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Mandible morphology and diet of the South American extinct metatherian predators (Mammalia, Metatheria, Sparassodonta)

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ABSTRACT: Sparassodonta is a diverse group of extinct metatherian predators that include forms with diets ranging from omnivores to hypercarnivores, including potential bone-crushers and sabre-tooth specialised species. Most of the previous dietary studies on the group were based on qualitative approaches or dental morphometric indexes and/or bite force estimations. In this study, we explore the evolution of mandible shape and diet of Sparassodonta in a comparative phylogenetic framework, using geometric morphometric tools and allometric and discriminant analyses. We analysed the mandible shape of 142 extant species of marsupials and placental carnivores, and 15 fossil sparassodont species. We found that the relationship between shape and size of the mandible is strongly structured by phylogeny, where the more derived borhyaenoids tend to possess stronger and larger mandibles. Derived borhyaenoid sparassodonts and basal borhyaenoids were classified as hypercarnivores (with short and robust mandibular body). Hathliacynid were classified as mesocarnivores or as hypercarnivores, but with lower probabilities and less specialised morphologies (with a long and slender mandible). Although dental morphology suggests that most of the species of Sparassodonta would have been hypercarnivores, the robustness of the mandible seems to be informative regarding the prey size and degree of specialisation. The relationship between mandibular size and shape, and talonid/trigonid relative size, is strongly influenced by the phylogenetic legacy, suggesting that ecological factors could have influenced the evolution of the sparassodonts.

KEY WORDS: Borhyaenoidea, evolutionary constraints, geometric morphometrics, Hathliacynidae, palaeoecology

Sparassodonta is a monophyletic group, basal to the crown group Marsupialia (Forasiepi 2009), which includes more than 50 species of extinct marsupial predators. They inhabited the South American continent during most of the Cenozoic (e.g., Marshall 1978; Forasiepi 2009; Prevosti *et al.* 2013), and shared the predatory guild with phorusrhacoid 'terror' birds, large terrestrial crocodiles (Sebecidae), giant snakes (Madtsoiidae) and, in the last part of the Tertiary, with placental carnivores (Carnivora) (Simpson 1950, 1980; Patterson & Pascual 1972; Reig 1981; Gasparini 1984; Albino 1996; Pascual 2006; Forasiepi *et al.* 2007; Riff *et al.* 2010; Prevosti & Soibelzon 2012; Prevosti *et al.* 2012a, b). The Sparassodonta had a wide range of body sizes and locomotor habits, from the scansorial opossum-like *Pseudonotictis pusillus* of about 1 kg, to the large terrestrial *Thylacosmilus atrox* of near 100 kg (Wroe *et al.* 1999, 2003, 2004, 2013; Argot 2003a, b, 2004a, b, c; Vizcaíno *et al.* 2010; Ercoli & Prevosti 2011; Ercoli *et al.* 2012; Prevosti *et al.* 2012b), and a variety of morphological adaptations to carnivory, reaching extreme morphotypes such as the sabertoothed *Thylacosmilus atrox* (Marshall 1977a; Goin & Pascual 1987; Argot 2004a; Forasiepi & Carlini 2010; Prevosti *et al.* 2010; Engelman & Croft 2014; Ercoli *et al.* 2014; Forasiepi *et al.* 2014). The stratigraphic range of Sparassodonta goes from early Paleocene

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(Tiupampan age, ≈64–62 Ma) to middle Pliocene (Chapadmalalan Age, ≈3.3 Ma), reaching their acme, with eleven species, during the late early Miocene (Santacrucian Age, 18–16 Ma) (Sinclair 1906; Argot 2004c; Forasiepi 2009; Prevosti *et al.* 2012b).

Most species of Sparassodonta are only known from isolated teeth or fragmentary mandibles, so previous authors made inferences of their diet by comparing the dentition of sparassodonts with that of living mammal carnivores (e.g., Marshall 1978). The dentition of sparassodonts is extremely specialised towards a carnivorous diet (Muizon & Lange-Badré 1997), but variations in tooth morphology suggest differences in the type of food ingested (Marshall 1977a, 1978, 1979, 1981). In genera where the skull and mandible are preserved (e.g., *Cladosictis*, *Borhyaena*, *Prothylacinus*), morphological differences lead to infer different biting capabilities. Additionally, postcranial evidence suggests a diversification of hunting and preying behaviours (Argot 2003a, b, 2004c; Blanco *et al.* 2011).

Sparassadonta is divided in two main clades, Hathliacynidae and Borhyaenoidea (see Forasiepi 2009). Hathliacynids include small to medium-sized sparassodonts (e.g., *Cladosictis* and *Sipalocyon*), most of them with scansorial habits, with pseudo-opposable pollex that enabled manipulative behaviour, and a generalised carnivorous dentition (Argot 2003b, 2004c; Forasiepi 2009; Ercoli *et al.* 2012; Prevosti *et al.* 2012b, 2013; Zimicz 2014). *Cladosictis patagonica* has been considered as having the most specialised dentition among hathliacynids, adapted toward hypercarnivory; however, it seems to be a species with a weak bite force when compared with other marsupials, suggesting that they only preyed on small vertebrates and perhaps had a more omnivorous diet (Blanco *et al.* 2011). Borhyaenoids are medium to large sized, and morphologically more diverse than the other clade, with most of the species showing a specialised diet towards hypercarnivory. Basal borhyaenoids, such as *Prothylacynus* and *Lycopsis,* were considered omnivores or mostly omnivores (Marshall 1977a, b, 1978, 1979, 1981), although their dental morphology, stomach contents remains (in the case of *Lycopsis longirostrus*) and the architecture of the postcranial skeleton suggests a more active predation (Marshall 1977b; Argot 2003a, 2004a, c). Proborhyaenidae (*Proborhyaena*, *Arminiheringia* and *Callistoe*) represent mostly a pre-Miocene radiation of hypercarnivore borhyaenoids (Marshall 1978), some of them considered as the largest bone cracker sparassodonts (Zimicz 2012; Forasiepi *et al.* 2015). The derived borhyaenoids (Borhyaenidae), Borhyaena and *Artodictis,* are regarded as large specialised carnivores, with robust and bulbously rooted teeth, and robust deep jaws, which led several authors to infer some capacity to crush bones (Argot 2004c; Forasiepi *et al.* 2004, 2015). Finally, the most derived borhyaenoids are the Thylacosmilidae, which convergently evolved a sabre-toothed morphology (Marshall 1976, 1978; Forasiepi & Carlini 2010).

Most of the palaeoecological reconstructions for the group were based on qualitative approaches (e.g., Marshall 1977a, 1978, 1979, 1981; Argot 2003a, b, 2004a, b; Forasiepi *et al.* 2004; Forasiepi 2009) or on dental morphometric indexes and bite force estimations (Blanco *et al.* 2011; Prevosti *et al.* 2012b, 2013). The analysis of the dental morphometric indexes suggested that most sparassodonts had hyper-carnivorous diets (Prevosti *et al.* 2012b, 2013), but this hypothesis has not yet been tested using a wider comparative sample and multivariate statistics analyses.

