# The Structure of the Mammalian Predator Guild in the Santa Cruz Formation (Late Early Miocene)

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# The Structure of the Mammalian Predator Guild in the Santa Cruz Formation (Late Early Miocene)

Marcos D. Ercoli · Francisco J. Prevosti ·
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**Abstract** The Santa Cruz Formation (late early Miocene, Santacrucian age) registers 11 species of mammalian predators (Metatheria, Sparassodonta). Together with large carnivorous flightless birds, they comprised the terrestrial predator guild. The Santacrucian sparassodonts were diverse in body size, had different locomotory habits, and were primarily hypercarnivores. The objective of this work is to analyze the guild structure of the sparassodonts of the Santa Cruz Formation, using the variables of body mass, diet, and locomotion as proxies. Furthermore, we analyze the interaction with other predators and potential prey. The univariated test V of Poole and Rathcke and the multivariated test of Clark-Evans were used to construct the models. In the multivariate test, we made a Principal Component Analysis to resume and standardize the variables. With body mass and locomotion we obtained an evenly spaced pattern of segregation for the sparassodont species, being non-significant and significant, respectively. The pattern was aggregated and significant only with diet. The analysis of all variables together resulted in an evenly spaced and significant pattern, which is consistent with character displacements (segregation of species throughout the morphospace) that would help to diminish interspecific competition during the Santacrucian age and would allow selection of prey species of different sizes and substrate specializations. When the body size pattern of predator birds and sparassodonts were plotted together, the pattern is evenly spaced and non-significant. Other factors, including locomotion, would differentiate these species and their ecological niches.

## Introduction

The Santa Cruz Formation (SCF) in southern Patagonia, Argentina, is the richest fossiliferous unit of the Cenozoic of South America (Vizcaíno et al. 2012a, b). The quantity and quality of fossils from this unit, including many complete skeletons, has provided the best collection of South American mammals (Vizcaíno et al. 2012a).

The coastal outcrops of the SCF (Fig. S1; modified from Cassini 2013) were deposited between 18 and 16 Ma (late early Miocene) under fluvial and aeolian conditions and with the presence of an intense volcanism that resulted in high sedimentation rates, while other deposits were dated between 22.5 or 19, and 14 Ma (Blisniuk et al. 2005; Perkins et al. 2012). The vegetation was a mixture of grass and arboreal components, defining a mosaic of open temperate humid and semi-arid forests, and occasional marshlands with a mixture of grasses and forbs (Barreda and Palazzesi 2007; Brea et al. 2012; Kay et al. 2012a).

The Santacrucian fauna developed in the context of South American isolation, before Great American Biotic Interchange (GABI) immigrants entered the southern hemisphere. The morphotypes and the combination of lineages represented in the Santacrucian mammal community have no present day

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counterpart and included therians (Eutheria and Metatheria represented by the crown groups and stem taxa) and survivors of Mesozoic lineages (Dryolestoidea; Rougier et al. 2012). The mammalian association, other than predators, ranged in body masses from less than 20 g to greater than 1000 kg and were represented by endemic native ungulates (Astrapotheria, Notoungulata, and Litopterna; Cassini et al. 2012), xenarthrans (Cingulata, Vermilingua, and Folivora; Bargo et al. 2012; Vizcaíno et al. 2012a), marsupials (Paucituberculata and Microbiotheria; Abello et al. 2012), rodents (Caviomorpha; Candela et al. 2012), and primates (Platyrrhini; Kay et al. 2012a). The predator guild, feeding on vertebrates, was occupied by metatherians (Sparassodonta; Fig. 1), birds (Phorusrhacidae, Cariamidae, Anseriformes, and Falconiformes), reptiles (Squamata), and frogs (Neobatrachia), the last being occasional predators of small vertebrates (Fernicola and Albino 2012).

Among birds, the "terror birds" (Phorusrhacidae) comprised cursorial and highly carnivorous species, from 4.5 to around 90 kg, the cariamids were about 1.5 kg, the large-sized anseriform *Brontornis* of more than 300 kg, and the falconids between 200 g to 2.3 kg (Degrange 2012; Degrange et al. 2012).

The predator mammals of the SCF were represented by 11 species of Sparassodonta with body masses from 1 kg to greater than 50 kg (Argot 2003a, b, 2004a, b; Wroe et al. 2004; Vizcaíno et al. 2010; Ercoli and Prevosti 2011; Prevosti et al. 2012; Fig. 1). This group demonstrates different locomotory habits (from scansorial to terrestrial forms with incipient cursorial capabilities; Argot 2004b; Ercoli et al. 2012), while all appeared to show a hypercarnivorous diet (Prevosti et al. 2013).

The paleoautecology (branch of paleoecology that studies the relationship of the extinct species with the environment; e.g., diet and locomotion) of sparassodonts has been studied using descriptive or quantitative approaches (Marshall 1977a, 1978; Argot 2004b; Forasiepi et al. 2004; Forasiepi 2009; Ercoli and Prevosti 2011; Ercoli et al. 2012; Prevosti et al. 2012; Fig. 1), while the few paleosynecological (branch of paleoecology that studies the relationships between extinct species; e.g., intraguild killing and prey-predator relationships) studies are descriptive narratives based on quantitative paleoautecological inferences. The possible competition between sparassodonts and phorusrhacids was discussed by Argot (2004b; see also Marshall 1978; Bond and Pascual 1983) who distinguished partial segregation of niches. Using the estimated body size of sparassodonts and other mammals, Prevosti et al. (2012) hypothesized about potential relationships between prey and predators in the SCF.

The main objective of this work is to evaluate the structure of the extinct South American mammalian predator guild with a quantitative approach. Our analysis is based on the fauna of the SCF, assuming temporal and geographical coexistence between the taxa. Some aspects of the morphology of the

Santacrucian sparassodonts are analyzed in the assumption that these features reflect the ecological requirements of the species. This study is to test the hypothesis that the guild of the Santacrucian terrestrial mammalian predators was structured by character displacement (morphological differentiation among coexisting species) to diminish interspecific competition (Dayan and Simberloff 2005).

