizcaíno et al. 2004) probably had a strong impact on the carnivorous didelphoid fauna, promoting a taxonomic and functional turnover (sensu Blois and Hadly 2009). The genera *Hyperdidelphys* and *Thylatheridium* became extinct after the Chapadmalalan SALMA. The only Chapadmalalan genera that survive into Barrancalobian were *Thylophorops* and *Sparassocynus,* each represented by one species. However, none of them survived into the Pleistocene. The last *Sparassocynus* (*S. derivatus*) was recorded in the Vorohuean, while the last *Thylophorops* (*T. lorenzinii*) was recovered from the Sanandresian subage of the Marplatan Age (Goin et al. 2009). The extinction of *Thylophorops* may be understood as a competitive interaction with placental hypocarnivores present in South America since the Chapadmalalan (see Prevosti et al. 2013). The post-Chapadmalalan didelphoids were all mesocarnivorous species (Table 1). The post-Pleistocene record of carnivorous didelphoids corresponds exclusively to members of this modern fauna. The genera *Didelphis* and *Lutreolina* have their oldest record in the Huayquerian and Montehermosan, respectively (Goin and Pardiñas 1996), and both survived into the present. In this sense, it is important to note that the recent radiation of carnivorous didelphoids has its origin in the late Miocene and the main components of the living fauna (e.g., *Didelphis* and *Lutreolina*) survived through the climatic crash of mid-late Pliocene.

In summary, the extinction of Hathliacynidae, a clade that originated during a greenhouse world, is related it seems with the sustained drop in global temperatures since the middle Miocene. Contrary to this, didelphoid carnivores survived and radiated in an icehouse world. Interesting, the generalist Didelphimorphia that coexisted with placental carnivores, presumably were at no physiological disadvantage, having similar metabolic rates to generalist placental species (McNab 2005; Cooper et al. 2009). As suggested by the fossil record, the extinction was the cost of the highly specialized carnivory for metatherians in South America (Forasiepi et al. 2009). The global cooling trend starting in the middle Miocene seems to be the major selective pressure acting on the carnivorous metatherian faunas. The application of modern techniques for estimating the physiology of fossil vertebrates (e.g., Chinsamy et al. 1995; Eagle et al. 2009; Köhler and Moyá-Solá 2009) can provide more clues to the ecological evolution of metatherians in South America.

Conclusions

The actual fossil record of the Hathliacynidae and the carnivorous Didelphoidea suggests that no competitive displacement or passive replacement took place between these groups of carnivorous metatherians during the Neogene. The Hathliacynidae were exclusively hypercarnivores of small- and medium-sized, while the didelphoids were restricted to meso- and hypocarnivorous diets even after the extinction of the hathliacynids. This dietary segregation contradicts the hypothesis of passive replacement of Hathliacynidae by the carnivorous Didelphoidea. The extinction of the first (Hathliacynidae), seems to be triggered by the Middle Miocene Transition that promoted a sustained decline in the global temperatures during more than 10 Ma. The onset of Northern Hemisphere Glaciation was probably the “death blow” for the Hathliacynidae. The climatic crash involved in the Chapadmalalan-Barrancalobian event caused a taxonomical turnover within the carnivorous Didelphoidea. The ancient genera *Hyperdidelphys*, *Thylophorops*, *Sparassocynus*, *Hesperocynus,* and *Thylateridium* became extinct before the Plio-Pleistocene transition. The late fossil record of this group corresponds entirely to members of the modern fauna of didelphoids.

Acknowledgments Many thanks to Yamila Gurovich for language correction and critical reading of the manuscript. Many thanks also to Francisco Prevosti for the critical reading of the manuscript. Thanks to David Flores and Itatí Olivares for allowing me to study the mammal collection at MACN and MLP, respectively. A special thanks to John Wible, Marcos Ercoli, and the two anonymous reviewers who highly improved this manuscript with their comments. The present study was supported by a postdoctoral research grant of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) to N. Zimicz.