The main aim of this study is to explore the evolution of mandible shape in Sparassodonta, Carnivora and Marsupialia, and its relation with diet, size and phylogeny. In order to accomplish this objective, we analysed mandible shape using 2D geometric morphometric methods and multivariate techniques in a wide sample of extant species to infer dietary habits in Sparassodonta species, in particular in santacrucian taxa. We also compared our results with previous dietary inferences (e.g., Wroe & Milne 2007; Goswami *et al.* 2011), especially with those based on dental anatomy (Marshall 1977a, 1978, 1979, 1981; Prevosti *et al.* 2013; Zimicz 2014). Finally, we discuss the implications of our results for the evolutionary history of the Sparassodonta.

1. Materials and methods

1.1. Materials and taxonomic sample

The dataset studied included a total of 498 mandibles belonging to 142 species of extant marsupials (Dasyuromorphia, Didelphimorphia, Peramelemorphia and Microbiotheria) and placental carnivores (Carnivora), in addition to the 35 fossil specimens belonging to 15 species of Sparassodonta (Supplementary file 1). For extant taxa, only adult specimens with fully erupted dentition were included and, when possible, we tried to sample an equal number of males and females, up to six per species. For extinct taxa, we included specimens with fully erupted dentition and no evident deformation; fragmentary material was included as long as all landmarks could be identified. Mandibles were photographed aligning the medial surface of the mandible resting on the table or camera stand base. The sparassodont species included in this study belong to the family Hathliacynidae Ameghino, 1894, and the superfamily Borhyaenoidea Simpson, 1930 (systematic arrangement after Forasiepi 2009) (Supplementary file 1).

Since we analysed lower carnassial morphology (i.e., trigonid/talonid development of m1 in Carnivora and m4 in marsupials), we did not include taxa with reduced dentition and no carnassials (e.g., the living Pinnipedia, *Proteles*). The lower fourth molar (m4) of metatherians was chosen as an analogue of the carnivore m1 because it usually presents the more carnassial-like shape, is placed closest to the condyle and, from a biomechanical point of view, it is in the 'correct' to be an analogue for a carnassial in an adult marsupial (see Werdelin 1986, 1987; Jones 2003; Prevosti *et al.* 2012a).

We classified the species according to their diet (Supplementary file 1) following the categories proposed by Van Valkenburgh (1989) with minor modifications:

- Hypercarnivores: most of their diet is composed by other vertebrates;
- Mesocarnivores: feed mainly on other vertebrates (usually smaller species than themselves), but also plants and invertebrates;
- Omnivores: plants and invertebrates represent a large proportion of the diet;
- Herbivores: feed mostly on plant materials;
- Insectivores: feed mostly on insects.

Data on extant species diet was taken from the bibliography (Supplementary file 1). We are aware of the limitations of classifying a continuous character such as diet in discrete categories, but since, for many of the species included, there are no detailed diet analyses by using this classification scheme, we were able to include a larger sample of extant species, improving the representation of the morphological variability present in living species of carnivores and marsupials. In the case of otters, although most of the species could be classified as piscivores since they eat a large proportion of fish, we classified them as hypercarnivores since fish are vertebrates; moreover changing their classification did not alter our results.

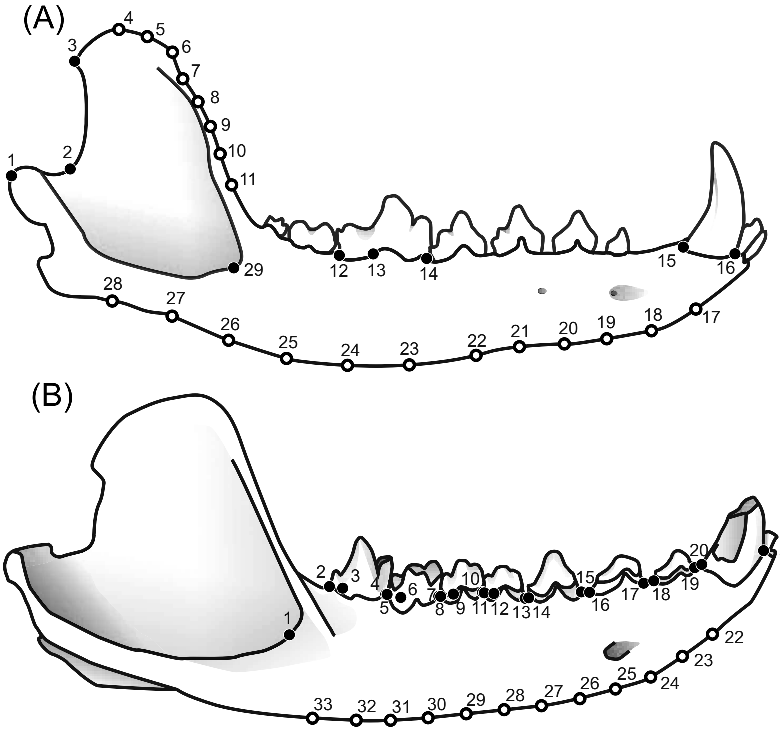

Figure 1 Configurations of landmarks (filled circles) and 'semi-landmarks' (open circles) used. (A) Set 1 in *Chrysocyon brachyurus* lower jaw: 1 = distal extreme of the mandible condyle; 2 = most concave point of mandible notch; 3 = dorso-caudal angle of the coronoid process; 4–11 = 'semi-landmarks'; 12 = distal extreme of the carnassial; 13 = distal border of the protoconid projected to the base of the crown of the carnassial; 14 = mesial extreme of the lower carnassial; 15 = distal extreme of the c1; 16 = mesial extreme of the c1; 17–28 = 'semi-landmarks'; 29 = anterior border of the masseteric fossa. (B) Set 2 in *Cladosictis patagonica* lower jaw: 1 = anterior border of the masseteric fossa; 2 = distal extreme of the m4; 3 = distal border of the protoconid projected to the base of the crown of the m4; 4 = mesial extreme of the m4; 5 = distal extreme of the m3; 6 = distal border of the protoconid projected to the base of the crown of the m3; 7 = mesial extreme of the m3; 8 = distal extreme of the m2; 9 = distal border of the protoconid projected to the base of the crown of the m2; 10 = mesial extreme of the m2; 11 = distal extreme of the m1; 12 = distal border of the protoconid projected to the base of the crown of the m1; 13 = mesial extreme of the m1; 14 = distal extreme of the p3; 15 = mesial extreme of the p3; 16 = distal extreme of the p2; 17 = mesial extreme of the p2; 18 = distal extreme of the p1; 19 = mesial extreme of the p1; 20 = distal extreme of the c1; 21 = mesial extreme of the c1; 22–33 = 'semi-landmarks'.

1.2. Geometric morphometrics

1.2.1. Landmarks. Two sets of landmarks were combined with different taxonomic groups to construct three samples. The first sample (MAND_TOT) includes the metatherians and eutherians using a configuration of 29 landmarks representing the whole mandible as defined by Prevosti *et al.* (2012a) (Fig. 1A). The second sample (MAND_MET) includes only metatherians and the same landmark configuration as the first analysis. Finally, a third sample (BODY_MET) was performed with metatherians, but using a configuration of 33 landmarks placed only on the mandibular body (Fig. 1B).