## Materials and Methods

We produced an analysis of the 11 sparassodont species from the SCF by comparing the morpho-functional disparity of the three principal ecological variables: body mass, diet, and locomotion (Table 1). We used body mass estimations of Ercoli and Prevosti (2011), which were obtained from allometric equations between the centroid size of the postcranial elements and body mass of extant predators. For incomplete specimens, body mass was calculated with the dental equation of Myers (2001; Ercoli and Prevosti 2011). Dietary inferences were taken from Prevosti et al. (2013), which are based on the Relative Grinding Area (RGA) index. The RGA index is the square root of the talonid area divided by the trigonid length and is inversely correlated with carnivory (Van Valkenburgh 1989). Locomotion was assessed using the Relative Warp axis of the geometric morphometric analysis of the shape of the distal humerus in anterior view and was taken from Ercoli et al. (2012). Unfortunately only five sparassodonts could be included in the locomotor analysis due to preservation.

We statistically evaluated the guild structure of the extinct South American predators. For univariate data (body size and RGA), we used the one-tail V test proposed by Poole and Rathcke (1979) and modified by Williams (1995). The V value is the variance in the distances between the species when sorted by one parameter (Williams 1995). For multivariate data, humerus shape or the combination of the proxies, we used the test of Clark and Evans (1954, 1979). The mean of the nearest neighbor distances was divided by the value expected by chance to obtain R. The tests were calculated with the computer program R 2.14.1 (R Development Core Team 2011) and the significance was estimated with 10,000 random samples from a uniform distribution that covers the range of values observed in each variable. For the univariate analyses, we use natural log-transformed variables to obtain a normal distribution. For the multivariated test in the humerus analysis, RW axes were used in the Clark-Evans test. In the analyses of the combination of the ecological proxies, we performed a Principal Component Analysis (PCA) and the principal component axes were used in the Clark-Evans test. In addition, we performed the V test for body mass of Santacrucian terrestrial birds, and birds together with sparassodonts.

**Fig. 1** Cranium and mandible of the Santacrucian sparassodonts. *Arctodictis munizi*, CORD PZ 1210 (**a, b**); *Borhyaena tuberata*, MPM-PV 3625 (**c**), MACN-A 12700 (**d**); *Prothylacynus patagonicus*, MACN-A 5931-5937, juvenile specimen (**e**), MACN-A 706-720 (**f**); *Lycopsis torresi*, MLP 11-113 (**g**); *Cladosictis patagonica*, MACN-A 5927-5929 (**h, i**); *Sipalocyon gracilis*, YPM PU15154 (**j**), YPM PU15373 (**k**); *Pseudonotictis pusillus*, MLP 11-26 (**l**); *Perathereutes pungens*, MACN-A 684 (**m**). Scale bar= 50 mm
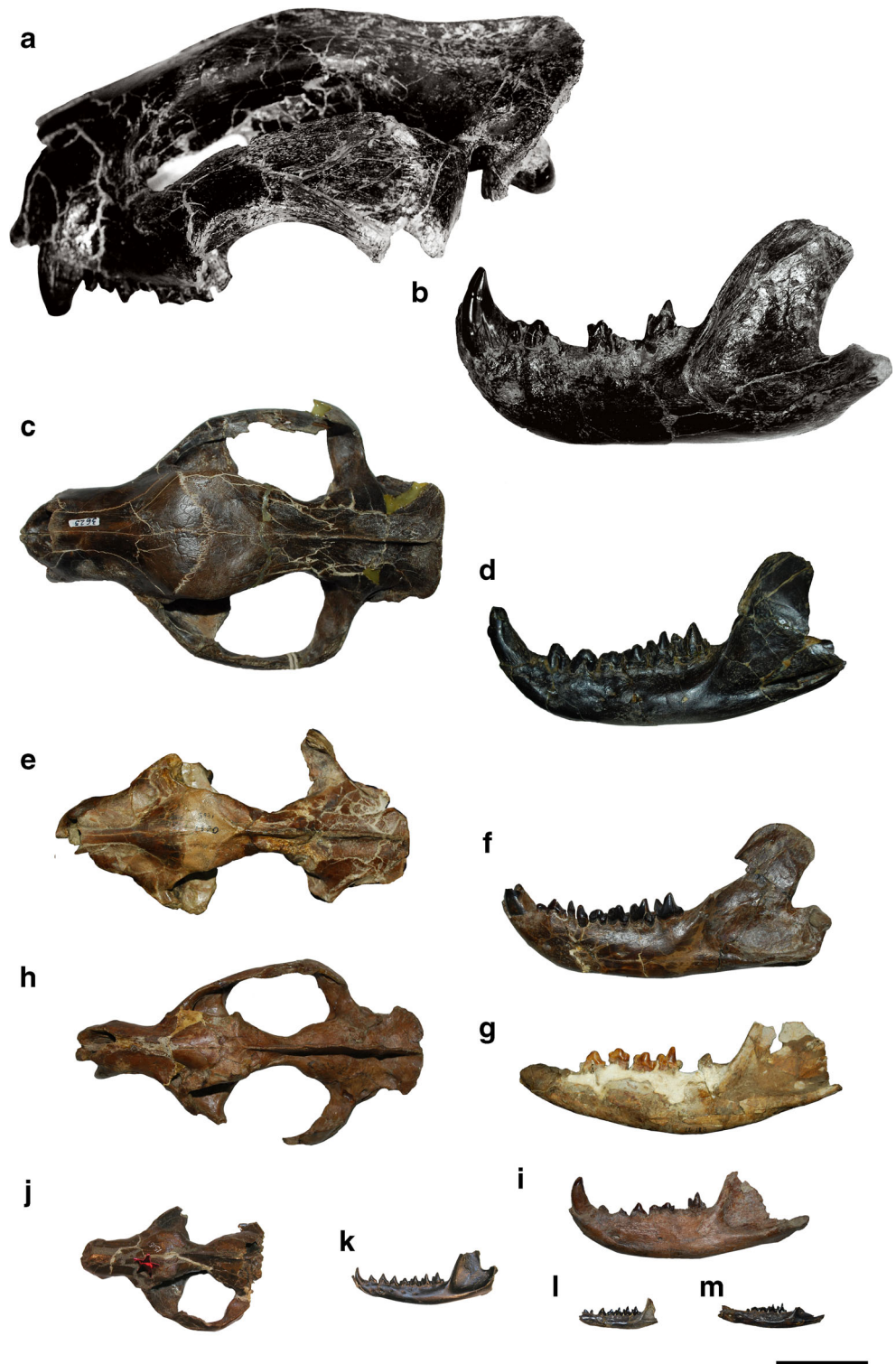