References

Alberdi MT, Ortiz Jaureguizar E, Prado JL (1995) Evolución de las comunidades de mamíferos del Cenozoico superior de la Provincia de Buenos Aires, Argentina. Rev Esp Pal 10: 30–36

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

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

Benton MJ (1983) Dinosaur success in the Triassic: a noncompetitive ecological model. Quart Rev Bio 58: 29–55

Bond M (1986) Los carnívoros terrestres fósiles de Argentina: resumen de su historia. Actas IV Congr Arg Pal Bioest 2: 167–171

Bond M, Carlini AA, Goin FJ, Legarreta L, Ortiz-Jaureguizar E, Pascual R, Uliana MA (1995) Episodes in South American land mammal evolution and sedimentation: testing their apparent concurrence in a Paleocene succession from central Patagonia. Actas VI Congr Arg Pal Bioest: 47–58

Blois JL, Hadly EA (2009) Mammalian response to Cenozoic climatic change. Annu Rev Earth Planet Sci 37:181–208

Bruch AB, Uhl D, Mosbrugger V (2007) Miocene climate in Europe: patterns and evolution a first synthesis of NECLIME. Palaeogeogr Palaeoclimatol Palaeoecol 253: 1–7

Carbone C, Teacher A, Rowcliffe JM (2007) The costs of carnivory. PLOS Biol 5(2): 363–368

Chinsamy A, Chiappe LM, Dodson P (1995) Mesozoic avian bone microstructure: physiological implications. Paleobiology 21:561–574

Cione AL, Tonni EP (2005). Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina. In: de Barrio RE, Etcheverry RO, Caballé MF, Llambías E (eds) Geología y Recursos Minerales de la Provincia de Buenos Aires. XVI Congreso Geológico Argentino, La Plata, pp 183–200

Cooper CE, Whiters PC, Cruz-Neto AP (2009). Metabolic, ventilatory, and hygric physiology of the gracile mouse opossum (*Gracilinanus agilis*). Physiol Biochem Zool 82(2):153–62

Eagle RA, Schauble EA, Tripati AK, Tutken T, Hulbert RC, Eiler JM (2009) Body temperatures of modern and extinct vertebrates from 13C-18O bond abundances in bioapatite. Proc Natl Acad Sci USA 107(23): 10377–10382

Ercoli MD (2010) Estudio de los hábitos locomotores en los Borhyaenoidea (Marsupialia, Sparassodonta) de la Formación Santa Cruz (Mioceno inferior de la provincia de Santa Cruz) a partir de la diferenciación morfológica en depredadores vivientes. Dissertation, Universidad Nacional de Buenos Aires

Ercoli MD, Prevosti FJ, Alvarez 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

Filippelli GM, Flores JA (2009) From the warm Pliocene to the cold Pleistocene: a tale of two oceans. Geology 37:959–960

Flores DA (2009) Phylogenetic analyses of postcranial skeletal morphology in dildelphid marsupials. Bull Mus Nat Hist 320: 1–81

Flower BP, Kennett JP (1994) The middle Miocene climate transition: east Antarctic ice sheet development, deep ocean circulation and global carbon cycling. Palaeogeogr Palaeoclimatol Palaeoecol 108: 537–555

Flynn JJ, Swisher III CC (1995) Cenozoic South American land mammal ages: correlation to global geochronologies. In: Berggren WA, Kent DV, Aubry MP, Hardenbol J (eds) Geochronology, Time Scales and Global Stratigraphic Correlation. Soc Sedimentol Geol Spec Pub 54: 317–333

Forasiepi AM (2009) Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. Monogr Mus Arg Cs Nat n s 6: 1–174

Forasiepi AM, Goin FJ, Martinelli AG (2009) Contribution to the knowledge of the Sparassocynidae (Mammalia, Metatheria, Didelphoidea), with comments on the age of the Aisol Formation (Neogene), Mendoza province, Argentina. J Vertebr Paleontol 29(4):1252–1263

Friscia AR, Van Valkenburgh B, Biknevicius AR (2007) An ecomorphological analysis of extant small carnivores. J Zool 272: 82–100

