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Differences in mandibular disparity between extant and extinct species of metatherian and placental carnivore clades

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There are a number of studies relating to skull morphology differences within the carnivoran clades of both placentals and metatherians. It is difficult to compare these studies because of differences in taxonomic sampling, for example some include fossil taxa while others include non-carnivoran placentals. As a consequence, we studied mandible morphology in a broad range of both extant and extinct carnivorous species, including Carnivora, Marsupialia and Sparassodonta to test for differences between these clades. We used geometric morphometrics and two disparity indexes, the variance and Procrustes distances mean. When including fossil species, we found no significant differences for both disparities in some analyses, except after the exclusion of the sabretooth morphotype. This can be explained by the extreme morphology of this morphotype, which increases the variance and reduces the disparity effect of the other species in the analyses. Using Procrustes distances, we found significant differences in disparity distances between Carnivora and Metatheria for most of the analyses. We also found significant differences using the variance index in some analyses. The mandibular disparity in Carnivora is greater than in carnivorous metatherian mammals for most of the cases and this can be related with differences in evolutionary history and constraints of both groups. The pattern found in the mandible is similar to that found in the face of the skull but was not observed in the braincase, due to differences in skull function and mandible function. ☐ *Carnivora, disparity, geometric morphometry, mandible, Metatheria.*

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Dietary habits have conditioned the evolution and morphology of mammals and are the primary driver of change in mammals (Crusafont-Pairó & Truyols-Santonja 1956, 1957, 1958; Turnbull 1970; Van Valkenburgh 1989; Meloro & Raia 2010; Ungar 2010; Figueirido *et al.* 2012). Examples of convergence as a function of dietary habits are found in the placental clades, Carnivora and Creodonta, and with the metatherians (marsupials and extinct relatives) mammals, Sparassodonta, Dasyuridae and some groups of Didelphoidea (Savage 1977; Van Valkenburgh 2007). Classic cases of morphological convergence in the skull are the placental sabretooth tigers (e.g. *Smilodon*) and the metatherian sabretooth (e.g. *Thylacosmilus*), and between placental wolves (*Canis lupus*) and the Tasmanian wolf (*Thylacinus cynocephalus*) (Riggs 1934; Gazin 1946; Marshall 1976; Emerson & Radinsky 1980; Goin & Pascual 1987; Martin 1989; Argot 2004; Van Valkenburgh 2007; Christiansen 2008a,b; Slater & Van Valkenburgh 2008; Prevosti *et al.* 2010). Despite the gross similarities, there are many morphological differences between each of the parings due to the evolutionary constraints of ancestry (see Gould 2002), which cause each clade to have different morphological patterns and evolutionary limitations (e.g. Werdelin 1986, 1987; Wroe & Milne 2007). Some authors have compared these clades using qualitative characters and cranial proportions. Werdelin (1986) implemented traditional multivariate techniques (i.e. correspondence analysis) and found similarities associated with diet type, but also that dasyurids occupy a morphometric space that does not overlap with that of carnivorans.

Other studies compared cranial, dental and mandible morphology of several carnivorous mammal lineages including representatives of Carnivora and Metatheria, and examined the morphologic patterns related to diet (e.g. Meloro & Raia 2010; Figueirido *et al.* 2011, 2012; Goswami *et al.* 2011; Prevosti *et al.*

2012). These works used geometric morphometrics as a tool for morphological analysis. Pinnipeds were not included in these analyses, mainly because they are aquatic and specialized forms with a simplified dentition (Jones *et al.* 2013) and therefore are difficult to compare with other representatives of Carnivora. *Proteles cristata* is an exception because is a hyaenid with a much reduced dentition related to its feeding specialization, similar to the pinnipeds' simplified dentition (Ungar 2010). However, the inclusion of these carnivorans will complete the disparity analysis within Carnivora, and explore the inclusion of an aquatic clade.

It is suggested that Marsupialia and Carnivora have a similar degree of disparity in the cranium (Goswami *et al.* 2011), with size range differentiating the groups (Prevosti *et al.* 2012). The lower jaw also shows significant disparity between the two groups (Prevosti *et al.* 2012). This later study examined the lower jaw instead of the cranium as in the first two studies, and did not include fossil taxa, both being possible factors in the differences. A recent work (Bennett & Goswami 2013) analysed the skull of several placental and marsupial mammals groups and found significantly less disparity in marsupials than in placentals, with the expectation of the neurocrania which have similar disparity values.

The effect on overall disparity via the inclusion of lower jaw morphology and the inclusion of a broader range of taxa is the focus of our study. We compare the disparate shapes of carnivore mandibles from different mammalian clades (Sparassodonta, Dedelphimorphia, Dasyuromorphia and Carnivora) with a sample of 708 specimens from 249 extant and extinct species, while taking into account (adjusting for) allometric pattern imposed by the size/shape relationship. We compare our results with published information about disparity in the shape of the mandible and skull of these clades, and discuss the potential causes for our findings.