We used landmarks of types I, II and III (*sensu* Bookstein 1991), which were digitised using the software tpsDig 2.09 (Rohlf 2006). Prior to the use of tpsDig, we used the program MakeFan6 (Sheets 2003) to place alignment 'fans' that helped to place type III landmarks (i.e., semi-landmarks) consistently. In the analyses of the whole mandible, fans were placed equiangular, radiating from the distal extreme of the mandibular condile (semi-landmarks 4–11) and equidistantly from the distal-most point of the mandibular condyle to the mesial-most point of the lower canine (semi-landmarks 17–28); whilst for the analysis of the mandibular body, they were placed equidistantly from the ventral margin projection of the landmark of the distal extreme of m4 to the ventral margin projection of the landmark of the distal extreme of the c1 (semi-landmarks 22–33) (see Bookstein 1997; Perez *et al.* 2006). The software tpsUtil 1.40 (Rohlf 2008) was used to compile image files and to perform other basic operations. Sliding of the semi-landmarks, as well as superimposition of landmark configurations through generalised Procrustes analysis (GPA; Goodall 1991; Rohlf 1999) was performed using the software tpsRelw 1.45 (Rohlf 2007).

1.2.2. Analyses. The discrimination of diet classes and the placement of fossils was explored through a between-group PCA (BgPCA; Bookstein 1989; Rohlf 1993; Zelditch *et al.* 2004; Mitterocker & Bookstein 2011) and with a discriminant analysis (DA) using the MASS library (Venables & Ripley 2002) for the software R (R Development Core Team 2010). For the BgPCA, we used the Procrustes coordinates of the specimens aligned previously. In the discriminant analysis, we used the scores of the BgPCA (five or four variables) as dependent variables, in order to control the negative impact of having many dependent variables (Neff & Marcus 1980; Kovarovic *et al.* 2011), but without discarding any morphological information. For the same reason, we used specimens and not species means in the DAs, and each specimen of Sparassodonta was classified independently. The same probability of classification was assigned to each group and the percentage of posterior correct reclassification was calculated using cross validation (CV; Reyment *et al.* 1984; Jackson 1993; Mendoza *et al.* 2002).

Aligned landmark coordinates were used to perform a multivariate regression between size and shape, using Procrustes coordinates (i.e., shape) as dependent variables and natural log-transformed centroid size (i.e., size) as the explanatory variable (Supplementary file 2). The significance of this relationship was analysed using permutations (10000 replicates). The regression analyses were performed using the software MorphoJ 1.02b (Klingenberg 2011). In order to take into account the phylogenetic structure of the data, we constructed a phylogenetic covariance matrix based on a combined phylogenetic tree (see below), and performed the same regression of size onto shape, but incorporating this matrix into the error term of the regression equations (PGLS (phylogenetic generalised least squares); Martins & Hansen 1997). These analyses were carried out using the package APE (Paradis *et al.* 2004) for R (R Development Core Team 2010).

The phylogenetic matrix was constructed from a combined phylogenetic tree, following the same procedures as in Prevosti *et al.* (2012a). The combined phylogenetic tree (Supplementary file 3) was built from recently published phylogenies (Krajewski & Westerman 2003; Flynn *et al.* 2005; Gaubert *et al.* 2005; Johnson *et al.* 2006; Koepfli *et al.* 2006, 2007, 2008; Beck 2008; Krause *et al.* 2008; Flores 2009; Patou *et al.* 2009; Sato *et al.* 2009; Wolsan & Sato 2009; Prevosti 2010, for living taxa; and Forasiepi *et al.* 2015 for Sparassodonta). For the phylogenetic relationships of *B. musteloides*, *Pe. pungens*, *Ps. pusillus* and *S. gracilis*, we followed Marshall (1981).

2. Results

2.1. Diet and shape variation

2.1.1. Analysis of the whole mandible in carnivorans and metatherians (MAND_TOT). BG-PC1 explained 58.31 % of the total variance. On the negative scores, we found specimens with a robust mandibular body, high coronoid process, ventrally displaced condyle, anteriorly expanded masseteric fossa (landmark 29), and large canines and carnassials (Fig. 2). Specimens with positive scores showed the opposite trend (Fig. 2). BG-PC2 explained 19.87 % of the total variance; specimens with positive scores showed mandibles with a broader coronoid process, a lower mandibular body in its anterior portion but higher in the posterior region, a well-developed subangular lobule, a small canine, and the carnassial placed more anteriorly and with a short trigonid and a long talonid. The opposite trend is observed in the negative end of this axis (Fig. 2).

Although there was a wide overlap between all diet categories, a pattern could be observed whereby hypercarnivores had negative scores on BG-PC1 and 2, and herbivores had negative scores for BG-PC1, but positive scores on BG-PC2. Mesocarnivores, insectivores and omnivores were widely overlapped in the centre of the distribution (Fig. 2). Sparassodonts had negative scores for BG-PC2, but are widely distributed along BG-PC1. Larger species (e.g., *Borhyaena*, *Thylacosmilus*, *Arctodictis*) are in the area dominated by hypercarnivores, whilst the smaller species (e.g., *Cladosictis*, *Sipalocyon*) overlapped with omnivores, mesocarnivores and insectivores (Fig. 2).

2.1.2. Analysis of the whole mandible in metatherians (MAND_MET). BG-PC1 explains 51.55 % of the total variance. Specimens with negative scores showed robust mandibles with a ventrally displaced condyle, posteriorly displaced carnassials (placed near the base of the coronoid process) that present a reduced talonid, an anteriorly displaced masseteric fossa, and large canines (Fig. 3). Specimens with positive scores showed the opposite morphological trend. BG-PC2 explains 35.67 % of the total variance, and changes are less evident than in BG-PC1. Specimens with positive scores showed mandibles with a broader coronoid process, a large and posteriorly displaced condyle, a more convex ventral border, and a more robust mandibular body (Fig. 3). Specimens with negative scores showed the opposite pattern (Fig. 3).

