

# The Evolution of the Cenozoic Terrestrial Mammalian Predator Guild in South America: Competition or Replacement?

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**Abstract** South America was isolated from other continents during most of the Cenozoic, developing a singular mammalian fauna. In contrast to North America, Europe, Asia, and Africa, up to the late Neogene, the carnivore adaptive zone in South America was populated by crocodiles (Sebecidae), large snakes (Madtsoiidae), large birds (Phorusrhacidae), and metatherian mammals (Sparassodonta). Sparassodonta were varied and comprised a wide range of body masses ( $\approx 2$ –50 kg) and food habits. Their diversity decreased towards the late Miocene (Huayquerian Stage/Age) and the group became extinct in the “middle” Pliocene ( $\approx 3$  Ma, Chapadmalalan Stage/Age). Several authors have suggested that the cause of this decline and extinction was the ingression of carnivorans to South America (about 6–7 Ma ago), because they competed with the Sparassodonta; although this hypothesis has been criticized in recent years. With the intention of

testing the hypothesis of “competitive displacement,” we review the fossil record of South American Sparassodonta and Carnivora, collect data about diversity, estimate size and diet, and determine first and last appearances. The diversity of Sparassodonta is low relative to that of Carnivora throughout the Cenozoic with the early Miocene (Santacrucian Stage/Age) showing the greatest diversity with 11 species. In the late Miocene-middle Pliocene (Huayquerian Stage/Age), the fossil record shows overlap of groups, and the Sparassodonta’s richness curve begins to decline with the first record of Carnivora. Despite this overlap, carnivorans diversity ranged from four or fewer species in the late Miocene-Pliocene to a peak of around 20 species in the early Pleistocene (Ensenadan Stage/Age). Carnivora was initially represented by small-sized, omnivorous species, with large omnivores first appearing in the Chapadmalalan Stage/Age. Over this period, Sparassodonta was represented by large and small hypercarnivores and a single large omnivorous species. From this review of the fossil record, it is suggested that factors other than competitive displacement may have caused the extinction of the Sparassodonta.

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## Introduction

Competition and competitive displacement in the fossil record have attracted the attention of numerous researchers, aiming to analyze different cases in which one taxon is replaced by another, a pattern that is represented as a “double edge” in the fossil record (e.g., Benton 1983a; Krause 1986; Van Valkenburgh 1999). These studies

consider classical ecological pairs such as gastropods and brachiopods (Gould and Calloway 1980; Sepkoski 2001), basal archosauromorphs and dinosaurs (Brusatte et al. 2008; Langer et al. 2009), multituberculates and rodents (Krause 1986), creodonts and carnivorans (Van Valkenburgh 1999; Friscia and Van Valkenburgh 2010), among others. One intriguing case in South America is the replacement of mammalian carnivores during the late Miocene-Pleistocene: the metatherian sparassodonts (Order Sparassodonta) disappeared and the carnivorans (Order Carnivora) arrived in South America and diversified. The sparassodonts were a group of continental predators endemic to South America that lived during the Paleocene-middle Pliocene and that developed some ecomorphs comparable to carnivorans (see Marshall 1977, 1978, 1979, 1981; Forasiepi et al. 2007; Forasiepi 2009). Carnivorans arrived in South America during the late Miocene-Pleistocene, through different immigrant waves (see Woodburne et al. 2006; Soibelzon and Prevosti 2007; Prevosti and Soibelzon *in press*). Early authors suggested that carnivorans competed with sparassodonts and caused their extinction (e.g., Simpson 1950, 1969, 1971, 1980; Patterson and Pascual 1972; Savage 1977); others questioned, criticized, or rejected the idea, the last receiving more support in recent years (Marshall 1977, 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 et al. 2007; Forasiepi 2009; Prevosti et al. 2009). Despite the evidence against the hypothesis of competitive displacement, several authors today continue using the idea in different contexts (e.g., Werdelin 1987; Wang et al. 2008).

Different models were used to explore the likelihood of competitive displacement (competitive exclusion or active displacement, *sensu* Krause 1986). The basic model predicts a “linear” decrease in diversity and/or abundance of one taxon associated with the increase in diversity and/or abundance in another (Benton 1983b; Krause 1986; Van Valkenburgh 1999). Other concepts use coupled logistic functions based on the Lotka Volterra equation, which describes local population sizes of competing species in local environments (Sepkoski 1996, 2001; Sepkoski et al. 2000). Under this model, both groups increase together in their diversity/abundance, until they reach a threshold; after that, the out-competed taxon starts to decline. Another framework postulates that both groups could compete for a long time, but an external perturbation is needed to decrease the diversity/abundance of one of them in favor of the other (the “incumbent replacement” *sensu* Rosenzweig and McCord 1991). The second taxon probably has better adaptations for the new environmental conditions, but the external perturbation was necessary for this taxon to occupy the new space at the expense of the other.

In summary, different models have been used to understand the evolution of two convergent clades occupying the same geographic area at the same time, but the natural relationships are more complex, and the effects of external factors (e.g., climatic changes, migratory events) could modify the expected pattern (Van Valkenburgh 1999). In this sense, the immigration of Carnivora into South America was a protracted event and different carnivoran lineages arrived at different times during the last 8–7 Ma. This scenario plus the climatic changes occurring in South America during the Neogene complicate the application of previous models to the relationships between the ecological groups.

In this paper, we test the Sparassodonta/Carnivora competitive displacement hypothesis, by considering the estimation of the diversity of each clade through time (based on the data of the fossil record) and the features that have been traditionally used to consider ecological vicariants (i.e., body mass and diet). Under this hypothesis we expect to find clear temporal and ecological overlap between these two carnivore clades.

## Abbreviations

The following institutions house the specimens studied (cited in text and [Electronic supplementary material](#)): **AMNH**, American Museum of Natural History, USA; **CEHA**, Centro de Estudios del Hombre Austral, Chile; **CORD PZ**, Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de Córdoba, Argentina; **DGM**, Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral, Brazil; **FMNH**, Field Museum of Natural History, USA; **GALY**, Grupo de Arqueología del Liceo de Young, República Oriental del Uruguay; **GP**, Instituto de Geociencias, Universidade de Sao Paulo, Brasil; **IGC**, Instituto de Geociencias, Universidade Federal de Minas Gerais, Brasil; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Argentina (MACN-A, Ameghino collection; MACN-PV, Vertebrate Paleontology collection; MACN-ZOOL, Mammalogy collection); **MARC**, Museo y Archivo Regional Castelli, Argentina; **MBLUZ**, Museo de Biología de la Universidad del Zulia, Venezuela; **MHJ**, Museo Histórico de Junín, Argentina; **MLP**, Museo de La Plata, Argentina (MLP-PV, Vertebrate Paleontology collection; MLP-M Mammalogy collection); **MMMP**, Museo Municipal de Mar de Plata “Lorenzo Scaglia,” Argentina; **MMPH**, Museo Municipal “Punta Hermengo,” Argentina; **MNHN-Bol**, Museo Nacional de Historia Natural de La Paz, Bolivia; **MNHNP-PAM**, Museum National de Histoire Naturelle, Pampean Collection, France; **MNRJ**: Museu Nacional e Universidade Federal do Rio de Janeiro, Brazil;

**MPD**, Museo Paleontológico de Daireux, Argentina; **MPEF**, Museo Paleontológico “Egidio Feruglio,” Argentina; **MPS**, Museo Paleontológico de San Pedro, Argentina; **MPV**, Museo Paleontológico de Valencia, Spain; **NHM**, Natural History Museum, England; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; **UCMP**, University of California Museum of Paleontology, USA; **UZM**, Zoological Museum University of Copenhagen, Denmark; **VF**, Museo Royo y Gómez, Universidad Central de Venezuela, Venezuela; **YPM-PU**, Yale Peabody Museum, Princeton University collection, USA.

The anatomical abbreviations “m,” used in the text, refers to lower molars. RGA: relative grinding area index.

## Material and Methods

### Geologic Units, Taxonomic Sample, and Diversity

In order to test the competitive displacement hypothesis, we measured the diversity of Sparassodonta and Carnivora in each age, following chronostratigraphic and biogeographic charts (from Tiupampan to Chasicuan ages: Flynn and Swisher 1995; Gelfo et al. 2009; Madden et al. 2010; Ré et al. 2010; and from Chasicuan to Recent: Cione and Tonni 2005, modified by Woodburne et al. 2006; Fig. 1). The geographical and chronological information of the fossil taxa included here was drawn from the literature (e.g., Marshall 1978, 1979, 1981; Patterson and Marshall 1978; Marshall et al. 1983; Pascual and Ortiz Jaureguizar 1990; Cione and Tonni 2001; Croft 2009; Forasiepi 2009; [Electronic supplementary material](#)) and from specimens housed at the above mentioned institutions.