Gelfo JN, Goin FJ, Woodburne MO, Muizon C de (2009) Biochronological relationships of the earliest South American Paleogene mammalian faunas. Palaeontology 52(1): 251–269

Goin FJ (1989) Late Cenozoic South American marsupial and placental carnivores: changes in predator–prey evolution. Abstr V Int Ther Cong 1: 271–272

Goin FJ (1991) Los Didelphoidea (Mammalia, Marsupialia) del Cenozoico Tardío de la Región Pampeana. Dissertation, Universidad Nacional de La Plata

Goin FJ (1995) Los marsupiales. In: Alberdi MT, Leone G, Tonni EP (eds) Evolución Biológica y Climática de la Región Pampeana durante los Últimos Cinco Millones de Años. Un ensayo de Correlación con el Mediterráneo Occidental Monografías del Museo Nacional de Ciencias Naturales, Madrid, pp 165–179

Goin FJ, Abello A, 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, Montalvo C (1988) Revisión sistemática y reconocimiento de una nueva especie del género *Thylatheridium* Reig (Marsupialia, Didelphidae). Ameghiniana 25:161–167

Goin FJ, Pardiñas UFJ (1996) Revisión de las especies del género *Hyperdidelphys* Ameghino, 1904 (Mammalia, Marsupialia, Didelphidae), su significado filogenético, estratigráfico y adaptativo en el Neógeno del Cono Sur Sudamericano. Est Geol 52: 327–359

Goin FJ, Zimicz N, de los Reyes M, Soibelzon L (2009) A new large didelphid of the genus *Thylophorops* (Mammalia: Didelphimorphia: Didelphidae), from the late Tertiary of the Pampean Region (Argentina). Zootaxa 2005: 35–46

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

Jansa SA, Forsman JF, Voss RS (2006) Different patterns of selection on nuclear genes IRBP and Dmpl affect the efficiency but not the outcome of phylogeny estimation for didelphids marsupials. Mol Phylogenet Evol 38: 363–380

Jansa SA, Voss RS (2005) Phylogenetic relationships of the marsupial genus *Hyladelphys* based on nuclear gene sequences and morphology. J Mammal 86:853–865

Köhler M, Moyá-Solá S (2009) Physiological and life history strategies of a fossil large mammal in a resource-limited environment. Proc Natl Acad Sci USA 106 (48): 20354–20358

Krause DW (1986) Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. In: Flanagan KM, Lillegraven JA (eds) Vertebrates, Phylogeny and Philosophy. Contrib Geol Univ Wyoming Spec Pap 3: 119–130

Lewis AR, Marchanta DR, Ashworthc AC, Hedenäs L, Hemmingf SR, Johnsong JV, Lengh ML, Machlusf ML, Newtoni AE, Rainej JI, Willenbringk JK, Williamsl M, Wolfem AP (2008) Mid-Miocene cooling and the extinction of tundra in continental Antarctica. Proc Natl Acad Sci USA 105 (31): 10677–10680

Madden RH, Kay RF, Vucetich MG, Carlini AA (2010) Gran Barranca: a 23-million-year record of middle Cenozoic faunal evolution in Patagonia. 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, Cambridge, pp 423–439

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

Marshall LG (1977b) Evolution of the carnivorous adaptative zone in South America. In: Hecht MK, Goody PC, Hecht BM (eds) Major Patterns in Vertebrate Evolution. Plenum Press, New York, pp 709–722

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

Marshall LG (1979) Review of the Prothylacyninae, an extinct subfamily of South American "dog-like" marsupials. Fieldiana Geol n ser 3: 1–50

Marshall LG (1981) Review of the Hathlyacyninae, an extinct subfamily of South American "dog-like" marsupials. Fieldiana Geol n ser 7: 1–120

Marshall LG, Cifelli RL (1990) Analysis of changing diversity patterns in Cenozoic Land Mammal Age faunas, South America. Palaeovertebrata 19: 169–210

Marshall LG, Hoffstetter R, Pascual R (1983) Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. Palaeovertebrata mém extra 1983: 1–93