We inferred typical and maximum prey size for each sparassodont taxon. Due to the absence of equations based on living marsupials or other mammalian predators, we followed the methodology described for body mass estimations, and the data published by Van Valkenburgh and Koepfli (1993) and Van Valkenburgh and Hertel (1998) for typical and maximum prey size (TPM and MPM), and predator body mass, for canids and felids, respectively. We combined these datasets in one equation, using least square regression of natural log-transformed data. Log bias de-transformation was corrected using the mean of these three coefficients (Quasi-Maximum Likelihood Estimator, QMLE; Smearing

**Table 1** Species and dataset analyzed in this study. Body Mass (BM) values were taken from Ercoli and Prevosti (2011), based on the centroid size values of the postcranial elements (a) and the equations of Myers (2001) based on dental measurements (b). The Relative Grinding Area (RGA) values were obtained from Prevosti et al. (2013), calculated on the m4. The Relative Warp (RW) coordinates of the first fourth axis of the morphospace of the humerus constructed by geometric morphometric analysis from the consensus of procrustes coordinates, taken from Ercoli et al. (2012)

| Species | Size | | Locomotion | | | |
|---|---|---|---|---|---|---|
| | BM (kg) | RGA | RW 1 | RW 2 | RW3 | RW4 |
| **Borhyaenoidea** | | | | | | |
| *Acrocyon sectorius* | 28.70[b] | 0.00 | | | | |
| *Arctodictis munizi* | 51.60[b] | 0.00 | | | | |
| *Borhyaena tuberata* | 36.42[a] | 0.00 | +0.1875 | −0.0024 | −0.0096 | +0.0079 |
| *Lycopsis torresi* | 19.40[b] | 0.30 | | | | |
| *Prothylacynus patagonicus* | 31.79[a] | 0.17 | −0.0848 | +0.0069 | −0.0565 | −0.0041 |
| **Hathliacynidae** | | | | | | |
| *Acyon tricuspidatus* | 8.00[b] | 0.30 | | | | |
| *Cladosictis patagonica* | 6.60[a] | 0.17 | +0.0003 | +0.0406 | +0.0146 | +0.0246 |
| *Pseudonotictis pusillus* | 1.17[a] | 0.30 | −0.0357 | −0.0641 | +0.0145 | +0,0090 |
| *Perathereutes pungens* | 2,50[b] | 0.34 | | | | |
| *Sipalocyon gracilis* | 2.11[a] | 0.33 | −0.0672 | +0.0190 | +0.0369 | −0.0216 |
| *Sipalocyon obusta* | 2.06[b] | 0.27 | | | | |

Estimate, SE; and Ratio Estimate, RE; Smith 1993). The Phylogenetic Eigenvector Regression (Diniz-Filho et al. 1998) was used to control the phylogenetic pattern using the topologies published by Johnson et al. (2006) for felids (the position of *Panthera onca* and *P. pardus* followed Davis et al. 2010) and Prevosti (2010) mainly for canids, complemented by Lindblad-Toh et al. (2005) for the position of the *Vulpes* species. Body mass of potential prey species of the SCF were taken from Vizcaíno et al. (2012b).

For our study, we chose a Coarse Grain Approach (e.g., Van Valkenburgh 1991) to examine the vertebrate taxa from the entire SCF. We included a time averaging of several million years, with the assumption of coexistence. Alternatively, it would be ideal to use single assemblages from individual localities and fossil levels (e.g., Vizcaíno et al. 2010; Kay et al. 2012b), but this generally offers an insufficient sample size for meaningful results, with loss of diversity and insufficient representation of predators (Prevosti et al. 2012; see also Croft 2013). Furthermore, the presence of time averaging could be excluded in a mass-death assemblage (quickly covered by sediments and without reworking), but not in most deposits, even if they are restricted to one fossil level of one locality as is the case of SCF assemblages (Flessa 2001). Because we are interested in broader patterns in the predator guild structure and the potential predator-prey relationships, we prefer the Coarse Grained Approach. Our results could be easily applied to samples limited to one fossil level/ locality.

The specimens of Sparassodonta mentioned in the text manuscript are housed in the following institutions: MPM-PV, Museo Regional Provincial "Padre M. J. Molina," Argentina; CORD-PZ, Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de Córdoba, Argentina; MACN-A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Ameghino Collection), Argentina; MLP, Museo de La Plata, Argentina; YPM: Yale Peabody Museum, USA (YPM PU).

## Results

The analysis of estimated values of the log transformed body mass for the 11 Santacrucian sparassodonts ($V=0.007$; $p=0.458$) suggests that the sample has a non-significant pattern of evenly spaced (uniform) distribution. The 11 species fall on the body mass axis in three widely distributed groups. The two main groups are the smaller hathliacynids and the larger borhyaenoids, while two medium-size hathliacynids, *Cladosictis patagonica* and *Acyon tricuspidatus*, lie between (Fig. 2a).

The analysis of the log transformed RGA values for the 11 Santacrucian sparassodonts ($V=0.0228$; $p=0.002$) demonstrates a significant pattern of aggregated distribution. The distribution of the species along the RGA axis reveals a clear clustered pattern. The three borhyaenids that have no talonid (*Acrocyon sectorius*, *Borhyaena tuberata*, and *Arctodictis munizi*) cluster together at zero. *Cladosictis patagonica* and *Prothylacinus patogonicus* form a second cluster on the middle of the axis. The remaining hathliacynids and borhyaenoids with basined and cuspated talonids form another group with greater values of RGA (Fig. 2b).
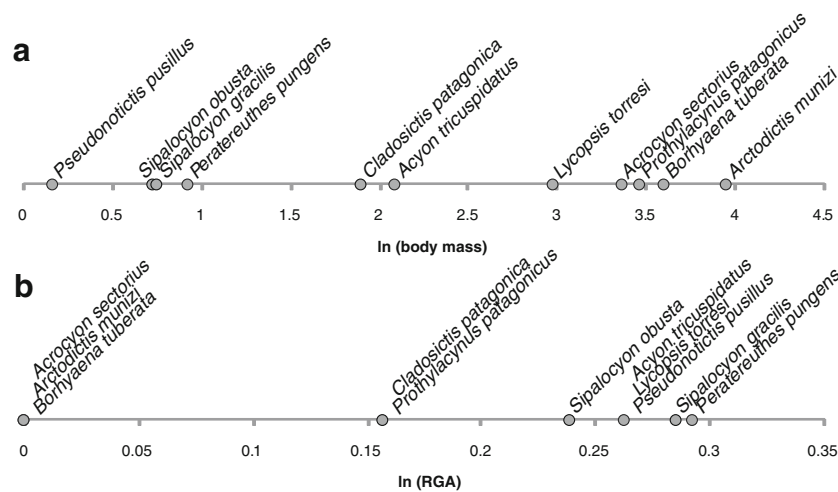
**Fig. 2** Distribution of Santacrucian sparassodont species in body mass axis (**a**), and the Relative Grinding Area (RGA) index axis (**b**)