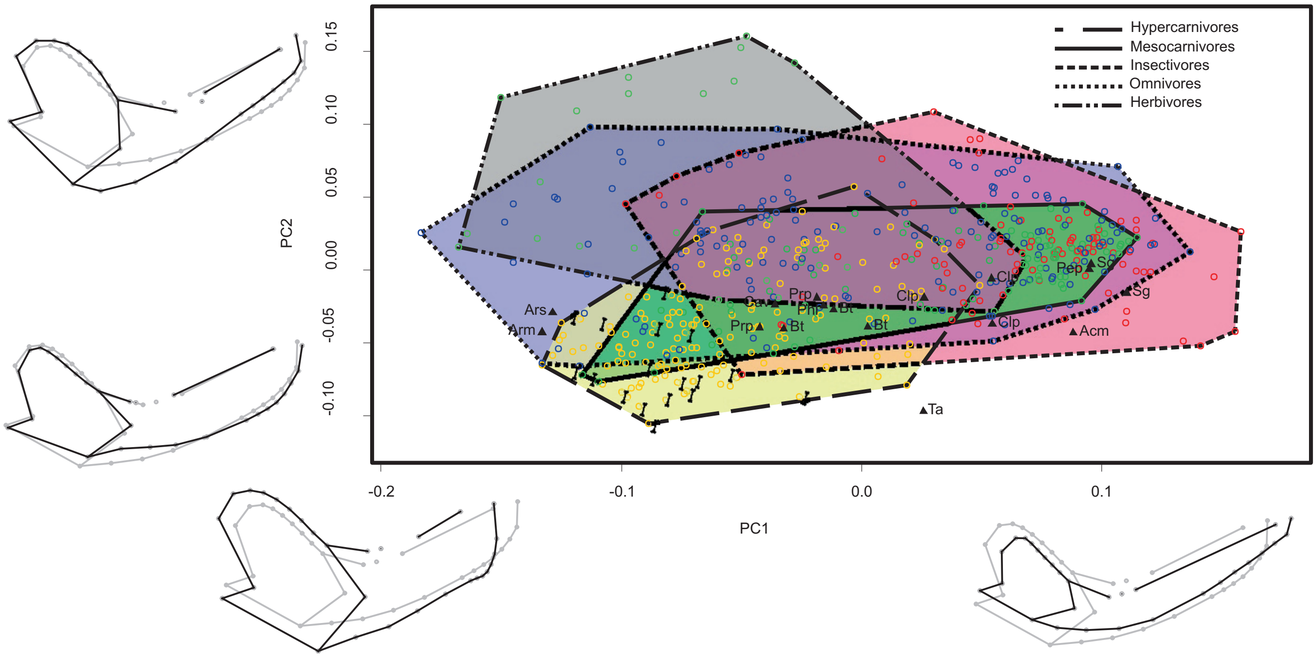

Figure 2 Graph showing the first two axes of between-group principal component analysis of the sample that includes carnivorans and metatherians and the whole mandible configuration (MAND_TOT). Mandible shapes at each end of each axis shown in black; consensus shapes in grey. Abbreviations: Acm = *Acyon myctoderos*; Arm = *Arctodictis munizi*; Ars = *Arctodictis sinclairi*; Bt = *Borhyaena tuberata*; Cav = *Callistoe vincei*; Clp = *Cladosictis patagonica*; Pep = *Perathereutes pungens*; Phl = *Pharsophorus lacerans*; Prp = *Prothylacynus patagonicus*; Sg = *Sipalocyon gracilis*; Ta = *Thylacosmilus atrox*. Yellow and long dashed line = hypercarnivores; pale green and continuous line = mesocarnivores; blue and dotted line = omnivores; red and short dashed line = insectivores; grey and two point-dashed = herbivores. Bones indicate ossifragous specimens.

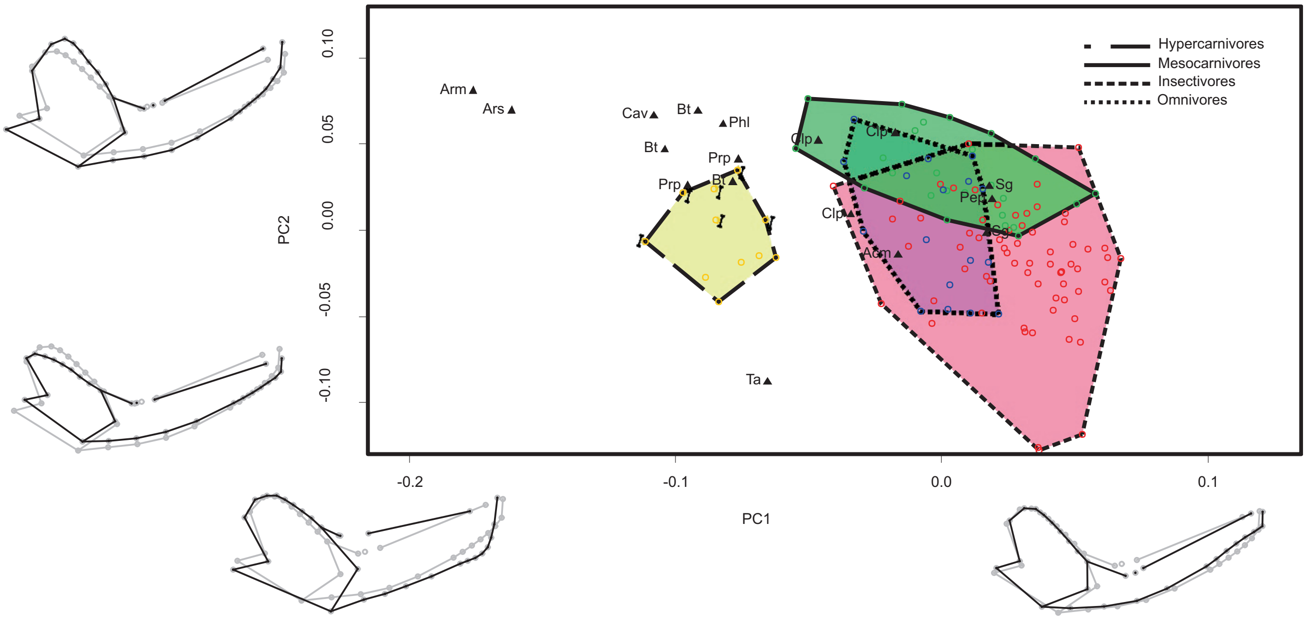

Figure 3 Graph showing the first two axes of between-group principal component analysis of the sample that includes the complete mandible configuration of metatherians (MAND_MET). Mandible shapes at each end of each axis shown in black; consensus shapes in grey. Abbreviations: Acm = *Acyon myctoderos*; Arm = *Arctodictis munizi*; Ars = *Arctodictis sinclairi*; Bt = *Borhyaena tuberata*; Cav = *Callistoe vincei*; Clp = *Cladosictis patagonica*; Pep = *Perathereutes pungens*; Phl = *Pharsophorus lacerans*; Prp = *Prothylacynus patagonicus*; Sg = *Sipalocyon gracilis*; Ta = *Thylacosmilus atrox*. Yellow and long dashed line = hypercarnivores; pale green and continuous line = mesocarnivores; blue and dotted line = omnivores; red and short dashed line = insectivores. Bones indicate ossifragous specimens.