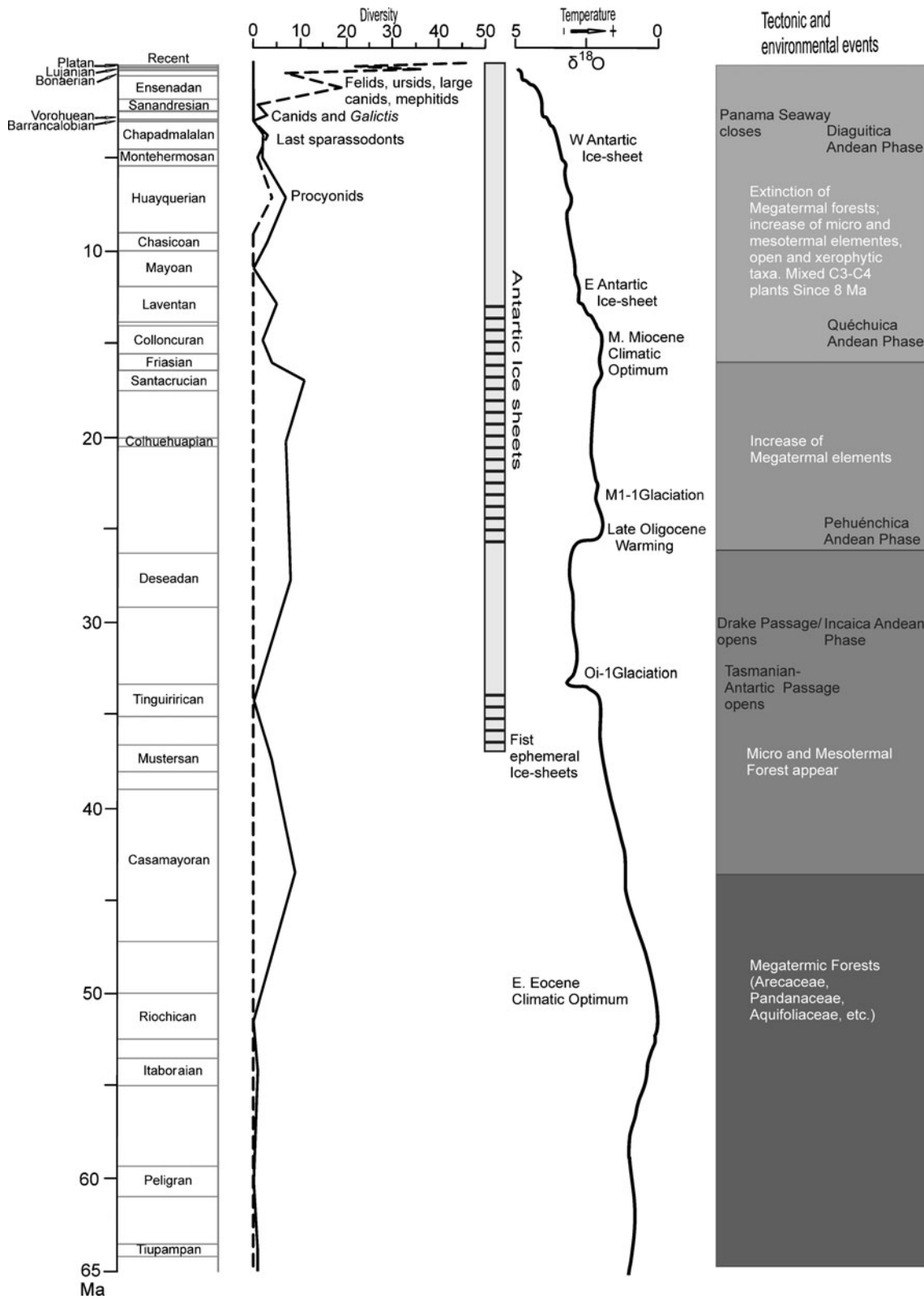
The taxonomy of Sparassodonta mainly follows Marshall (1978, 1979, 1981), Goin and Pascual (1987), Marshall et al. (1990), Babot (2005), and Forasiepi (2009). Sparassodonta is considered as a stem taxon within Methateria, but not part of the crown group Marsupialia (see Forasiepi 2009); it includes 58 nominal species ([Electronic supplementary material](#)). In the present study, *Notogale tenuis*, *Procladosictis erecta*, and *Pseudocladosictis determinabile* are excluded. Their taxonomic validity has been questioned by several authors (e.g., Simpson 1948; Marshall 1981; Forasiepi 2009), because the type material lacks diagnostic features and thus, they are considered *nomina vana* (following Marshall 1981). The taxonomy of Carnivora mainly follows Kraglievich (1930), Berta (1989), Berman (1994), Seymour (1999), Soibelzon (2004), Prevosti (2006a, b, 2010), and additional published information (e.g., Berta and Marshall 1978; Bond 1986; Mones and Rinderknecht 2004; Pomi and Prevosti 2005; Prevosti et al. 2005; Prevosti and

Rincón 2007; Prevosti and Pomi 2007; Soibelzon and Rincón 2007; Prevosti and Ferrero 2008). It includes 82 terrestrial taxa, of which 37 are extinct and 45 are living representatives ([Electronic supplementary material](#)). Some groups, such as foxes and procyonids lack new and comprehensive revisions; thus, the dubious taxa (e.g., “*Canis*” *peruanus*, *Galictis intermedia*) have been excluded from this analysis. Unpublished new species, for both Sparassodonta and Carnivora (e.g., Zetti 1972; Berman 1987, 1994; Babot 2005), were not included.

We used the term “adaptive zone” in a descriptive sense (following Van Valen 1971), assuming that two non-related taxa occupied a similar ecological position/function (“niche”) if they had a similar body size and diet (inferred by a similar dental morphology), and they are not related by any evolutive processes. The term “diversity” refers to all the taxa (measured as the total number of species) during a given period of time (considering South American Stages/Ages as time unit). The terms “competitive displacement” and “opportunistic replacement” follow Benton (1983b; Krause 1986). In this context, competitive displacement has to be defined under two conditions: (1) the diversity of one clade declines while the diversity of a second clade increases; and (2) the lack of association with climatic or floral changes (Benton 1983b; Krause 1986). Point (1) implicitly states the existence of temporal, geographic, and ecological overlap. Opportunistic replacement implies that (1) one group radiates upon the extinction of the other; (2) the rate of replacement is rapid; (3) the groups are not found together or the replaced group is found when the other is not dominant; and (4) replacement could be associated with climatic or floral changes (Benton 1983b:42; Krause 1986:97).

We calculated the number of “range-through taxon” (also known as a “Lazarus taxon”; i.e., one taxon found in underlying and overlying ages or strata, but absent in the intermediate ones, sensu Smith 1994), the correlation (Spearman R) between diversity and the number of sites per age, and the temporal span of each age to detect possible biases in the fossil record (Maas et al. 1995; Fortelius et al. 1996; Foote 2000; Palombo et al. 2008). We did not include first and last records for each species because these resulted in the same pattern as the diversity figures.

The inclusion of “ghost lineages” (i.e., taxa that are predicted to occur by the internal branching structure of the phylogenetic tree, sensu Norell 1992) for measuring diversity could improve the results of the analyses (e.g., Cavin and Forey 2007). Unfortunately, we are unable to use them because the available phylogenies of Sparassodonta do not include all the recognized species, and because Carnivora invaded South America several times and their South American representatives do not form a monophyletic group.



**Fig. 1** South American Age chart, sparassodont and carnivoran diversity, temperature line, climatic, environmental, and tectonic events. Grey boxes correspond to different floral changes (darker is older). Antarctic Ice sheets: dashed bar represent minimal ice (< than the 50% of

present ice volume) while gray represent full glatiation (more of the 50% of present ice volume; see Zachos et al. 2001). See the text for details



## Ecological Inferences: Body Size and Diet

To evaluate the ecological superposition between sparassodonts and carnivorans, we compiled information from the literature and estimated size and diet habits of fossil species.