McNab BK (2005) Uniformity in the basal metabolic rate of marsupials: its causes and consequences. Rev Chilena Hist Nat 78: 183–198

McNab BK (2008) An analysis of the factors that influence the level and scaling of mammalian BMR. Compa Biochem Physiol Part A 151: 5–28

Meachen-Samuels J, Van Valkenburgh B (2009) Craniodental indicators of prey size preference in the Felidae. Biol J Linn Soc 96**:** 784–799

Meng J, McKenna MC (1998) Faunal turnover of Palaeogene mammals from the Mongolian Plateau. Nature 394: 364–367

Muizon C de (1991) La fauna de mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucía) Bolivia. En Suarez-Soruco R (ed) Fósiles y Facies de Bolivia, Volumen, I Vertebrados. Revista Técnica de Yacimientos Petrolíferos Fiscales de Bolivia 12:575–624

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

Muizon C de, 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 Marsupial Carnivores. CSIRO Publishing, Collingwood, pp 43–62

Ortiz Jaureguizar E (1989) Analysis of the compositional changes of the South American mammal fauna during the Miocene-Pliocene (Panaraucanian Faunistic Cycle). Abstr V Int Ther Cong 1: 277–278

Ortiz Jaureguizar E (2001) Cambios en la diversidad de los mamíferos sudamericanos durante el lapso Mioceno Superior-Holoceno: el caso pampeano. In: Meléndez G, Herrera Z, Delvene G, Azanza B (eds) Los Fósiles y la Paleogeografía. Publ del SEPAZ Univ Zaragoza 5: 397–403

Palmqvist P, Martínez-Navarro B, Pérez-Claros JA, Torregrosa V, Figuerido B, Jiménez-Arenas JM, Patrocinio Espigares M, Ros-MontoyaS, De Renzi M (2011) The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. Quaternary Internatl 12: 1–19

Pascual R, Bond M (1986) Evolución de los marsupiales cenozoicos de Argentina. Actas IV Congr Arg Pal Bioest 2: 143–150

Pascual R, Ortiz Jaureguizar E (1990) Evolving climates and mammal faunas in Cenozoic South American. J Hum Evol 19: 23–60

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

Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast A, Erk FC, Glass B (eds) Evolution, Mammals and Southern Continents. State University of New York Press, New York, pp 274–309

Prevosti FJ, Forasiepi AM, Ercoli MD, Turazzini GF (2012) Chapter 11: 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: High Latitude Paleocommunities Of The Santa Cruz Formation. Cambridge University Press, Cambridge, pp 173–193

Prevosti FJ, Forasiepi AM, Soibelzon LH, Zimicz N (2009) Sparassodonta vs. Carnivora: ecological relationships between carnivorous mammals in South America. Abstr X Int Mamm Congr 1: 61–62

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

Prothero DR (1994) The late Eocene-Oligocene extinctions. Annu Rev Earth Planet Sci 22:145–165

Ré G, Bellosi E, Heizler M, Vilas J, Madden RH, Carlini AA, Kay RF, Vucetich, MG (2010) A geochronology for the Sarmiento Formation at Gran Barranca. 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, Cambridge, pp 46–60

Reig OA (1981) Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. Monographíae Naturae 1: 1–162

Reig OA, Simpson GG (1972) *Sparassocynus* (Marsupialia, Didelphidae), a peculiar mammal from the late Cenozoic of Argentina. J Zool 167:511–539

Rosenzweig ML, McCord RD (1991) Incumbent replacement: evidence for long-term evolutionary progress. Paleobiology 17: 202–213

Savage RJG (1977) Evolution of carnivorous mammals. Palaeontology 20: 237–271

Sepkoski JJr (1996) Patterns of Phanerozoic extinctions: a perspective from global databases. In: Walliser H (ed) Global Events and Event Stratigraphy. Springer, Berlin, pp 35–52

Sepkoski JJr (2001) Competition in evolution. In: Briggs DEG, Crowther PR (eds) Paleobiology II. Blackwell Sciences, Oxford, pp 171–175