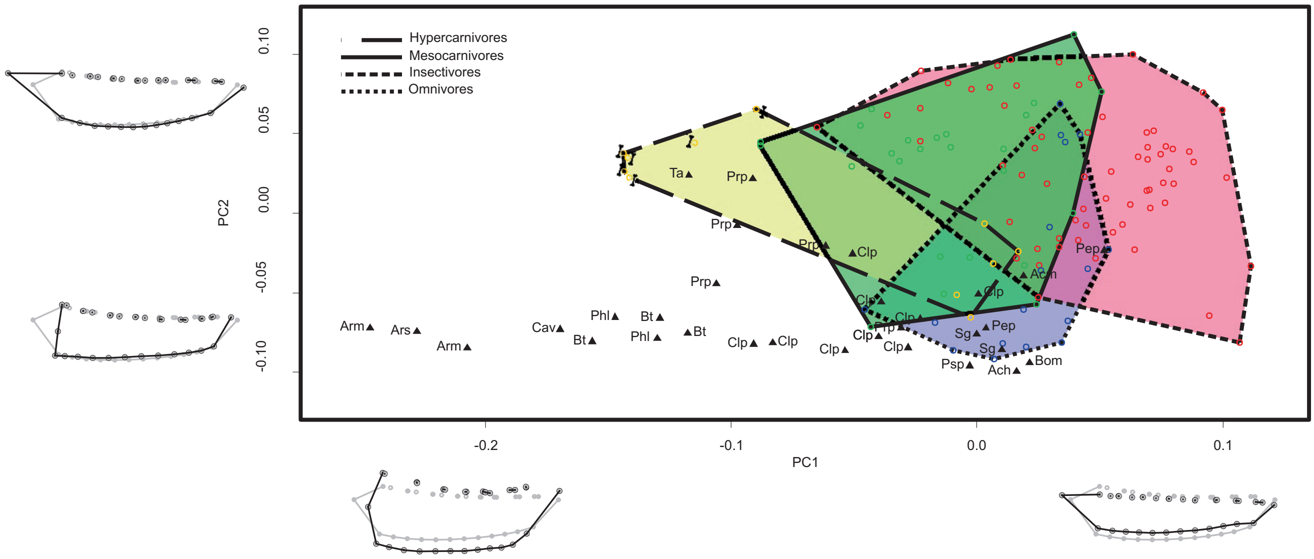

Figure 4 Graph showing the first two axes of between-group principal component analysis of the sample that includes only the mandibular body configuration of metatherians (BODY_MET). Mandible shapes at each end of each axis shown in black; consensus shapes in grey. Abbreviations: Ach = *Acyon herrerae*; Acm = *Acyon myctoderos*; Arm = *Arctodictis munizi*; Ars = *Arctodictis sinclairi*; Bhm = *Borhyaneidium musteloides*; Bt = *Borhyaena tuberata*; Cav = *Callistoe vincei*; Clp = *Cladosictis patagonica*; Pep = *Perathereutes pungens*; Phl = *Pharsophorus lacerans*; Prp = *Prothylacynus patagonicus*; Psp = *Pseudonitictis pusillus*; Sg = *Sipalocyon gracilis*; Ta = *Thylacosmilus atrox*. Yellow and long dashed line = hypercarnivores; pale green and continuous line = mesocarnivores; blue and dotted line = omnivores; red and short dashed line = insectivores. Bones indicate ossifragous specimens.

Hypercarnivores were completely separated from the other groups and placed toward the negative scores of BG-PC1, but omnivores, mesocarnivores and insectivores are widely overlapped on both axes (Fig. 3). Sparassodonts were aligned with hypercarnivores on BG-PC1, but most species showed higher BG-PC2 scores; whilst *Thylacosmilus* showed smaller scores for that axis (Fig. 3). *Cladosictis*, *Sipalocyon*, *Acyon* and *Perathereutes* overlapped with omnivores, mesocarnivores or insectivores.

Table 1 Confusion matrices of the Discriminant Analyses (AD). MAND_TOT = complete mandible configuration and the whole taxonomic sample explained; MAND_MET = the analysis of the complete mandible configuration of metatherians; BODY_MET = configuration of the mandible body of metatherians; PRCP = percentage of correct posterior reclassification (global percentage shown in bold).

MAND_TOT

	herbivore	hypercarnivore	insectivore	mesocarnivore	omnivore	PRCP
herbivore	16	2	4	0	4	61.54
hypercarnivore	9	106	1	27	5	71.62
insectivore	8	4	57	17	5	62.64
mesocarnivore	1	13	34	33	6	37.93
omnivore	45	18	51	21	26	16.15
Error (%)	12.28	7.21	17.54	12.67	7.80	**46.39**

MAND_MET

	hypercarnivore	insectivore	mesocarnivore	omnivore	PRCP
hypercarnivore	11	0	0	0	100.00
insectivore	0	47	11	8	71.21
mesocarnivore	1	3	18	3	72.00
omnivore	0	4	0	13	76.47
Error (%)	1.12	5.88	9.24	9.24	**74.78**

BODY_MET

	hypercarnivore	insectivore	mesocarnivore	omnivore	PRCP
hypercarnivore	6	0	1	4	54.55
insectivore	0	44	9	13	66.67
mesocarnivore	4	7	9	5	36.00
omnivore	1	5	0	11	64.71
Error (%)	7.14	10.08	8.40	18.49	**58.82**

Table 2 Summary of a posteriori diet classification of fossil species: 1 = analysis of the whole mandible configuration and complete taxonomic sample (MAND_TOT); 2 = analysis that included the whole mandible configuration, but only metatherians (MAND_MET); 3 = analysis restricted to the mandible body configuration of metatherians (BODY_MET). Symbols indicate the posterior probability of assignation for each analysis: ** = 0.99–0.900; * = 0.899–0.800; ^ = 0.799–0.500; ‘ = <0.499. Differences in the percentages or the categories between specimens of the same species are indicated.

Species	Insectivore	Omnivore	Mesocarnivore	Hypercarnivore
Acyon myctoderos		3^	1^, 2’	
Acyon herrerae				3*
Arctodictis munizi				1*, 2**, 3**
Arctodictis sinclairi				1^, 2**, 3**
Borhyaena tuberata			1^	2**, 3**
Borhyaenidium musteloides		3*		
Callistoe vincei			1^	2**, 3**
Perathereutes pungens		3’	1^, 2^	3^
Cladosictis patagonica		2’, 3^	1^, 2**, ^	3**, *, ^
Pharsophorus lacerans			1^	2**, 3**
Prothylacynus patagonicus				1^, 2**, 3**, *
Pseudonotictis pusillus		3*		
Sipalocyon gracilis	2’	1’, 3*	1*, 2**, ’	
Thylacosmilus atrox				1^, 2**, 3**

2.1.3. Analysis of the mandibular body in metatherians (BODY_MET). BG-PC1 explained 48.92 % of the total variance. Specimens with negative scores showed a shorter and more robust mandibular body, anteriorly displaced masseteric fossa, larger canines, reduced p1 and larger molars with a highly reduced talonid (Fig. 4). Specimens with positive scores show the opposite trend (Fig. 4). BG-PC2 explained 31.62 % of the total variance, and towards its negative end specimens showed a larger p2 and p3, and an anteriorly displaced masseteric fossa (Fig. 4). Specimens with positive scores show the opposite trend (Fig. 4).

Diet categories were widely overlapped, but in BG-PC1 we observed a trend, where several insectivores had higher BG-PC1 scores than the rest, whilst some hypercarnivores (specimens of *Sarcophilus*) had lower scores than the remaining specimens (Fig. 4). Sparasodonts mostly shared the BG-PC1 morphospace with hypercarnivores, but some had lower scores in that axis, and most of them showed lower BG-PC2 scores. *Cladosictis*, *Sipalocyon*, *Acyon* and *Perathereutes* were overlapped with omnivores, mesocarnivores and insectivores (Fig. 4).