Body size was arbitrarily divided in three categories according to mass: small (below 7 kg), medium (between 7 and 15 kg), and large (above 15 kg). We present the distribution of body mass per each group and age in Fig. 2a–c. For the extinct sparassodonts, body mass was calculated following the regression equations of Gordon (2003), constructed on the basis of didelphid and dasyurid marsupials. We calculated body mass from all molar loci (where the material allowed) and the results were averaged to obtain a single value in order to compare them with previous estimations (see Argot 2003a, b, 2004a, b, c; Wroe et al. 2004) and with other mammals of similar ecological habits. The averaged weights obtained from dental measurements are indicated in the [Electronic supplementary material](#). For Carnivora, body mass was taken from Christiansen and Harris (2005), Prevosti (2006a), Prevosti and Vizcaíno (2006), Soibelzon and Tartarini (2009), or estimated with the Van Valkenburgh (1990) formula based on the lower carnassial m1. For living species, body mass was taken from Eisenberg (1989), Silva and Downing (1995), Larivière (1999), Nowak (1999, 2005), Parera (2002), Sunquist and Sunquist (2002), and Sillero Zubiri et al. (2004) ([Electronic supplementary material](#)). Some fossil taxa are represented by one or only a few specimens whose dentition is partially or imperfectly known. In such cases, the size category listed in the [Electronic supplementary material](#) is that of their close and similar-sized relative.

Diet was estimated using a dental index based on the relative grinding area (RGA) of the m4 for Sparassodonta and the m1 for Carnivora. These teeth have pronounced carnivorous features and are analogous between Sparassodonta and Carnivora (Werdelin 1987). The index is the square root of the total grinding area divided by the length of the trigonid (modified from Van Valkenburgh 1991). Despite the fact that the m4 ratio was measured for most sparassodonts, there are some taxa for which this tooth is unknown. In those cases, the m3 was used in the calculation, assuming a small reduction in the talonid grinding area in the m4, or else the category provided in the table is based on an estimation already made for a sister species, or other species with similar tooth pattern ([Electronic supplementary material](#)). The RGA index has a minimum of 0 in hypercarnivorous species without talonid (e.g., borhyaenids, felids) and higher than 1 in extremely omnivorous species with very large talonids (e.g., bears, *Potos flavus*). The use of other dental indices that include more teeth (e.g., Friscia and Van Valkenburgh 2010) is inappropriate for incomplete taxa, and this is the case for several fossil species in our analysis.

Based on the diet habits of living carnivorans and marsupials (e.g., Strahan 1995; Nowak 1999; Viera and Astúa de Moraes 2003; Wilson and Mittermeier 2009) and the morphometric index, we classified the species into the following categories: hypercarnivorous (species that feed mostly on other vertebrates chiefly mammals), mesocarnivorous (species with diets mostly composed of vertebrates but with important consumption of insects, fruits, or other non-vertebrate items), and omnivorous (species that incorporate a large proportion of non-vertebrate items, such as insects or vegetables) (cf. Van Valkenburgh and Koepfli 1993). In the case of extinct species, a taxon is considered hypercarnivorous, when the RGA index is lower than 0.48; mesocarnivorous when the index ranges between 0.48 and 0.54; and omnivorous when it is larger than 0.54 (the lower index observed in a living omnivorous marsupial, *Parantechinus apicalis*). The limit between living hypercarnivores and other dietary types is clear, but the limit between omnivores and mesocarnivores is ambiguous and determined arbitrarily. In Carnivora, the overlap is due to canids, because some omnivore and mesocarnivore canids have similar RGA values, filling the gap between hypercarnivores and omnivores as defined by the RGA. The domestic dog has a mesocarnivore index and an omnivore diet, but we considered that this is the result of anthropogenic influence and not a “natural” response (its agriotype, *Canis lupus*, has a hypercarnivore diet). In living marsupials, there is considerably overlap. There are mesocarnivores with RGA values of 0.76 (*Lutreolina crassicaudata*); thus we cannot exclude the possibility that some fossils assigned to the omnivore class could have a mesocarnivore diet. For fossil Carnivora, the classification based on RGA is consistent with the published paleoecological data (Berta 1989; Van Valkenburgh 1991; Van Valkenburgh and Koepfli 1993; Berman 1994; Van Valkenburgh and Hertel 1998; Prevosti 2006a; Prevosti and Vizcaíno 2006; Soibelzon and Tartarini 2009; Figueirido and Soibelzon 2009; see [Electronic supplementary material](#)).

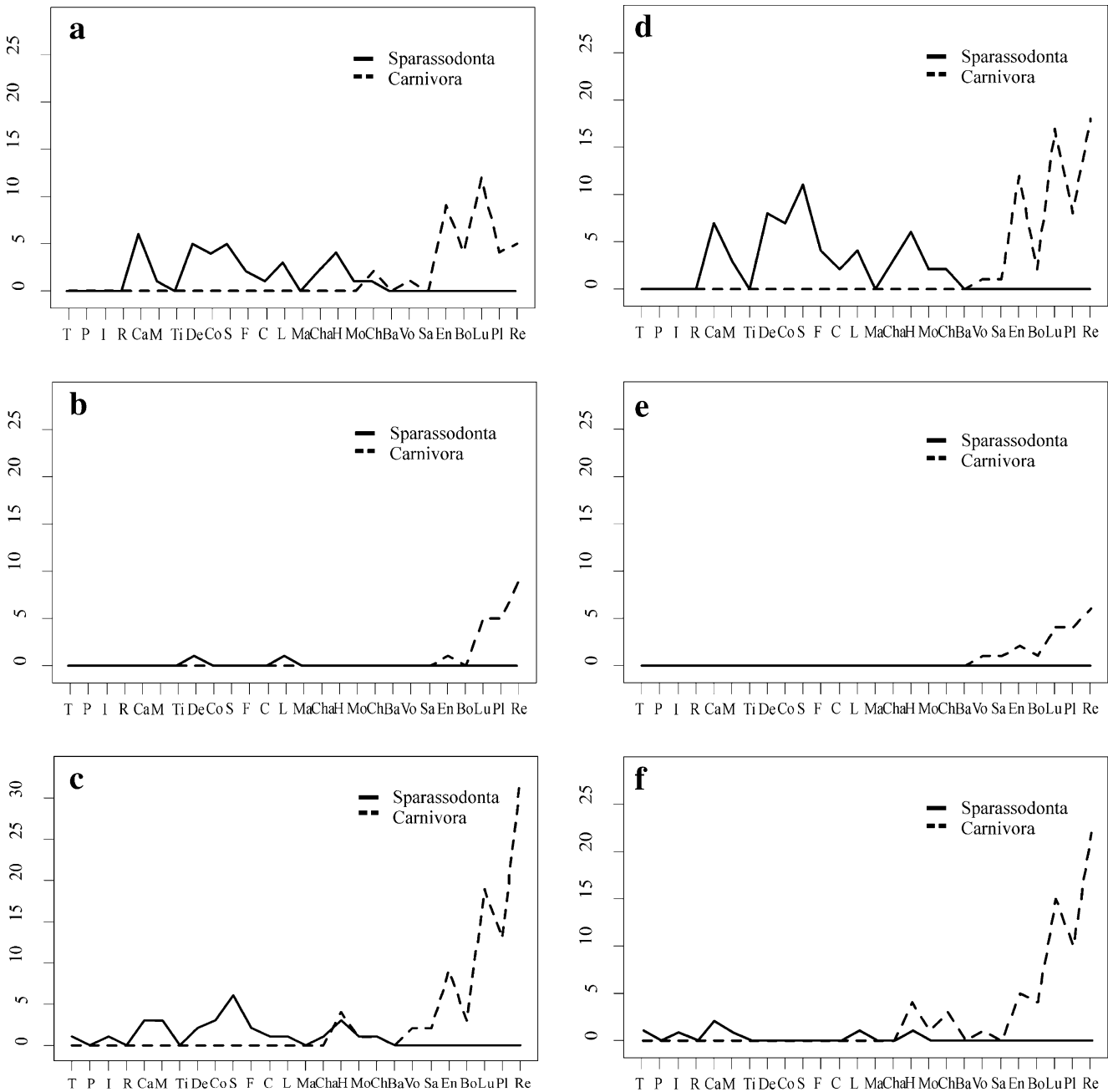
## Results

### Diversity, Body Size, and Diet

For most ages, Sparassodonta had a low diversity of five taxa or less. It rose to a maximum of 11 taxa in the Santacrucian related directly to the quality of the fossil record (see below; Fig. 1). The Casamayoran provided nine taxa, and eight in the Deseadan and Colhuehuapian. The Huayquerian was represented by seven species (Fig. 1; Table 1). The number of taxa fell finally to two in the Chapadmalalan: the highly derived sabertooth *Thylacosmilus atrox* and the Hathliacynidae *Borhyaenidium riggsi*