The analysis of the RWs values of the morphospace of the humerus was completed with five Santacrucian sparassodonts that have postcranial material (*B. tuberata*, *Pr. patagonicus*, *C. patagonica*, *Sipalocyon gracilis*, and *Pseudonotictis pusillus*). The values obtained ($R = 2.30$; $p < 0.0001$) suggest a significant pattern of evenly spaced distribution with all the species roughly equidistantly separated. The distances between the nearest species vary only one order of magnitude (Fig. 3a, b).

The analysis of the PCs values of log transformed RGA and the RWs values of the morphospace of humerus of the five species reveals a significant pattern of evenly spaced distribution ($R = 3.31$; $p < 0.0001$). An even clearer evenly spaced pattern was obtained on analyzing the PCs values of log transformed body mass and the RWs values of the morphospace of humerus ($R = 3.66$; $p < 0.0001$). In these morphospaces, the species distribution reflects a stronger evenly spaced pattern than demonstrated by the humerus shape alone. However, the PCs values of log transformed RGA and body mass for the 11 species result in a random pattern ($R = 1.11$; $p < 0.2703$, consistent with the same analysis including only the five species with postcranial remains).

The analysis of the PCs values of all variables together for the five Santacrucian sparassodonts reveals a significant pattern of evenly spaced distribution ($R = 2.24$; $p < 0.0001$). The species are roughly equidistant and the distances between the nearest species vary approximately by one order of magnitude (Fig. 3c, d). *Borhyaena tuberata* separates from other species because of it greatest size in the group, a humerus with robust distal articular condyle, and minimum RGA value. *Cladosictis patagonica* is larger than *S. gracilis* and *Ps. pusillus*, and the humerus has more robust articular condyles and a more reduced lateral epicondylar crest than *Pr. patagonicus*. *Sipalocyon gracilis* differs from other species of the group with its smaller size and greater RGA value. *Pseudonotictis*

*pusillus* is the smallest of the group and has a wide and distally expanded medial condyle in the humerus, particularly in comparison with *C. patagonica*.

In the prey size estimation analyses (Fig. 4; Supporting Information Table S1), the MPM equation ($\ln MPM = \ln$ body mass $*1.241 + 0$) is significant, with a $R2 = 0.743$, and a percentage of predicted error (PE%) of 30.15. The log bias coefficients are QMLE$=1.25$, SE$=1.26$, RE$=1.12$. The TPM equation ($\ln TPM = \ln$ body mass $*1.77 + 0$) is significant, but has a poorer fit, with a $R2 = 0.568$, and a percentage of predicted error (PE%) of 135.52. The log bias coefficients are QMLE$=1.94$, SE$=1.87$, RE$=1.04$.

## Discussion

Ecological Relationships Between Sparassodont Species

Our results show that the sparassodonts of the SCF had an evenly spaced distribution in the morphospace by locomotor analysis and combining this ecological proxy variable together with body mass, diet, or both (Figs. 2a, b and 3). The stronger evenly spaced pattern was obtained combining locomotion and body mass together. The character segregation could be interpreted as the result of niche partition by historical competition (Argot 2004b; Ercoli and Prevosti 2011; Prevosti et al. 2012). Alternatively, the lack of a significant evenly spaced distribution does not necessarily mean that there was strong competition in the assemblage, especially when there is little overlap between species in the studied variables (e.g., body mass).