2.2. Diet classification

The data set that showed the highest total percentage of correct classification (after cross-validation) in the discriminant analysis was MAND_MET, with 74.74 % of correct classification, followed by BODY_MET with 58.82 %, whilst MAND_TOT only classified correctly 46.39 % of the specimens (Table 1). It is noteworthy that the discriminant analysis of the MAND_

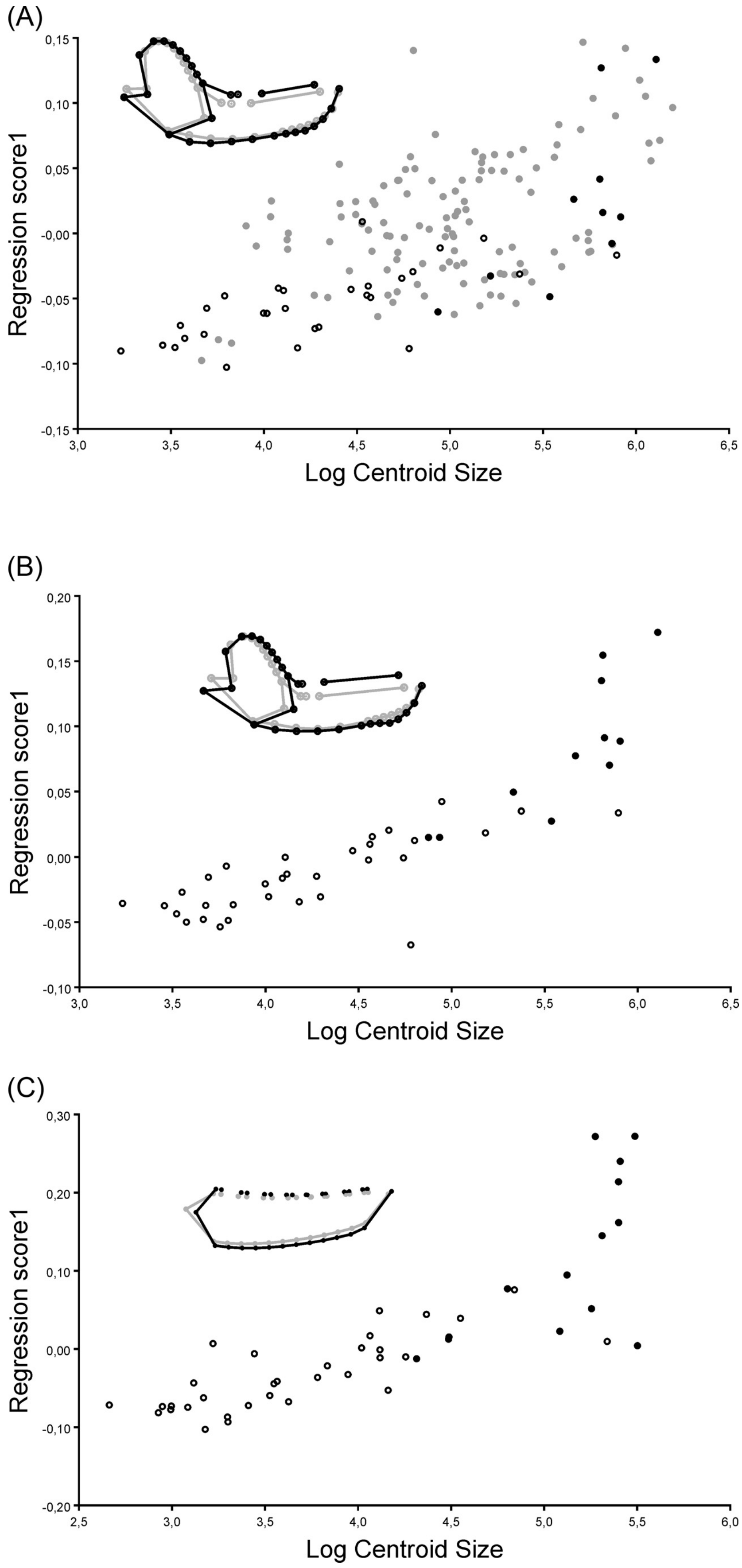

Figure 5 Regression graphics between shape and centroid size, and shape variability of the allometric analyses, representing the shape for the zero value of the log of centroid size in grey and the shape of mandible for the two value of the log of centroid size in black. (A) analysis that includes the complete mandible configuration and the whole taxonomic sample explained (MAND_TOT); (B) analysis of the complete mandible configuration of metatherians (MAND_MET); (C) analysis that includes only the configuration of the mandibular body of metatherians (BODY_MET). Filled black circles indicate specimens of Sparassodonta; open black circles indicate specimens of Marsupialia; filled grey circles indicate specimens of Carnivora.

MET dataset classified correctly 100 % of the living hypercarnivores, whilst the remaining analyses showed a percentage of correct classification of 71.62 % (MAND_TOT) and 54.54 % (BODY_MET) for that diet category (Table 1). The results shown in Table 1 indicate that these functions are useful to separate hypercarnivores, but not to discriminate the other categories.

In the discriminant analyses, *Ac. myctoderos* was classified as a mesocarnivore or omnivore with low-moderate posterior probabilities (PP) and *Ac. herrerae* was classified as a hypercarnivore with high PP (Table 2). *Cladosictis patagonica* was classified as an omnivore with high-moderate PP, and as a hypercarnivore with very high PP. *Sipalocyon gracilis* was classified as an insectivore or omnivore with low-moderate PP, and as a mesocarnivore with very high PP. *Borhyaenidium musteloides* and *Ps. pusillus* were classified as omnivores with high PP, whilst *Pe. Pungens* was classified as a mesocarnivore, omnivore or hypercanivore with low-moderate PP. Large sparassodonts (*Arctodictis*, *Borhyaena*, *Callistoe*, *Thylacosmilus* and *Pharsophorus*) were identified as hypercarnivores, mostly with very high PP, but *Borhyaena*, *Callistoe*, and *Pharsophorus* were also classified as mesocarnivores with moderate PP with the MAND_TOT function (Table 2; Supplementary file 4).

2.3. Allometry

In the allometric analysis of the MAND_TOT dataset, size explained 9.38 % of shape variation. Smaller specimens had slender mandibles, with a dorsally displaced condyle, anteriorly displaced carnassials with long talonids and a small canine. Larger specimens had robust mandibles, with a ventrally displaced condyle, large canines and carnassials with a reduced talonid (Fig 5A). The relationship between size and shape was statistically significant; both without taking into account the phylogenetic effect ($P < 0.0001$) and when including the phylogenetic effect in the PGLS analysis (Wilks' Lambda $F = 0.213$, $P < 0.0001$).

In the allometric analysis of the MAND_MET dataset, size explained 18.30 % of shape variability. The smaller specimens had slender mandibles, with dorsally displaced condyle, small carnassials and small canines; larger specimens had robust mandibles, with ventrally displaced condyle, large canines, large carnassials with reduced talonid, and an incipient symphyseal process (Fig. 5B). The relationship between size and shape was statistically significant when the phylogenetic effect was not considered ($P < 0.001$), but the PGLS analysis showed a non-significant relationship between size and shape (Wilks' Lambda $F = 0.008$, $P = 0.154$).