(Figs. 1, 2, 3; [Electronic supplementary material](#)). Large sparassodont abundance follows the peaks of the group diversity (six species in the Deseadan and five in the Casamayoran and Santacrucian, four in the Huayquerian and Colhuehuapian, and three species in the Laventan; Fig. 2a). Medium-sized sparassodonts are represented by only

one taxon in the Deseadan, and another in the Laventan (Fig. 2b). Small sparassodonts are well represented only in the Santacrucian (six species), followed by the Casamayoran, Colhuehuapian, and Huayquerian with considerably fewer taxa (about three species for each age; Fig. 2c). In summary, the large-sized sparassodont curve follows a pattern similar



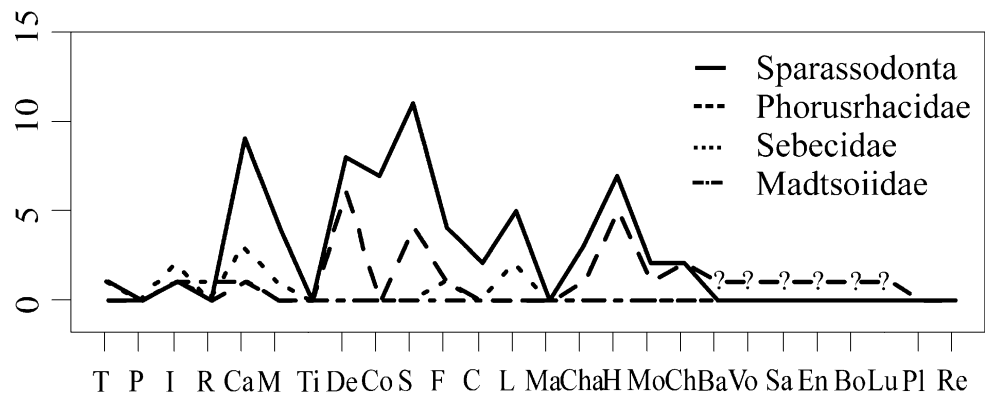
**Fig. 2** Distribution of South America sparassodonts and carnivores separated by body size (**a** large; **b** medium; **c** small) and by diet (**d** hypercarnivores; **e** mesocarnivores; **f** omnivores). *T* Tiupampán; *P* Peligran; *I* Itaboraian; *R* Riochican; *Ca* Casamayoran; *M* Mustersan; *Ti* Tinguirirican; *De* Deseadan; *Co* Colhuehuapian; *S* Santacrucian; *F*

Friasian; *C* Colloncuran; *L* Laventan; *Ma* Mayoan; *Cha* Chasicuan; *H* Huayquerian; *Mo* Montehermosan; *Ch* Chapadmalalan; *Ba* Barranquense; *Vo* Vorohuean; *Sa* Sanandresian; *En* Ensenadan; *Bo* Bonaerian; *Lu* Lujanian; *Pl* Platan; *Re* Recent

**Table 1** Diversity of sparassodonts, carnivorans, Phorusracidae, Sebecidae, and Madtsoiidae in South America during each age, age span (Ma), number of localities per age, and the number of large, medium, small, hypercarnivore, mesocarnivore, and omnivore taxa of sparassodonts and carnivores in each age. Time span is in Ma. *S* sparassodonta; *C* carnivora; *Div* diversity; *L* number of “range-through taxon”; *Hyper* hypercarnivores; *Meso* mesocarnivores; *Omn* omnivores; *Phor* Phorusracidae; *Sebec* Sebecidae; *Madtso* Madtsoiidae

Age	# Sites	Time Span	Div S	Div C	L S	L C	Large S	Large C	Medium S	Medium C	Small S	Small C	Hyper S	Hyper C	Meso S	Meso C	Omn S	Omn C	Phor	Sebec	Madtso
Tiupampan	2	0.7	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Peligran	4	1.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Itaboraian	2	1.5	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	2	1
Riochican	8	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Casamayoran	32	7	9	0	0	0	6	0	0	0	3	0	7	0	0	2	0	1	3	1	1
Mustersan	7	1.4	4	0	0	0	1	0	0	0	3	0	3	0	0	0	1	0	0	1	0
Tinguirirican	2	1.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Descadan	23	2.9	8	0	0	0	5	0	1	0	2	0	8	0	0	0	0	0	6	0	0
Colhuehuapian	17	0.4	7	0	0	0	4	0	0	0	3	0	7	0	0	0	0	0	0	0	0
Santaacruccian	43	1.2	11	0	0	0	5	0	0	0	6	0	11	0	0	0	0	0	4	0	0
Friasian	4	0.8	4	0	0	0	2	0	0	0	2	0	4	0	0	0	0	0	1	1	0
Colloncuran	27	1.5	2	0	0	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0
Laventian	5	2	5	0	0	0	3	0	1	0	1	0	4	0	0	0	1	0	0	2	0
Mayoan	8	1.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chasicooan	5	1	3	0	0	0	2	0	0	0	1	0	3	0	0	0	0	0	1	0	0
Huayquerian	36	3.7	7	4	0	0	4	0	0	0	3	4	6	0	0	1	4	5	0	0	0
Montehermosan	8	0.8	2	1	0	0	1	0	0	0	1	1	2	0	0	0	1	1	0	0	0
Chapadmalalan	12	1.5	2	3	0	0	1	2	0	0	1	1	2	0	0	0	3	2	0	0	0
Barrancalobian	1	0.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1?	0	0
Yorohuean	2	0.5	0	3	0	0	0	1	0	0	0	2	0	1	0	1	0	1	1?	0	0
Sanandresian	3	0.8	0	2	0	1	0	0	0	0	0	2	0	1	0	1	0	1?	0	0	0
Ensenadan	13	1.3	0	19	0	0	0	9	0	1	0	9	0	0	2	0	5	1?	0	0	0
Bonaerian	8	0.37	0	7	0	5	0	4	0	0	0	3	0	2	0	1	0	4	1?	0	0
Lujanian	108	0.122	0	36	0	0	0	12	0	5	0	19	0	17	0	4	0	15	1?	0	0
Platan	135	0.079	0	22	0	10	0	4	0	5	0	13	0	8	0	4	0	10	0	0	0
Recent	–	0.005	0	46	0	0	0	5	0	9	0	32	0	18	0	6	0	22	0	0	0

**Fig. 3** Diversity of sparassodonts and non-mammalian predators. ?: dubious records. Other references as in Fig. 2



to the general diversity line; small sized taxa have a clear peak in the late early Miocene (Santacrucian; Fig. 2a), whereas medium-sized species are occasionally represented with one species during some ages (Fig. 2c).

The diversity of Carnivora was low during the Huayquerian-Sanandresian, when less than five representatives were recorded for each age (Fig. 1; Table 1). Their diversity increased in the Ensenadan with about 20 taxa. Since then, the diversity increased, with a drop in the Bonaerian and Platan (Fig. 1). During the Huayquerian and Montehermosan, the carnivorans were small and represented by procyonids (four and one species, respectively; Fig. 2c). In contrast, in the Chapadmalalan, they reached large sizes (one small- and two large-sized species; Fig. 2a). During the Vorohuean and Sanandresian small mustelids and canids were added to the record, whereas, since the Ensenadan, all the families and morphotypes (see below) have been recognized. In summary, small carnivorans follow the same pattern as that of the Carnivora diversity line, large carnivorans are only recorded in the Chapadmalalan, Vorohuean, and since the Ensenadan when they increased notably, and medium-sized carnivorans are only recorded since the Ensenadan (Fig. 2b–c).