It has been noted that body mass of the Santacrucian sparassodonts varies from 1 kg (*Ps. pusillus* and *Peratthereutes pungens*) to more than 50 kg (e.g., *Ar. munizi*) (Fig. 2). The pattern of distribution of body mass values is evenly spaced, although the statistical analysis reveals that the structure does
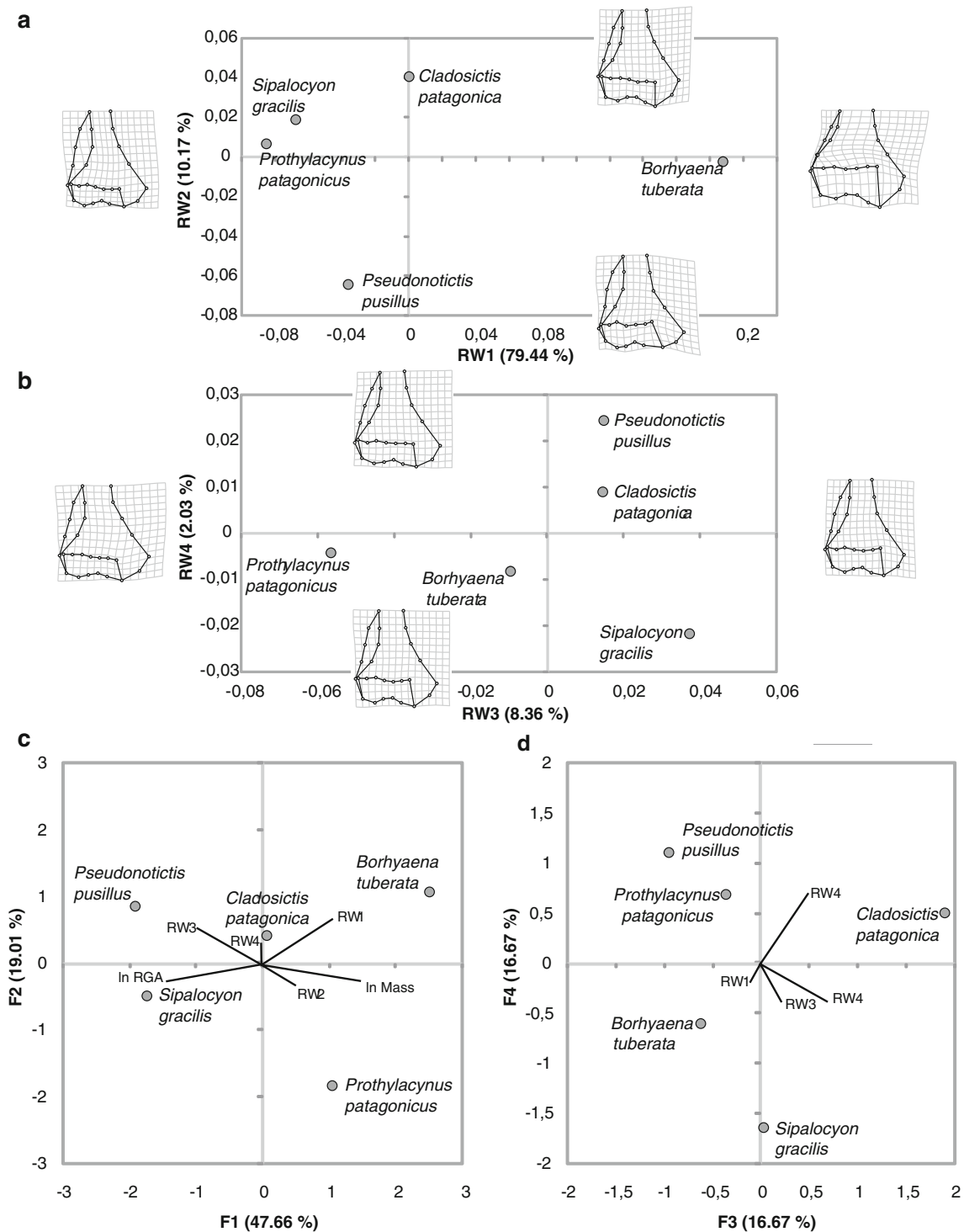
**Fig. 3** Morphospace of humerus shape of the five Santacrucian sparassodonts with this element preserved, Relative Warps 1 vs. 2 (**a**), and Relative Warps 3 vs. 4 (**b**). Multidimentional space of all proxies variables resumed by a Principal Component Analysis, Factor 1 vs. 2 (**c**), and Factor 3 vs. 4 (**d**)

not differ significantly from random cases. The analysis of body mass together with the locomotor proxy reveals a clearer, evenly spaced pattern than the analysis of body mass or the humerus alone. This demonstrates that an emerging multidimensional

character displacement occurs when body mass combined together with other variables promote the segregation of the species in the morphospace. Species with similar postcranial morphology, and assumed similar locomotor strategies,
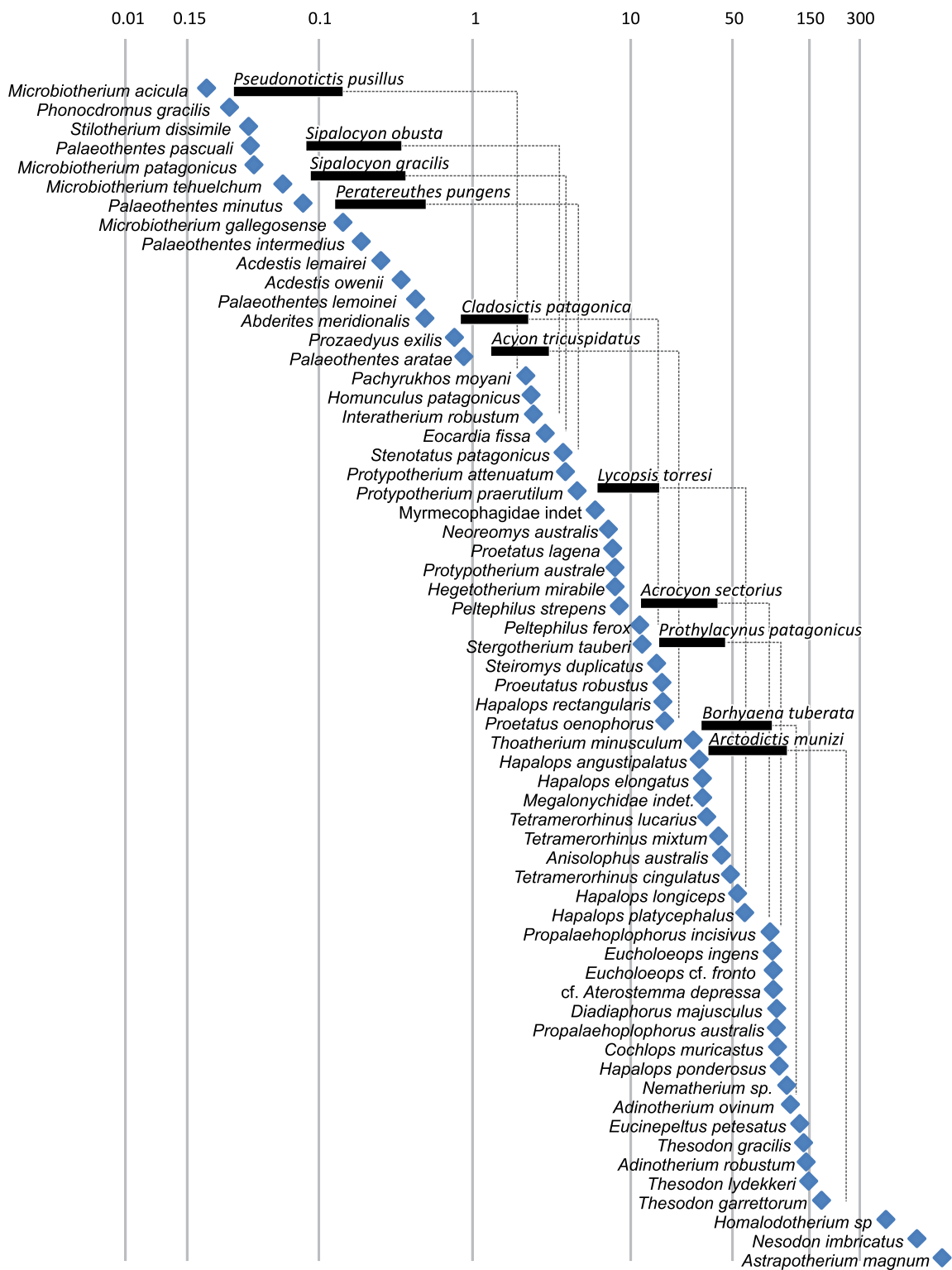
**Fig. 4** Typical and maximum prey size for the 11 Santacrucian sparassodont species. The horizontal axis indicates body mass. Gray diamonds represent the mean body mass estimates of some potential prey present of the Santa Cruz Formation. Black bars represent the range estimates typical prey size (TPM) for sparassodont species. Dotted lines indicate the mean estimated value of the maximum prey size (MPM)

occupied alternative ecological niches by means of different body mass (Ercoli and Prevosti 2011).