In the allometric analysis of the BODY_MET dataset, size explained 31.74 % of the shape variability. The smaller specimens showed a dorsoventrally compressed mandibular body, with a posteriorly displaced masseteric fossa, molars with well-developed talonids, and small canines; larger specimens showed a dorsoventrally expanded mandibular body, with an anteriorly displaced masseteric fossa, large molars with a reduced or absent talonid, reduced first premolars and large canines (Fig. 5C). The relationship between size and shape was statistically significant when the phylogenetic effect was not considered ($P < 0.001$), but when taking the phylogenetic effect into account in the PGLS analysis, a non-significant relationship between size and shape was recovered (Wilks' Lambda $F = 0.070$, $P = 0.766$).

3. Discussion

3.1. Reconstruction of dietary habits

The BgPCA and the discriminant analyses showed an overlap between most of the diet categories, hypercarnivores being the category that presented a better separation from the others (Figs 2–4; Table 1). This pattern was found in other studies (e.g., Prevosti *et al.* 2012a) and is to be expected, since most hypercarnivorous species have a very specialised mandibular morphology, with large carnassials with reduced talonids, reduced postcarnassial molars, a robust mandibular body and a ventrally displaced mandibular condyle; whilst groups that eat different items, apart from vertebrates, share a more generalised mandibular shape (Van Valkenburgh 1989; Meloro *et al.* 2008; Meloro & Raia 2010; Prevosti *et al.* 2012a). Overlapping between diet classes could also be influenced by allometric constraints and the phylogenetic legacy, due to evolutionary constraints, as was found in other studies of mandible and skull shape (e.g., Wroe and Milne 2007; Meloro *et al.* 2008; Meloro & Raia 2010; Goswami *et al.* 2011; Prevosti *et al.* 2012a). This overlap had an impact in the discrimination power of the AD functions, which had a moderate or low percentage of global posterior correct reclassification (46–75 %) but, with the exception of the BODY_MET dataset, hypercarnivores had a high percentage of correct reclassification (72 % and 100 %, respectively), and few non-hypercarnivores specimens were classified in this class (<7 %). Thus, even though total percentages of posterior correct reclassification are not very high, these functions, in combination with the distribution of the specimens in the BgPCA, can be used to distinguish hypercarnivores from other diet categories. Another issue that could be affecting the performance of the analyses is the construction of discrete classes from continuous variables such as diet, mainly when the classes do not present a clear separation (e.g., omnivore *vs.* mesocarnivore). This problem could be exacerbated by the absence of good ecological data for some species and the intraspecific seasonal or geographic variation of diet.

The distribution of sparassodonts in the plots of the BgPCA (Figs 2–4) and their classification with the DAs (Table 2) is evidence that there is a wide variety of mandibular shapes in the group, and that larger genera (*Borhyaena*, *Arctodictis*, *Callistoe*, *Pharsophorus*, *Thylacosmilus* and *Prothylacynus*) were more similar to extant carnivoran hypercarnivores. This can be explained by the fact that large sparassodonts have a short and robust mandibular body, with a ventrally displaced condyle, anteriorly expanded masseteric fossa, and a large carnassial with a reduced talonid, that is displaced posteriorly (Figs 2–4). These morphological traits are interpreted as a specialisation to consume high percentages of meat and hunt prey that could be larger than the carnivore itself (Van Valkenburgh 1989; Meloro *et al.* 2008; Meloro & Raia 2010; Prevosti *et al.* 2012a). A robust mandibular body (i.e., short and high) is good for supporting high stresses (Therrien 2005; Prevosti *et al.* 2012a), which is important when dealing with large prey or processing hard objects such as bones, as was proposed for larger sparassodonts (e.g., *Arctodictis*; Forasiepi *et al.* 2004, 2015; see also Prevosti *et al.* 2012b). Since borhyeanoids have some morphological features (e.g., strong mandible body and premolars) that were interpreted as indicators of ossifragous habits (Forasiepi *et al.* 2004, 2015), we explored the position of the living ossifragous taxa (e.g., *Hyaena*, *Crocuta*, *Gulo*, *Sarcophilus*) in our analyses. In the MAND_TOT analysis, ossifragous species are placed overlapped with hypercarnivores and some mesocarnivores and omnivores, but towards the negative end of the hypercarnivore distribution in both axes. That morphospace is shared with derived borhyaenoids (Fig. 2; e.g., *Borhyaena*, *Callistoe*, *Pharsophorus*, *Prothylacynus*). Something similar can be seen in the analyses that only included Metatherians, where the extant *Sarcophilus* is overlapped with those taxa in the first axis (Figs 3, 4). These observations suggest that derived borhyaenoids could have been hypercarnivores, with the capacity to consume carcasses and crack bones, similar to the living *Crocuta* or *Sarcophilus*.

Contrary to larger species, hathliacynids shared the morphospace with non-hypercarnivorous species (omnivores, insectivores and mesocarnivores), mostly due to their longer and slender mandibular body (Figs 2–4). Consequently, the discriminant analyses classified most hathliacynids as omnivores or mesocarnivores. However, *Acyon herrerae*, and some specimens of *Cladosictis*, were also identified as hypercarnivores (Table 2; Supplementary file 4), something that could be indicating that these species had a tendency to consume more meat than other hathylacinids (as was supported by other studies; Prevosti *et al.* 2012b, 2013) or, in the case of *Cladosictis*, indicating intraspecific variability in the diet. Therefore, hathliacynids had less carnivorous diets than the borhyaenoids studied here, and probably (mainly due to the shape of their mandible and their body size) did not hunt frequently on prey larger than themselves (see Ercoli *et al.* 2014). *Dasyurus* spp. (e.g., *D. maculatus*) could be a good model for these sparassodonts, because it has a mesocarnivore diet and generally hunts prey smaller than its own body mass (Strahan 1995; Attard *et al.* 2014).

Our results are mostly congruent with the palaeoecological interpretation of Marshall (1978), who concluded that sparassodonts had different degrees of feeding adaptations, with a trend towards a specialisation on a carnivorous and hypercarnivorous diet. Marshall (1978) considered hathliacynids and basal borhyaenoids (e.g., *Pr. patagonicus*) as predominantly omnivorous, but Argot (2003b), based on the morpho-functional analysis of postcranial elements, inferred that *Pr. patagonicus* was an active predator with ambush habits; an interpretation that is in agreement with our results (*Pr. patagonicus* was classified as a hypercarnivore in the DA).

In recent studies based on a dental morphometric index (relative grinding area (RGA) of the fourth lower molar) all the sparassodonts studied here fall into the hypercarnivore category (Prevosti *et al.* 2012b, 2013; Zimicz 2014), whilst we found omnivorous or mesocarnivorous diets for some species. It is possible that the agreement between Marshall's (1978) results and ours is because the geometric morphometric analyses conducted here captured the same morphological traits that Marshall used. Indeed, it is not clear why our results were so different from the analyses based on the RGA index, mainly because we included landmarks from the lower carnassial in our analyses. One possible explanation is that since the lower carnassial represents a small subset of landmarks in the global configuration of the mandible, the changes of the mandibular shape as a whole subordinated the morphological differences of the carnassials (i.e., any changes in the carnassial will be very small compared to changes in each part of the mandible), reducing its impact in diet discrimination. This is combined with the fact that hathliacynids have a mandibular morphotype that is not commonly present in living predators, which combines a relatively long and slender mandibular body with a carnassial with a reduced talonid. Thus, it is possible that hathliacynids were in fact more carnivorous than here inferred, and that mandible shape is more related to other factors such as prey size. The latter interpretation agrees with the interpretation of Ercoli *et al.* (2014), who concluded that hathliacynids of the Santa Cruz Formation hunted on small prey, but that borhyaenoids could prey more frequently on vertebrates larger than themselves.