Sparassodonta was a clade represented primarily by hypercarnivores and, as it was expected, the curve of hypercarnivores follows that of diversity (Fig. 2d). No mesocarnivores were detected, and only one or two species of omnivores were restricted to the Tiupampan, Itaboraian, Casamayoran, Mustersan, Laventan, and Huayquerian (Fig. 2e–f). The last sparassodonts were hypercarnivores, with the exception of one large species from the Huayquerian (*Stylocynus paranensis*; Fig. 4c–d), which was an omnivore (but see below). The first known South American Carnivora (Huayquerian) were omnivores (first represented by small-bodied taxa; large omnivore carnivorans are known only since the Chapadmalalan; Fig. 4). Hypercarnivores and mesocarnivores are known since the Vorohuean, but first they comprise small-bodied taxa. Hypercarnivores became diverse and included large species only since the Ensenadan.

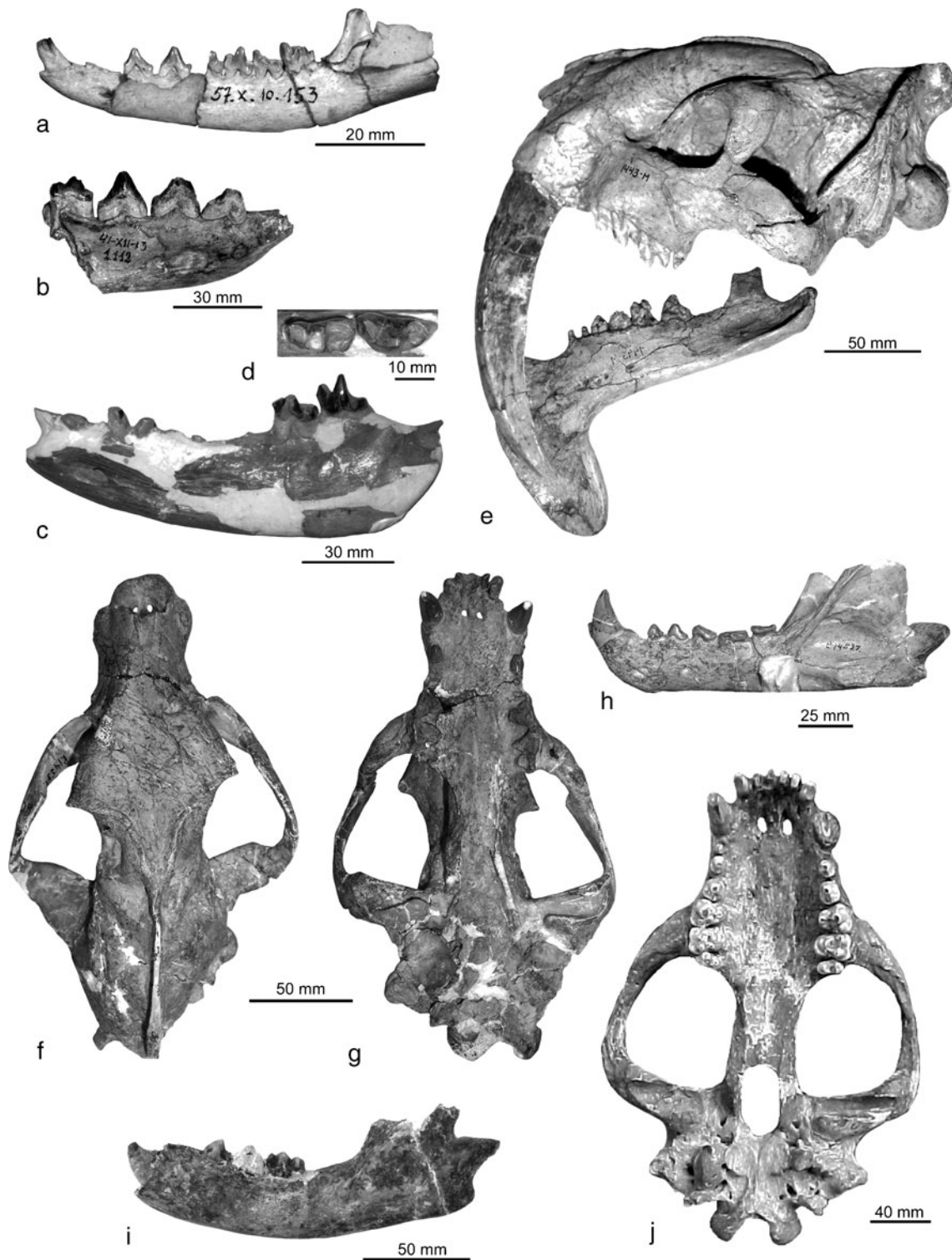
#### Fossil Record Quality

According to our results, the relationship between age time span and global diversity is not significant (Spearman  $R=-0.24$ ,  $p.=0.233$ ); in contrast, there is a highly positive coefficient between global diversity and the number of paleontological sites per age (Spearman  $R=0.77$ ,  $p.<0.0001$ ).

More than 43 localities represent the Santacrucian age, which coupled to the greatest diversity of sparassodonts result in 21 locations and 11 species. Following this are the Casamayoran and Huayquerian assemblages, which are represented by more than 30 fossil localities each. From about ten of these localities, nine Casamayoran and seven Huayquerian sparassodont species were recovered (Table 1). The general pattern is that ages with few localities (e.g., Peligran, Vorohuean) have no record or the recovered species include few predator species. In contrast, eight localities are known for the Montehermosan age and only three sparassodont species were recovered. Carnivora shows the same pattern: the diversity is high in the Lujanian and Platan with more than 100 localities with fossil carnivorans, and low in the Vorohuean, and Sanandresian (three and two species, respectively) represented by less than five fossil localities. In addition, there are some interesting contra examples: the Huayquerian has twice the localities as the Ensenadan, but only four carnivoran species in the former versus 19 in the latter. Similarly, three and nine carnivoran species have been found in the Bonaerian and Chapadmalalan, respectively, but the Bonaerian has eight localities and the Chapadmalalan has 12 (Table 1).

The range-through taxa are few for both carnivorous groups. Sparassodonta has only one range-through taxon in the Riochican that corresponds to *Patene simpsoni*. Most other known species are restricted to one age (Table 1). Among the Carnivora, the range-through taxa are registered in the Barrancalobian, the Sanandresian (one range-through taxon each), the Bonaerian (five range-through taxa), and Platan (ten range-through taxa; Table 1).





**Fig. 4** Last known sparassodonts and first South American carnivorans. **a** *Borhyaenidium musteloides* (MLP 57-X-10-153), left dentary in lateral view; **b** *Stylocynus paranensis* (MLP 41-XII-13-1112), fragment of right dentary in lateral view; **c** *Stylocynus paranensis* (MLP 11-94), nearly complete left dentary in lateral view; **d** same specimen showing the m3–m4 in occlusal view; **e** *Thylacosmilus atrox* (MMP 1443) nearly

complete skull and dentary in lateral view; **f** and **g** *Cyonasua brevirostris* (FMNH 14537) nearly complete skull in dorsal and ventral views; **h** *C. brevirostris* (same specimen as **f**), left dentary in lateral view; **i** *Chapalmalania* cf. *Ch. altaeformis* (FMNH 14401), nearly complete left dentary in lateral view; **j** *Chapalmalania ortognatha* (MMP 1121), fragmentary skull in ventral view

## Discussion

### Diversity Pattern and Ecological Overlap

The diversity lines indicate that since the late Miocene (Huayquerian) the diversity of sparassodonts declined until they were last recorded in the “middle” Pliocene (Chapadmalan; Figs. 1, 2, 3; Table 1). The late Miocene is when the first carnivorans are recorded in South America. Therefore, this concurrence of data could be used to support the competitive displacement hypothesis (see Simpson 1980; Patterson and Pascual 1972; Savage 1977; Werdelin 1987; Wang et al. 2008). A close examination of the curve shows, however, that both groups decline in the Montehermosan, which is not expected under the classical model of competition (Krause 1986; Van Valkenburgh 1999; Friscia and Van Valkenburgh 2010; but see below). In addition, there is no temporal or ecological superposition; all carnivorans recorded during the Huayquerian-Chapadmalalan span were small omnivores with the exception of the Chapadmalalan, in which large omnivorous species were added (Fig. 2). Huayquerian-Chapadmalalan sparassodonts were both small-sized and large-sized hypercarnivores, with the exception of one large omnivore species recorded in the Huayquerian (Fig. 2).