The Santacrucian sparassodonts have molars with reduced Relative Grinding Area (RGA from 0.34 in *Pe. pungens* to

zero in *B. tuberata, Acr. sectorius,* and *Ar. munizi*; Prevosti et al. 2013), which suggest a hypercanivorous diet. The morphological description of several species (Marshall 1977b, 1978; Argot 2004a; Forasiepi et al. 2004; Blanco et al. 2011) is consistent with this inference, although other dissimilar features of the morphology are not distinguished with the RGA. Our results based on the RGA indexes show that the Santacrucian species are grouped in clusters, defining a significant aggregated pattern (Fig. 2b). So, considering diet alone, it would result in strong competition between some species. However, when the locomotor and diet proxies are considered together, a clearer and more marked distribution emerges than observed on the morphospace of the humerus alone. This result points to an emerging multidimensional character displacement, with diet contributing to the segregation in the morphospace of some species with similar locomotor type (e.g., *S. gracilis* and *C. patagonica*). This result also reveals that smaller variations of this proxy, strongly correlated with size and structured by phylogeny (Prevosti et al. 2012, 2013), is sufficient to diminish interspecific competition.

Evolutionary constraints (Werdelin 1986, 1987), the global biogeographic pattern and its associated biotic components (Sánchez-Villagra 2013) could have played a role in reducing the disparity of morphologies in metatherians. The cluster of species with RGA=0 has been considered a monophyletic clade (Borhyaenidae; Forasiepi 2009) formed by medium to large-sized species. Among the non-zero RGA values (Hathliacynidae and basal borhyaenoids), the smallest hathliacynids (*Pe. pungens*, *Ps. pusillus*, and *Sipalocyon* spp.) have higher RGA values than the larger species (*C. patagonica*). Excluding *Ac. tricuspidatus*, there is a clear positive correlation between body mass and hypercarnivory, as observed in placental predators (Van Valkenburgh et al. 2004; Raia et al. 2012). This is consistent with the energy balance in acquiring large body masses that require the consumption of larger prey and larger quantities of meat (Carbone et al. 1999, 2007; Van Valkenburgh et al. 2004).

It is also possible that the RGA is not a good dietary predictor for carnivorous metatherians. The index allows comparisons with a wide sample of taxa, including the recent species in which diet is known. However, it results in a simplification, and several aspect of diet cannot be explained. For example, it is impossible to recognized bone-cracker forms, the inclusion of insects in diet, or the prey-size, which can be deduced with other analyses (e.g., Blanco et al. 2011; Zimicz 2011; Prevosti et al. 2012). *Borhyaena tuberata* and *Ar. munizi* were considered as opportunist bone-crackers (*B. tuberata*: Argot 2004b contra Blanco et al. 2011; *Ar. munizi*: Forasiepi et al. 2004; Prevosti et al. 2012) because of the tall mandible, strongly connected (*B. tuberata*) or fused (*Ar. munizi*) symphysis, long tooth roots, bulbous cusps, and microfractures in the tooth enamel. Although some bone-crackers are active

predators (e.g., *Crocuta crocuta*, Wilson and Mittermeier 2009), they are usually associated with the presence of other more efficient predators that partially consume and abandon the carcasses (Viranta 1996; Argot 2004b). In the Santacrucian ecosystems, this primary role could be occupied by birds (i.e., Phorusrhacidae) and sparassodonts could then have taken advantage of the animals already dead by robbery or attacked weakened animals by diseases, injury or age.

*Perathereutes pungens*, *S. gracilis*, *Ac. tricuspidatus*, and *Ps. pusillus* have larger talonid basins. Argot (2003a), through comparative descriptions, and Blanco et al. (2011), through analysis of the bite mechanism and force, suggested that *C. patagonica* had low bite force and more specialized capabilities in capturing small prey than *Pr. patagonicus* and *B. tuberata*. *Prothylacynus patagonicus*, with moderate bite force, strong neck, and manipulative and scansorial capabilities could have ambushed, caught, dragged, and moved large prey. Feeding strategies that could reduce the intraspecific competition are not evidenced in the RGA.

The morphology of the postcranium suggests that the Santacrucian predator guild included species with different locomotory habits. *Sipalocyon gracilis* and *Pr. patagonicus* have wide lateral epicondylar crest and very low articular condyle, suggesting strong muscular control of the forearm and carpus, and a wide range of movements of the elbow that can be related to scansorial or arboreal adaptations (Argot 2004a, b; Ercoli et al. 2012). *Pseudonotictis pusillus* has a similar morphology of the distal humerus with a wide and distally located medial epicondyle, suggesting similar use of the environment. Among them, *Pr. patagonicus* seems to be more specialized in using the arboreal substrate with better developed grasping capabilities (Argot 2003a; Ercoli et al. 2012). *Cladosictis patagonica* differs from the other taxa by having a high and vertical medial margin of the articular condyle, with deeper trochlea, and proximo-distally expanded medial epicondyle, suggesting strong movements of the elbow partially restricted to the parasagittal plane. *Cladosictis patagonica* was probably less specialized in the use of the arboreal substrate and could have digging capabilities (Muizon 1998; Argot 2003a, b, 2004b; Ercoli et al. 2012). *Borhyaena tuberata* has higher and deeper trochlea, reduced lateral epicondylar crest and medial epicondyle, which suggest a more restricted parasagittal movement at the elbow level and reduced manipulation capabilities. A similar humerus morphology was recorded in *Ar. sinclairi* (Forasiepi 2009) from the Colhuehuapian (the South American Land Mammal Age that precedes the Santacrucian age), and then traced for the Santacrucian *Ar. munizi*. If so, *B. tuberata* and *Ar. munizi* were more terrestrial and with less manipulation capabilities than other sparassodonts in the SCF and *B. tuberata* the most adapted for cursoriality (Sinclair 1906; Marshall 1977a; Muizon 1998; Argot 2003a; Ercoli et al. 2012). In our analysis of shape of humerus, the Santacrucian sparassodonts show a

significant evenly spaced pattern of distribution, reflecting the different locomotor specializations. An evenly spaced pattern of species distribution is obtained for all paired analysis in which the locomotion proxy was included. These results support the hypothesis of character displacement, and the pattern of segregation seen here is significantly different than expected by chance. Different locomotor specializations in the coexistent species would be a crucial factor to diminish the intraspecific competition.