Sepkoski JJr, McKinney FK, Lidgard S (2000) Competitive displacement among post-Paleozoic cyclostome and cheilostome bryozoans. Paleobiology 26: 7–18

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

Simpson GG (1969) South American mammals. In: Fitkau EJ, Illies J, Klinge H, Schwabe GH, Sioli H (eds) Biogeography and Ecology in South America. N.V. Publishers, Netherlands, pp 876–909

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

Simpson GG (1974) Notes on Didelphidae (Mammalia, Marsupialia) from the Huayquerian (Pliocene) of Argentina. Am Mus Novitates 2559:1–15

Simpson GG (1980) Splendid Isolation. The Curious History of South American Mammals. Yale University Press, New Haven, 266 pp

Smith FA, Lyons KS, Ernest SKM, Jones KE, Kaufman DM, Dayan T, Marquet PA, Brown JH, Haskell JP (2003) Body mass of late Quaternary mammals. Ecology 84(12): 3403

Soibelzon LH, Prevosti FJ (2007) Los carnívoros (Carnivora, Mammalia) terrestres del Cuaternario de América del Sur. In: Pons GX, Vicens D (eds) Geomorfología Litoral i Quaternari. Homenatge a Joan Cuerda Barceló. Monografia de la Societat d'Història Natural, Palma de Mallorca, pp 49–68

Stehlin HG (1909) Remarques sur les faunules de mammiferes des couches eocenes et oligocenes du Bassin de Paris. Bull Soc Geol Fr 4(9):488–520

Steiner C, Tilak M, Douzery E, Catzeflis FM (2005) New data from a transthyretin nuclear intron suggest an Oligocene to Miocene diversification of living South America opossums. Mol Phylogenet Evol 35: 363–379

Szalay FS (1994) Evolutionary History of the Marsupials and Analysis of Osteological Characters. Cambridge University Press, Cambridge, 481 pp

Tiedemann R, Sarnthein M, Shackleton NJ (1994) Astronomic timescale for the Pliocene Atlantic δ18O and dust flux records of Ocean Drilling Program site 659: Paleoceanography 9: 619–638

Van Valkenburgh B (1991) Iterative evolution of hypercarnivory in canids (Mammalia: Carnivore): evolutionary interactions among sympatric predators. Paleobiology 17(4): 340–362

Van Valkenburgh B (1999) Major patterns in the history of carnivorous mammals. Annu Rev Earth Planet Sci 27: 463–493

Van Valkenburgh B (2007) Déjà vu: the evolution of feeding morphologies in the Carnivora. Integr Comp Biol 47: 147–163

Van Valkenburgh B, Koepfli KP (1993) Cranial and dental adaptations to predation in canids. Symp Zool Soc London 65: 15–37

Viera E, Astúa de Moraes D (2003) Carnivory and insectivory in Neotropical marsupials. In: Jones ME, Dickman C, Archer M (eds) Predators with Pouches: the Biology of Carnivorous Marsupials. CSIRO Publications, Collingwood, pp 271–284

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

Vizcaíno SF, Fariña RA, Zárate MA, Bargo MS, Schultz P (2004) Palaeoecological implications of the mid-Pliocene faunal turnover in the Pampean Region (Argentina). Palaeogeogr Palaeoclimatol Palaeoecol 213: 101–113

Werdelin L (1987) Jaw geometry and molar morphology in marsupial carnivores: analysis of a constraint and its macroevolutionary consequences. Paleobiology 13: 342–350

Woodburne M, Cione AL, Tonni, EP (2006) Central American Provincialism and the Great American Biotic Interchange. In: Carranza-Castañeda O, Lindsay EH (eds) Advances in Late Tertiary Vertebrate Paleontology in Mexico and the Great American Biotic Interchange. Publ Especial Inst Geol y Centro de Geociencias Univ Nac Autónoma México 4: 73–101

Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN, López GM, Iglesias A, Zimicz AN (2014) Paleogene Land Mammal Faunas of South America; a response to global climatic changes and indigenous floral diversity. J Mammal Evol 21: 1–73

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693

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