In modern ecosystems, niche differentiation exists in some sympatric species. It includes diet partitioning based on body size, horizontal (type of vegetation and structure) and vertical (arboreal) habitat dimensions, and temporal activities (e.g., nocturnal vs. diurnal patterns) (Rosenzweig 1968; Sunquist et al. 1989; Johnson and Franklin 1994; Van Valkenburgh and Wayne 1994; Dayan and Simberloff 1996; Maehr 1997; Jones and Barmuta 1998, 2000; Dickman 2003). Competition between mammalian predators was also registered, particularly when resources were limiting. This resulted in an increase in the abundance and distribution of the dominant species to the exclusion of the subordinate species from a particular area (Dickman 1988; Sunquist et al. 1989; Johnson and Franklin 1994; Maehr 1997; Glen and Dickman 2008).

In Australia, niche overlap, displacement, and predation were detected between native marsupials and the recently introduced carnivorans (i.e., *Felis catus*, *Vulpes vulpes*, *Canis familiaris*), where the native species were negatively influenced (Jones et al. 2003; Glen and Dickman 2005, 2008; Saunders et al. 2010). On the contrary, the removal of placentals resulted in the increase of native predator populations (e.g., Morris et al. 2003; Wilson et al. 2003; Glen and Dickman 2008; Saunders et al. 2010). These studies also indicate that diet and body size influenced intraguild predation and aggression, and that larger species dominated over smaller (Dickman 1986; Palomares and Caro 1999; Donadio and Buskirk 2006). Based on the

information at hand, it is not expected that the small procyonids of the Huayquerian-Montehermosan would displace the contemporaneous large sparassodonts or even the smaller, specialized sparassodonts, such as the *Borhyaenidium* species (Fig. 4a). However, a certain level of predation cannot be completely discounted, considering that in current communities, ecological “non-equivalent” taxa may interact negatively under particular circumstances (Palomares and Caro 1999; Donadio and Buskirk 2006).

Most sparassodonts were hypercarnivores (Electronic supplementary material); thus the ecological superposition between procyonids and sparassodonts was limited. The only exception would be *Stylocynus paranaensis* (Fig. 4c–d), which was a large omnivore according to the RGA index (0.61), although a mesocarnivore diet could not be completely discarded. As shown previously (Materials and methods), among marsupials the RGA has limitations: the living opossum *Lutreolina crassicaudata* is a mesocarnivore preying mostly on small mammals, birds, reptiles, fishes, and insects (Nowak 1999) but its RGA index is 0.76, even higher than in *S. paranensis*. Moreover, and because of the considerably larger size of *S. paranensis* relative to species of *Cyonasua* (Fig. 4f–g), if there was a negative interaction, the former is more likely to have been the dominant species, based on the models of current predator interactions (e.g., Dickman 1986; Palomares and Caro 1999; Donadio and Buskirk 2006). If the giant, omnivorous, bear-like procyonid *Chapalmalania* (e.g., Kraglievich and Olazábal 1959; Fig. 4i–j) would be considered as the ecological counterpart of *S. paranensis*, there is no temporal overlap between them (a gap of more than 2 Ma exists between the first record of the former and the record of the sparassodont). Another possibility is that competition would have occurred between this large procyonid and the saber-toothed *Thylacosmylus atrox* (Fig. 4e), the last large sparassodont, during the Chapadmalan, but the very different ecotypes of these predators weaken the idea. On the contrary and from another point of view, the absence of strict omnivorous sparassodonts during the late Miocene-Pliocene would have facilitated the diversification of the omnivorous *Cyonasua-Chapalmalania* (Prevosti and Pardiñas in press).

For the competitive displacement hypothesis to be supported, considering that most sparassodonts were hypercarnivores, there must be temporal overlap between ecological counterparts of similar size. Review of the fossil record is not in agreement with this expectation. There is a gap of about 0.8 Ma. between the first record of a small hypercarnivore carnivorans (*Galictis sargentini*) and the last small sparassodonts (i.e., *Borhyaenidium riggsi*) and the gap is larger (about 1.2–2 Ma) between the first record of medium and large hypercarnivore carnivorans (*Smilodon*) and last large sparassodonts (i.e., *Thylacosmylus atrox*). It

bears mentioning that the supposed presence of a mustelid (Lutrinae?) in the Huayquerian of Argentina (Verzi and Montalvo 2008), was later demonstrated to be a didelphimorphian marsupial (Prevosti and Pardiñas 2009). According to the fossil record, it is highly improbable that weasels could cause the extinction of sparassodonts. If negative interaction occurred between weasels and metatherians, it is more likely that it affected carnivorous didelphimorphians of similar size (e.g., Marshall 1977; Goin 1989, 1995; Ortiz Jaureguizar 1989, 2001; Marshall and Cifelli 1990) during the Pliocene.

In conclusion, there is no evidence of temporal overlap between carnivoran and sparassodont ecological counterparts. There is no an adequate framework to hypothesize that carnivorans outcompeted and displaced the Sparassodonta during the late Miocene-Pliocene.

### Fossil Record Quality and Bias

The positive correlation between number of taxa and number of localities per age clearly indicates that sample size affects the diversity. This was previously noticed by Marshall and Cifelli (1990), who presented diversity lines roughly similar in shape to those recorded here (Figs. 1, 2, 3). More recently, Prevosti and Soibelzon (*in press*) found a similar bias for the late Miocene-Holocene carnivoran record. Nonetheless, the very low diversity registered during the Huayquerian-Sanandresian and the high diversity of the Ensenadan-Recent were interpreted as a real pattern and not bias of the fossil record (see arguments supporting this view in Prevosti and Soibelzon *in press*).

There are other strong biases coupled with sample size: (1) for most of the Paleogene and early Neogene (until the late Miocene) most of the fossil-bearing localities are in Patagonia, and after that they are in extra-Patagonian regions (e.g., Pascual and Odreman Rivas 1971; Patterson and Pascual 1972). The Lujanian is the only age that is well sampled along the entire continent (Marshall and Cifelli 1990; Prevosti and Soibelzon *in press*). Thus, our diversity curves represent mostly a regional pattern rather than a continental one. (2) Some mammalian assemblages are only partially known, requiring clarification and new fossil collections (e.g., hitherto, there is no record of mammalian predators for the Tinguirirican and Mayoan ages, which were undoubtedly present but have not been collected or yet identified; e.g., Flynn et al. 2003). (3) Some other assemblages (e.g., Colloncuran) are historically known (e.g., Roth 1899), but the faunas have not been reviewed recently. The two species of predators currently known for the Colloncuran ([Electronic supplementary material](#)) are clearly underestimated. (4) Paleogene diversity is less well known than those of the Neogene. Despite the fact that there is an increasing number of studies focused on Paleogene mam-

malian associations, the Paleogene is hitherto insufficiently known. Temporal gaps are larger during the Paleogene than Neogene (the discovery of new associations gradually fills some gaps; e.g., Tejedor et al. 2009) and the geochronology requires adjustments. (5) Some ages present particular problems for the current study. During more than 50 years the Casamayoran was regarded as a single unit (e.g., Simpson 1948, 1967; Marshall et al. 1983). More recently (Cifelli 1985), it was separated in two subages, the Vacan (49–44 Ma BP) and Barrancan (41.6–39 Ma BP), that together comprise around 10 Ma (Madden et al. 2005; Ré et al. 2010). By referring to the Casamayoran we are probably mixing faunas, but with the available data, especially from old collections, we cannot perform a study with a finer division of this age.

Taking into account these biases, it is possible to argue that the failure to find support for the competitive hypothesis is because the South American fossil record is incomplete, which precludes recognition of temporal overlap between ecologically equivalent sparassodonts and carnivorans. Nonetheless, we considered that the long gap between the last record of the large Sparassodonta in the Chapadmalalan and the first records of large-medium hypercarnivore Carnivora (Felidae and some clades of Canidae) in the Ensenadan (Fig. 1) is not a bias but a pattern of the fossil record. Small hypercarnivores (Mustelidae, *Galictis* spp.) are scarce but known since the Vorohuean. During the Ensenadan-Holocene their record is also sparse and sporadic. Foxes are known since the Vorohuean and during Ensenadan-Lujanian ages; *Smilodon* and foxes are the most frequently recovered carnivorans (Fig. 1). Thus, if *Smilodon* was present before the Ensenadan, we would expect to find it together with mustelids and foxes in older levels.