When the variables of body size, locomotion, and diet are analyzed together the pattern of distribution of the Santacrucian sparassodonts is evenly spaced. Locomotor diversification is the principal ecological factor that may have allowed the coexistence of the 11 mammalian predator species during the Santacrucian age. Body size and secondarily diet diminished the intraspecific competition, but those factors are not sufficient to completely segregate the taxa in the morphospace (Ercoli and Prevosti 2011). For example, dietary choice could diminish the competitive interaction between *C. patagonica* and *Ac. tricuspidatus*, which are similar in size, or more clearly between the highly hypercarnivore borhyaenids and *Pr. patagonicus.* The analyses of diet and locomotion, and body mass and locomotion provide a more marked evenly spaced pattern than is obtained when all three variables are analyzed together. This demonstrates that locomotion is the key factor in the predator guild in the SCF. Other ecological variables, not contemplated in our analysis (e.g., diurnal vs. nocturnal habits; e.g., Kay et al. 2012a), could provide in the future a better understanding of the niche segregation of the Santacrucian sparassodonts.

Studies with living carnivore communities show that intraguild interference and killing is common in recent Carnivora. Diet overlap, high taxonomic diversity, and primarily similar body size increase the chance of competition, with the larger species employing aggressive displacement strategies by chasing and even killing the smaller predators (Palomares and Caro 1999; Donadio and Buskirk 2006; Hunter and Caro 2008). This behavior is most prevalent when the larger predators are between 2 to 5.6 times the body size of the preyed predator species (Donadio and Buskirk 2006). It is reasonable to conclude that this pattern would have been equally likely among sparassodonts. Although we found good intraguild segregation that would have minimized competition between sparassodont species, intraguild competence, interference and predation, particularly in time of low resource availability (Jones and Barmuta 2000), would be likely. Within sparassodonts, candidate pairs that met the killer/killed body mass rate suggested by Donadio and Buskirk (2006) would include *Artodictis* displacing *Lycopsis*; *Lycopsis*, *Borhyaena*, and *Prothylacynus* displacing *Cladosictis* (adding *Acyon* in the case of *Borhyaena*), and finally, *Cladosictis* and *Acyon*, displacing *Sipalocyon*, *Perathereutes*, and *Pseudonotictis* (Table 1 for body masses).

Ecological Relationships with Bird Predators

Birds were the second major group of predators in the SCF. These include four phorusrhacid species, one cariamid, one anatid, and two falconids (Degrange 2012; Degrange et al. 2012). The largest species was the anatid *Brontornis burmeisteri* in excess of 300 kg and probably a scavenger (Tonni 1977). The largest of the "terror birds" was *Phorusrhacos longissimus* of about 100 kg. This species was considered an active predator of large prey because of its rigid cranium, high bite force, and stockiness of neck and limbs (Degrange 2012; Degrange et al. 2012). Smaller predators are represented by the "terror birds" *Patagornis marshi* (30 kg), *Psilopterus lemonei* (10 kg), and *Psilopterus bachmanni* (4.5 kg), and the cariamid *Cariama santacrucensis* (1.5 kg). When the pattern of body mass of terrestrial birds is analyzed, we obtained an evenly spaced pattern of distribution ($V=0.001$, $p=0.0027$ including *Brontornis*; $V=0.002$, $p=0.0089$, excluding *Brontornis*), with almost no superposition in the distribution of the species in the morphospace. In contrast, in the analysis of body mass of terrestrial birds and sparassodonts together, the pattern is non-significant ($V=0.002$, $p=0.2493$). These results do not confirm the presence of an ecological character displacement, although most sparassodonts mostly alternate with the "terror birds" species, with only a clear cluster between *Acr. sectorius, Pr. patagonicus,* and *Patagornis marshi* (Fig. S2). Thus, if the ecological impact of body size (i.e., prey size) can be taken as a comparable proxy between birds and mammals, potential competition is clearer between these three species. Although, other factors could affect the relationship between the two taxonomic groups and their direct comparison. These analyses include the implicit assumption that a terrestrial bird of a given body mass is more affected by competition with a sparassodont of similar size than with others mammalian predators. Degrange (2012) suggested that predator birds as phorusrhacids cannot hunt on prey greater than themselves, because birds cannot use the forelimbs to manipulate their prey and only depend on the movements of the head, neck, and hind limbs. However, some of the larger extant predator birds (e.g., eagles) regularly overpower animals as large or larger than themselves (Hutchins 2003). The present day does not provide any flightless carnivorous birds to draw comparisons with, leaving predation strategies to speculation.

The locomotory specializations between terrestrial birds and mammals are very different, and may be a relevant factor of segregation. The morphology of the limbs of terrestrial birds suggests strong cursorial specializations (Degrange et al. 2012), which are not found in sparassodonts. Recent studies on the SCF suggest that the environments was heterogeneous, with patches of forests, semi-arid forests, and open areas (Barreda and Palazzesi 2007; Brea et al. 2012; Kay et al. 2012a). This landscapes offered suitable habitats to accommodate the different predators with their different locomotor

specializations (Argot 2004b), diminishing interactions between terrestrial birds and sparassodonts.

We agree with the hypothesis that the terrestrial birds occupied a different ecological niche to the sparassodonts in the SCF (Argot 2004b). Historical competition (Croft 2001, 2006) and locomotory differences segregated the taxa into different predatory strategies. This could impact on the evolution of the sparassodonts, a group that failed to develop a strict cursorial morphotype.