The three datasets analysed here also allowed us to explore the use of samples that include different morphotypes (more limited in the ones that includes only metatherians), the inclusion of more distant lineages (i.e., Carnivora in the MAND_TOT sample), and the possibility of classifying more incomplete fossils (BODY_MET). It is clear that MAND_MET is the best discriminant function (Table 1) for living species with known diet, but several sparassodonts were placed outside the morphospace of the living taxa used to construct this function (Fig. 3), something that could bias the classifications because fossils could belong to a category not covered by any of the living species included (see Reyment *et al.* 1984; Legendre & Legendre 1998). This problem is not present in the analysis based on the MAND_TOT dataset (Fig. 2). On the other hand, the analysis of only the mandibular body (BODY_MET) allowed us to include incomplete fossils of other species such as *Borhyaenidium musteloides*, *Acyon herrerae*, and *Pseudonotictis pusillus*. Moreover, the inclusion of more landmarks in this analysis let us contemplate other morphological features for the inferences (Fig. 4; Table 2).

3.2. Mandible shape, body size, carnassial shape and sparassodont evolution

The allometric and multivariate analyses presented here, and the positive significant relation between the first axis of the analyses and the centroid size, showed a correlation between mandible size and shape (Figs. 2–5). A covariance of carnassial shape, dental morphology and body size has been reported previously by several authors (Marshall 1977a, 1978, 1979, 1981; Forasiepi 2009; Prevosti *et al.* 2012b, 2013; Ercoli *et al.* 2014), since taxa with short and robust mandibles were shown to have large body sizes and molars with extremely reduced talonids (RGA near 0). On the contrary, smaller taxa have longer and slender mandibles, and molars with more developed talonids (Marshall 1977a, 1978, 1979, 1981; Forasiepi 2009; Prevosti *et al.* 2012b, 2013). The morpho-functional diversity of sparassodonts is also related to the phylogenetic relationships of the group, because most of the small species, with generalised mandibles, are basal sparassodonts or hathliacynids, and the larger species, with shorter and robust mandibles, are borhyaenoids (see also Forasiepi 2009). The strong influence of the phylogenetic legacy in the relationship between shape, diet and size can also be observed in the shape–size regression of whole metatherian analyses (Fig. 5). The significant relationship between shape and size changed to non-significant levels when phylogeny was taken into account, suggesting that the associated changes in shape and size follow the structure of the phylogenetic relationships, occurring together in specific clades. The phylogenetic structure of mandible size and shape also indicates that ecological factors (diet in this case) have influenced the evolution of Sparassodonta, since more carnivore habits were derived changes of borhyaenoids. On the other hand, smaller and slender mandibles could be indirectly conditioned by the predominant scansorial locomotion habits of hathliacynids (e.g., *Cladosictis*, *Sipalocyon*, *Pseudonotictis*) since scansorial and arboreal mammals tend to be small-bodied (Van Valkenburgh 1987; Argot 2003b, 2004c; Ercoli *et al.* 2012). The association of large body sizes and more carnivorous habits was also found in the evolution of some groups of placental carnivores (Felidae and Canidae; Carbone *et al.* 1999; Van Valkenburgh *et al.* 2004), and could be explained by metabolical constraints, because species larger than 15–25 kg (Carbone *et al.* 1999, 2007) are mostly obligated to hunt on larger prey. This constraint could explain the covariation of mandibular size, body size and mandibular shape observed in sparassodonts, and could be one of the factors that controlled the diversification and morphological evolution of sparassodonts.

Some species not included in our analyses because their fossils were too fragmentary, such as *Stylocynus* and *Lycopsis*, apparently escape this pattern of covariation between size, mandible shape and carnassial shape. Although they have a relatively large body size and a long and slender mandibular body, the

RGA index for *Stylocynus* indicates that it was an omnivore or mesocarnivore, whilst for *Lycopsis*, the index has higher values than other borhyaenoids (Prevosti *et al.* 2012b, 2013). The new borhyaenid described by Engelman & Croft (2014) could be another exception, because it has a small body size, hypercarnivore habits and a short rostrum that could be correlated with a mandible with a short and robust body (something that it is not possible to corroborate because it is only known from cranial remains). These exceptions show that sparassodonts had a wide variability of ecomorphs, something that agrees with the disparity observed in living carnivorans, which include large omnivores and small carnivores with similar morphologies (e.g., Prevosti *et al.* 2012a).

The analyses performed here suggest that Sparassodonts have less disparity in the mandibular shape and smaller ecological amplitude than Carnivora, as was recently tested and linked to evolutionary and functional constraints (Echarri & Prevosti 2015; see also Werdelin 1987; Prevosti *et al.* 2012b). Sparassodont also appear to have less mandibular shape disparity than the extant marsupials used here as potential living analogues; but this should be tested with other methods, since the between-group PCA cannot be used to test this, and also the difference in sample size could bias the comparison (see Echarri & Prevosti 2015).

Finally, our results could be relevant to the discussion of the existence of competence between the last sparassodonts and the first Carnivora that invaded South America in the Late Miocene (see Prevosti *et al.* 2013; Zimicz 2014), because some species could be less carnivorous than previously thought. For example, *Borhyaenidium musteloides* could be omnivorous, as were the first South American carnivorans (i.e., *Cyonasua*). However, these changes do no alter the main pattern described in previous papers (see Prevosti *et al.* 2013; Zimicz 2014), because this sparassodont is smaller than *Cyonasua* or *Chapalmalania* (1.6 vs >6 kg, respectively), and its dentition is much less specialised to an omnivorous diet (*Cyonasua* and *Chapalmalania* have very few effective shearing crests on their molars) (Prevosti *et al.* 2013; Prevosti & Pereira 2014).

4. Conclusions

The mandible shape of Sparassodonta species suggests a hypercarnivore diet for borhyaenoids, whilst hathliacynids could have had less carnivorous diets (omnivores or mesocarnivores). Our results also showed differences with the diets inferred using the RGA index (relative molar grinding area), which assigned all the studied sparassodonts to the hypercarnivore class. Alternatively, mandible shape could be related to relative prey size, and species with shorter and robust mandibles could have preyed on larger prey (similar or larger than their own body size) and taxa with long and slender mandibles could have hunted only small prey, as was recently proposed for the Santacrucian fauna (Ercoli *et al.* 2014).

The shape of the mandible of Sparassodonta is covariate with body size and molar morphology, since larger taxa have lower molars with reduced talonids (RGA near 0) and short and robust mandibles, whilst smaller species present the opposite pattern (larger but still hypercarnivore RGA values, and longer and slender mandibles). This pattern is congruent with the phylogenetic placement of those species, suggesting that ecological factors have influenced the evolution of the sparassodonts. The metabolic constraint on the diet of large species, which was described in Carnivora (Carbone *et al.* 1999, 2007; Van Valkenbugh *et al.* 2004), could be involved in the correlation between mandible size and diet that we found, as well as in the evolutionary history of Sparassodonta.

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