On the other hand, the Chapadmalalan is well known, especially through very rich outcrops of the Chapadmalal Formation, which were extensively sampled for more than a century (see Cione and Tonni 1995). Several specimens of *Cyonasua*, some of *Chapadmalania*, *Thylacosmilus*, one specimen of *Borhyaenidium*, and even “terror birds” were collected. The supposed presence of felids was refuted (see Prevosti 2006b; Prevosti et al. 2006; Prevosti and Pomi 2007) and the presence of mephitids (*Conepatus*) is at least dubious (Cione and Tonni 1995; Woodburne et al. 2006; Woodburne 2010). Based on the extensive studies already performed, we assume that mammalian diversity would not increase significantly with new fossil collections. The diversity of sparassodonts and carnivorans is presently very low, but we do not believe this to be related to a bias in the fossil record.

In summary, despite the biases recognized earlier, the fossil record is the only tool at hand to interpret the diversity, evolution, and ecological patterns of the past. The



Neogene and in particular the time span since the beginnings of the diversification of carnivorans in South America (i.e., Huayquerian, Chapadmalalan, Ensenadan-Recent) is well represented. The low diversity of carnivorans registered in the Chapadmalalan-Sanandresian is assumed to reflect the real pattern.

#### Ecological Comparison Between Carnivora and Sparassodonta

Previous inferences about the ecology of sparassodonts were based on comparisons of their dentition with that of living marsupials and carnivorans. Hathliacynids and basal borhyaenids (*Prothylacynus patagonicus* and *Lycopsis torresi*) were considered omnivores or predominantly omnivores (Marshall 1977, 1978, 1979, 1981), were compared with didelphids, mustelids, or canids (Marshall 1977, 1978), and were assumed to have the capacity to prey on small vertebrates (e.g., small mammals, reptiles, birds, and amphibians), invertebrates, and eggs (Argot 2004a). In particular, *P. patagonicus* and *L. torresi* were compared with ursids and procyonids (Marshall 1977, 1978). Large borhyaenids (i.e., *Borhyaena tuberata*, *Acrocyon sectorius*, and *Arctodictis munizi*) were considered specialized carnivores, similar to canids and felids (Marshall 1977, 1978). The robust nature of the teeth, bulbous roots, and robust, deep, sometimes fused, dentaries support the assumption that they probably had the capacity to break hard materials like bones, as currently occurs among scavengers, but they were probably not specialized bone-cracking species as are living hyaenids (Marshall 1977, 1978; Argot 2004a; Forasiepi et al. 2004). In a more recent analysis, Wroe et al. (2004) argued that most sparassodonts were hypercarnivores. Use of the dental index RGA supports the inferences of Wroe et al. (2004) that most sparassodonts were hypercarnivore species (about 90.77%) and only few were omnivorous (the remaining 9.23%; [Electronic supplementary material](#)). The large proportion of hypercarnivores contrasts with modern and past carnivoran communities that always contain some proportion of omnivores and mesocarnivores (e.g., Van Valkenburgh 1999, 2007). Our results do not support a strict analogy between these metatherians and canids, ursids, procyonids, or even hyaenas as was stated earlier (Marshall 1977, 1978, 1979, 1981). There were no omnivorous sparassodonts comparable to eutherian carnivorans (e.g., *Nasua*, *Procyon*). Even the Huayquerian *Stylocynus paranensis*, classically compared with omnivorous taxa, has smaller talonids and more pointed cusps than living procyonids and mephitids (e.g., Marshall 1979; Babot and Ortiz 2008). In addition, sparassodont species with better developed talonids (e.g., *Nemolestes spalacotherinus*, *Patene simpsoni*, *P. coluapiensis*; *Stylocynus paranensis*, *Hondadelphys fieldsi*,

and *Allqokirus australis* if this taxon is a sparassodont) occupy a basal position in the phylogenetic tree (Forasiepi 2009). In this context, broad talonids would represent the plesiomorphic condition of the group. The talonid of hathliacynids and some borhyaenids (e.g., *Pseudothylacynus*, *Lycopsis*, *Prothylacynus*, and *Pseudolycopsis*) are within the range of living hypercarnivores. Some borhyaenids (e.g., *Borhyaena*, *Arctodictis*) and thylacosmilids have virtually no talonids, such as in Felidae and other hypercarnivore clades (i.e., Nimravidae). *Thylacosmilus* was compared with felid saber-tooth cats (Machaerodontinae; Patterson and Pascual 1972; Marshall 1976, 1977, 1978), due to the hypertrophy of upper canines and other associated features, or compared with derived nimravids (*Barbourofelis*; Prevosti et al. 2010), based on the shape of the skull and jaw.

Analysis of the postcranial anatomy of sparassodonts (Argot 2003a, b, 2004a, b, c; Ercoli 2010) suggests that they had generalized limbs, ranging from scansorial species (e.g., *Prothylacynus*) to more terrestrial ones (e.g., *Borhyaena*). The combination of a dentition specialized to hypercarnivory and a generalized postcranium is not commonly found among carnivorans, with the exception of some mustelids (e.g., *Gulo gulo*).

Reduced variation in dental morphology of the Sparassodonta with regard to carnivorans could be explained by the presence of phylogenetic constraints associated with the pattern of tooth replacement in metatherians (Werdelin 1987; see Goswami et al. 2011 for a different view). During ontogeny, lower molars erupt successively and occupy the optimal position from a biomechanical point of view, until the mandible reaches adult size and the m4 takes the most favorable position. Thus, during development each lower molar functions as a carnassial, at least temporally. The specialization in each loci would not permit that some molars to be specialized for grinding and smashing food, as happens with the m2–m3 in Carnivora (Werdelin 1987). The restriction of the Sparassodonta to hypercarnivory is present in nearly the entire clade (the exceptions are the basal taxa, as mentioned above), resembling the placental Felidae (e.g., Van Valkenburgh 1999, 2007).

#### Extinction of the Sparassodonta

As discussed above, we did not find evidence that carnivorans competed with and eventually displaced the sparassodonts during the late Miocene-Pliocene (see also Goin 1989; Forasiepi et al. 2007). Other hypotheses are competition with “terror birds” (Phorusrhacidae; Marshall 1977, 1978; Marshall and Cifelli 1990; see also Croft 2006) or with clades of didelphimorphian marsupials (Sparassocynidae, *Thylophorops*, *Thylatheridium*, *Hyperdidelphys*) that developed highly carnivorous taxa during the late

Mioceno-Pliocene, affecting in the particular the Hathliacynidae (Marshall 1977, 1978, partim; Goin 1989; Goin and Pardiñas 1996). Other hypotheses attribute the decline and extinction of Sparassodonta to Andean orogenic phases and the resulting environmental changes (Marshall 1977, 1978, in part; Marshall and Cifelli 1990, in part; Forasiepi et al. 2007).

Marshall and Cifelli (1990; see also Marshall 1977, 1978) suggested that “terror birds” were highly cursorial taxa that displaced large borhyaenids during the late Miocene-early Pliocene, when savannas, pampas, and open environments expanded. Assessment of “terror bird” diversity (see Alvarenga and Höfling 2003; Agnolin 2009) shows that the number of species was low during the Cenozoic, with few peaks: one in the Santacrucian with six species and the other in the Huayquerian with five species (Fig. 3). The last records with reliable stratigraphic data are from Chapadmalalan beds, but there is mention of a specimen from the “Pliocene-lower Pleistocene” (Montehermosan-Ensenadan) of Uruguay (Tambussi et al. 1999; Agnolin 2009). In addition, there is a recently described specimen from the late Pleistocene (Lujanian) of Uruguay that was classified as Phorusrhacidae (Alvarenga et al. 2009), but it could belong to *Ciconiiforme* indet. (F. Agnolin 2010, pers. comm.). The biochron of the group and the diversity line of Phorusrhacidae are roughly similar to that of Sparassodonta, and particularly similar to that of large sparassodonts (Fig. 4). Thus, the evidence does not support that the radiation of the “terror birds” in the late Miocene-Pliocene would cause the decline and extinction of sparassodonts. Similarly, other non-mammalian terrestrial predators do not likely influence the extinction of sparassodonts. The diversity of sebecid crocodiles and madtsoiid snakes was always low during the Cenozoic (Gasparini 1996; Albino 1996; Paolillo and Linares 2007; Riff et al. 2010) and their extinction preceded that of sparassodonts (Fig. 4).