Potential Predator-Prey Relationships

The mammalian assemblage of the SCF is the richest from the Cenozoic of South America. Previous paleoautoecological studies (Tauber 1997a, b; Argot 2003a, b, 2004a, b; Vizcaíno et al. 2012b) provided the starting point to examine the paleosynecological relationships of the SCF predators. Croft (2001, 2006) considered that the number of sparassodont species is smaller in comparison with the number of potential prey. This author based his conclusions on a predator/prey ratio lower than the expected found in placental assemblages (see also Vizcaíno et al. 2010). Alternatively, recent reviews (Kay et al. 2012b; Prevosti et al. 2012) suggested that the sparassodont diversity was higher than previously thought, and that the predator/prey rate of the SCF was similar to that observed in living associations.

The TPM and MPM estimation were both significant. However, the TPM should be considered with caution because the PE% is very high and the R2 is low. Based on the results obtained in this paper, *Ar. munizi*, the largest sparassodont in the SCF, could have mainly preyed upon animals between 30 kg to 90 kg, to an extreme upper limit of 300 kg. This would include litopterns (e.g., *Thesodon*, *Tetramerorhinus,* and *Diadiaphorus*), sloths (*Hapalops* and *Eucholoeops*) and toxodontids (*Adinotherium*) (Fig. 4). This prey body-mass range includes the juveniles of the largest herbivores (Prevosti et al. 2012), while the adults would be out of scope (*Homalodotherium*, *Nesodon*, and *Astrapotherium*). These very large herbivores possibly could be preyed by the largest phorusrhacids or even lack any potential predator. *Arctodictis munizi* has bone-cracking morphological features that enable scavenging on these massive herbivores (Forasiepi 2009; Prevosti et al. 2012). *Borhyaena tuberata* has a smaller body mass resulting in a TPM between 17 kg and 48 kg, and a MPM of 128 kg. This range would have included the megalonychids and megatheriids such as the *Hapalops* species but the large adult litopterns (e.g., *Theosodon* species) are higher than the predicted MPM. The terrestrial capabilities and the more developed cursorial capabilities in *Borhyaena* compared with other Santacrucian sparassodonts (Argot 2003a; Ercoli et al. 2012) would favor hunting more agile herbivores in the SCF environment.

*Acrocyon sectorius, Pr. patagonicus,* and *L. torresi* with the TPM between 6 kg to 37 kg would have preyed upon smaller vertebrates (Fig. 4), with a MPM between 59 and 109 kg. The prey diversity on this body mass range is large in the SCF and includes rodents (e.g., *Neoreomys* for *L. torresi*, *Steiromys* for the three species), cingulates (*Peltephilus*, *Stegotherium*, *Proeutatus*), sloths (*Hapalops*) and notoungulates (*Hegetotherium, Protypotherium*). The possibility of these taxa hunting on semiarboreal forms, such as *Steiromys* and *Hapalops*, agrees with the scansorial locomotion inference for *Pr. patagonicus*. *Neoreomys* as a potential prey for *L. torresi* agrees with its inferred more terrestrial locomotion (Argot 2004a, b). *Lycopsis longirostrus* preyed upon *Scleromys* (Dinomyidae) as this rodent was found during preparation in the area of the digestive cavity of the sparassodont (Marshall 1977b), and agrees with the inclusion of terrestrial rodents in diet of the SCF sparassodonts.

The largest hathliacynids *C. patagonica* and *Ac. tricuspidatus* would have typically preyed upon species between 1 kg and 3 kg, although larger taxa were not excluded (maximun MPM about 16–20 kg). The TPM includes rodents (*Eocardia*), notoungulates (*Interatherium*), small marsupials (*Palaeothentes*), cingulates (*Prozaedyus*, *Stenotatus*), and primates (*Homunculus*) (Prevosti et al. 2012). The fossorial capabilities suggested for *C. patagonica* (Ercoli et al. 2012), and the prey size inferred for the taxon agree with the possibility of preying on fossorial mammals (e.g., *Pachyrukhos*, *Protypotherium*, *Hegetotherium*, *Interatherium*; Cassini et al. 2012). Opportunist items, such as amphibians, reptiles, invertebrates, birds, and eggs, available on terrestrial and arboreal substrates should be also considered (Argot 2004b).

The TPM for the smallest Santacrucian species, *Pe. pungens*, *S. obusta*, *S. gracilis*, and *Ps. pusillus*, suggest predation on the smaller marsupials (microbiotherians and paucituberculatans). The scansorial locomotion inferred for these sparassodonts (Argot 2003b, 2004b; Ercoli et al. 2012) would allow opportunities in both substrates. The inclusion in the diet of other non-mammalian items would be likely.

These estimations are congruent with the predator-prey relationship observed in living placentals, where carnivores with an average body mass above 25 kg mainly feed on terrestrial herbivorous mammals with a body mass similar to their own or larger (Carbone et al. 1999), and ideally between half and twice their own body mass (at least in large carnivores, see Owen Smith and Mills 2008). Smaller carnivore placental mammals display less specialized diet and locomotion traits (Jenkins 1974; Prevosti et al. 2012). The smallest sparassodonts were probably similar in their behavior due to fewer potential vertebrate prey and their smaller physical scale (Prevosti et al. 2012).

**Concluding Remarks**

The Cenozoic of South America had a predator guild of great breadth, with metatherian mammals (Sparassodonta) and

birds (principally the Phorusrhacidae), as well as other reptiles and occasionally frogs. There is no current analog in modern ecosystems to compare and understand the mechanism of the autoecological and synecological interactions that existed, so other methodologies must be sought. The SCF provides a rich vertebrate fossil record in which to explore these interactions. Our study employs different statistical procedures to allow an insight of the Santacrucian paleoguild of predators, using autoecological and quantitative information available for each species, and to study some of the interspecific ecological interactions.

The guild reconstruction of the Santacrucian sparassodonts suggests that there was a good ecological separation within species, imposed by the combination of primarily locomotion and body size and secondarily diet.

The terrestrial birds and the sparassodonts would have partially overlapped in body mass, although other factors including locomotory and habitat preferences probably reduced competition.

The proxies of body size and especially locomotion had the greatest influence in the evenly spaced pattern structure of the guild and allowed major differences of the repertory of potential prey for each species. The character displacement observed in these ecological variables would diminish the interspecific competition, allowing the coexistence of 11 Santacrucian metatherian hypercarnivorous species.

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