The last hathliacynids (*Borhyaenidium*, *Notocynus*, *Notictis*) show a temporal overlap with carnivorous didelphids that appeared in the Huayquerian-Vorohuean (Sparassocynidae, *Hyperdidelphys*, *Thylateridium*, *Lutreolina*, *Thylophorops*), but Sparassocynidae, *Lutreolina*, and *Thylateridium* are smaller than hathliacynids (0.2–0.6 kg versus 0.89–1.98 kg, respectively; pers. obs.). *Thylophorops* and *Hyperdidelphys* overlap them in size (0.88–7.49 kg; Goin et al. 2009), but all of these species have RGA indexes clearly above the hypercarnivore range (i.e., values of 0.52–0.74; pers. obs), suggesting a less carnivorous diet than in the Hathliacynidae. These differences point to the existence of a potential niche separation between these two metatherian groups, and to an opportunistic replacement rather than a competitive displacement. A revision of the carnivorous didelphimorphians would

clarify the potential interactions between these metatherian groups.

Since the beginning of the Cenozoic, South America was affected by the principal phases of orogeny that resulted in building of the current Andean Range. The major phases are the Incaica (30 Ma), Pehuénchica (25 Ma), Quéchuica (15.5 Ma), and Diaguítica (4.5 Ma) (Yrigoyen 1979; Leanza and Hugo 1997). At the Eocene-Oligocene boundary, the Incaica Phase coupled with the final opening of the Drake Passage and the establishment of the Antarctic Circumpolar Current with the consequent appearance of the first permanent ice-sheet in Antarctica (the O<sub>1</sub> Glacial Event: Zachos et al 2001), promoted the most abrupt and rapid fall on environmental temperature recorded for the Cenozoic. This change in the climatic condition marked the end of the greenhouse period and their impact on the continental faunal and floral assemblages was drastic in South America, particularly in Patagonia (Barreda and Palazzesi 2007; Goin et al. 2010). Pascual and colleagues (Pascual and Odreman Rivas 1971; Patterson and Pascual 1972; Pascual et al. 1985; Pascual and Ortiz Jaureguizar 1990) noted that the middle Miocene phase of Andean orogeny, which is related to the significant increase in the elevation of the Main Cordillera, is coincident with the beginning of desertification of Patagonia and the northward woodland retreat. A replacement of forest by more open and xerophytic vegetation took place in the middle-late Miocene; in particular open forests composed of *Schinus*, *Prosopis*, *Celtis*, with shrubs of Ephedraceae, and Asteraceae are registered in the late Miocene (Barreda and Palazzesi 2007; Barreda et al. 2008; Dozo et al. 2010). Mixed floras with C3–C4 species are detected since 8 Ma in localities between 21°–35° S in Bolivia and Argentina, suggesting the presence of extensive grasslands (MacFadden et al. 1996). During the middle and late Miocene a marine transgression, accompanied by the development of large lakes and extensive fluvial systems, dissected South America into separated portions of land (Campbell et al. 2006; Cozzuol 2006; Latrubesse et al. 2007). During the middle Miocene-Recent, a gradual global temperature decrease occurred causing the establishment of permanent ice-sheets in western Antarctica and the onset of glaciation in the North Pole (Zachos et al. 2001; Fig. 1). These climatic and environmental changes affected the biotic associations of terrestrial ecosystems and consequently could cause the decline and extinction of several autochthonous groups (e.g., Ortiz Jaureguizar 1986; Pascual and Ortiz Jaureguizar 1990). Several South American “native ungulates” (e.g., Astrapotheria, Leontinidae, Adianthidae, Notohippidae) became extinct at the middle Miocene, but some xenarthrans experience a radiation (Megalonychidae, Megatheriidae, and Mylodontidae) (Marshall and Cifelli 1990). Despite restricted radiations in Toxodontidae, “na-



tive ungulates” experienced a continuous decline during the middle Miocene-Pleistocene, with a steep reduction in the Pliocene and disappearance during the Pleistocene-Holocene as part of the last mass extinction (Marshall and Cifelli 1990; Bond et al. 1995). A faunal turnover occurred during the “middle” Pliocene (e.g., Kraglievich 1952; Tonni et al. 1992). Some authors suggest this is related to environmental changes triggered by Andean orogeny rather than competition with North American immigrants (e.g., Ortiz Jaureguizar et al., 1995; Cione and Tonni, 2001), while others argue for impact of a meteor in the Pampean Region during the late Chapadmalalan (~3.3 Ma) as the cause of this faunistic change (Schultz et al. 1998; Vizcaíno et al. 2004).

The decrease in Sparassodonta diversity and their extinction in the “middle” Pliocene are part of this faunal turnover that apparently follows a stochastic pattern in which a mixture of biological and physical factors resulted in the final extinction of the clade (following Benton 1983a). The diversity of sparassodonts does not seem to have a direct correlation with total annual rainfall or vegetation, but rather with the diversity of medium-sized mammals (Croft 2001). Environmental changes occurred during the late Miocene-Pliocene triggered by episodes of Cenozoic Andean deformation. Nonetheless, these changes were not contemporaneous throughout the continent and the diastrophic phases, when precisely dated, did not coincide in different segments along the Andes (Garzzone et al. 2008; Ramos 2009; Bershaw et al. 2010). Thus northern parts of South America could have experienced different environmental changes during this time but sparassodonts became extinct from the entire continent. On the other hand, the diversity line of sparassodonts during the late Miocene-Pliocene (Figs. 1, 2, 3) roughly matches that of other groups, such as Notoungulata and Litopterna (Bond et al. 1995), with the exception that these groups became extinct at the end of the Pleistocene. It is expected that changes in the community would affect the predator guild and in particular the extremely specialized sparassodonts. Large-sized carnivores with a dietary specialization towards hypercarnivory are more vulnerable to extinction than non-hypercarnivore species (Van Valkenburgh et al. 2004) and this is the evolutionary trend of sparassodonts. In addition, if sparassodonts had an imperfect homeothermy, as do living marsupials, with consequent correlation between lactation and rain season (McNab 1986, 2005, 2008; Green 1997; Krockenberger 2006), the decrease in temperature and increase in aridity during the late Miocene when xerophytic vegetation and open environments were established in South America (Barreda and Palazzesi 2007; Barreda et al. 2008) would have influenced the decline of the group. Nonetheless, it is not clear whether the extrapolation from living marsupials to sparassodonts is correct.

Major taxonomic groups diversified and then declined to extinction during the history of the Earth, being replaced by others. Explanations that concerns only biological (e.g., competitive displacement) or physical (e.g., climatic changes) factors are deterministic (Benton 1983a). For the sparassodonts, we cannot apply the hypothesis that carnivores out competed and displaced the group during the late Miocene-Pliocene Great American Biotic Interchange. Direct competition with other non-mammalian predators seems equally unlikely. There is no direct association between the Andean orogenic phases and the extinction of sparassodonts. Nor does the impact of a meteor (Schultz et al. 1998; Vizcaíno et al. 2004) explain the decline in the diversity line since the late Miocene. Based on the information at hand, there are a combination of biological factors such as prey species decline and vulnerability of the group to extinction, along with the physical factors of global environmental changes, which under a stochastic approach require that not one but a series of causes are interrelated, needing not one but several complementary explanations to fully describe the phenomenon. Metatherian evolution in South America was influenced by climatic and environmental factors that promoted radiations and extinction events at the macrotaxonomic level (Goin et al. 2010).

## Conclusions

There was a temporal overlap between Sparassodonta and Carnivora in South America during the late Miocene-“middle” Pliocene, but there does not appear to have been an ecological one. Most sparassodonts were hypercarnivores and the late Miocene-“middle” Pliocene carnivores were omnivorous. This does not support the competitive displacement hypothesis and is more in line with an opportunistic ecological replacement, where the incoming carnivores occupied the space left by the extinct sparassodonts.

“Terror birds” had low diversity throughout the Cenozoic and do not appear to have been the cause of decline and extinction of the Sparassodonta. Nor do sebecid crocodiles or madtsoiid snakes, the groups that developed predator strategies in the terrestrial ecosystems. There was temporal and apparently some ecological overlap between thylacynids and some clades of carnivorous didelphimorphians, but there was also a potential ecological partition between them due to size and diet (didelphimorphians were smaller and less carnivorous).

The decline and extinction of the Sparassodonta appear to be part of a larger faunistic change under a stochastic approach, related to the combination of biological and physical factors. More information from northern South

America is needed to test whether this is a continental pattern or one limited to the southern part of the continent.

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