Materials and methods

Specimens and taxa

We analysed 708 images of lower jaws in lateral view (preferably the right dentary) of 249 extant and extinct species of carnivorous mammalian clades (Carnivora, Sparassodonta, Dasyuromorphia and Didelphimorphia) deposited in several institutions (Table S1). Only adult specimens were selected, and the complete tooth eruption and the fusion between the basisphenoid and basioccipital were used as proxies for adulthood.

From the total, 590 images correspond to 162 extant species, from which 40 images are from 12 species of the aquatic Pinnipedia. This clade was excluded from some analyses to compare our results against previous publications (e.g. Goswami 2006; Goswami *et al.* 2011; Prevosti *et al.* 2012). The remaining 118 images are from 87 extinct species. Similarly, these taxa were excluded from some analyses with the aim of evaluating their impact in the general results.

The mandibles were photographed in lateral view, with the medial surface of the mandible resting on the table or camera stand base. The studied specimens are in several museums: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Florida Museum of Natural History (UF); Frick Collection, Division of Palaeontology, American Museum of Natural History (F:AM); Instituto Miguel Lillo (IML); Instituto Miguel Lillo, Paleontología de Vertebrados (PVL); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Colección Nacional de Paleovertebrados (MACN); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Colección Nacional de Mastozoología (MACN-Ma); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM); Museo de La Plata (MLP); Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de Córdoba (CORD-PZ); Museo Municipal de Cs. Naturales y Tradicional de Mar de Plata 'Lorenzo Scaglia' (MMMP); Museo Paleontológico 'Egidio Feruglio' (MPEF); Museo Regional Provincial Padre Manuel Jesús Molina (MPM); Museo Regional Provincial Padre Manuel Jesús Molina, Colección de Paleovertebrados (MPM-Pv); Muséum National d'Histoire Naturelle (MNHN); National Museum of Natural History, Smithsonian Institution, Mammalogy (USNM Ma); National Museum of Natural History, Smithsonian Institution, Paleobiology (USNM); Naturhistoriska Riksmuseet (NHR); Rijksmuseum van Natuurlijke Historie (RMNH); Texas Memorial Museum (TMM); Uiversity of Nebraska State Museum (UNSM); Yale Peabody Museum (YPM) and Yale Peabody Museum, collection of Princeton University (YPM PU). In addition, we also used 50 images of 47 species figured in the literature (Table S1).

Geometric morphometrics analysis

Images were processed using tpsUtil 1.26 (Rohlf 2004). The landmarks were digitized using tpsDig 2.05 (Rohlf 2005). The configurations were superimposed and adjusted by Procrustes analysis using tpsRelw 1.36 (Rohlf 2003). Procrustes coordinate

values are listed in Table S2. The resulting coordinates were subject of a principal components analysis (PCA) and a regressions analysis between the centroid size and the Procrustes coordinates using MorphoJ (see Monteiro & dos Reis 1999; Adams *et al.* 2004; Zelditch *et al.* 2004; Klingenberg 2011). We defined the different types of landmarks according by following Bookstein (1991). The semilandmarks (Type 3) (Bookstein 1997) were digitized using MakeFan6 (Sheets 2003) and were placed equiangulary radiating from the distal extreme of the mandibular condyle (semilandmarks 4–11). The balance of the semilandmarks (17–28 in the analysis without pinnipeds and 14–25 and 27–32 in the analysis with pinnipeds) was placed equidistantly in two groups: one from the distal-most point of the mandibular condyle to mesial-most point of the lower carnassial, and the second from the latter to the mesial-most point of the lower canine. We used the criterion of minimizing Procrustes distances while superimposing configurations and the slip criterion for semilandmarks to minimize the bending energy (Bookstein 1997).

We used two different sets of landmarks. One set (Fig. 1A) comprises nine landmarks and 20 semilandmarks. Three landmarks were located at the base of the carnassial (the first landmark in the mesial-most point margin, the second is between trigonid and talonid, and the third one is at the distal-most point).

Following Prevosti *et al.* (2012), the m1 is the carnassial in Carnivora and analogous to the m4 in Metatheria. The m4 in carnivorous metatherians is the more carnassial tooth among lower molars, with larger trigonid and reduced talonid. Biomechanically, the m1 of carnivorans and the m4 of metatherians are located in the most advantageous position halfway between the condyle and the canine (Werdelin 1986, 1987).

The second set (Fig. 1B) does not include the landmarks related to carnassial because pinnipeds and *Proteles cristata* are homodont and dental homology with other mammals cannot be established. We considered a total of six landmarks and added 18 semilandmarks in the alveolar region of the mandible.

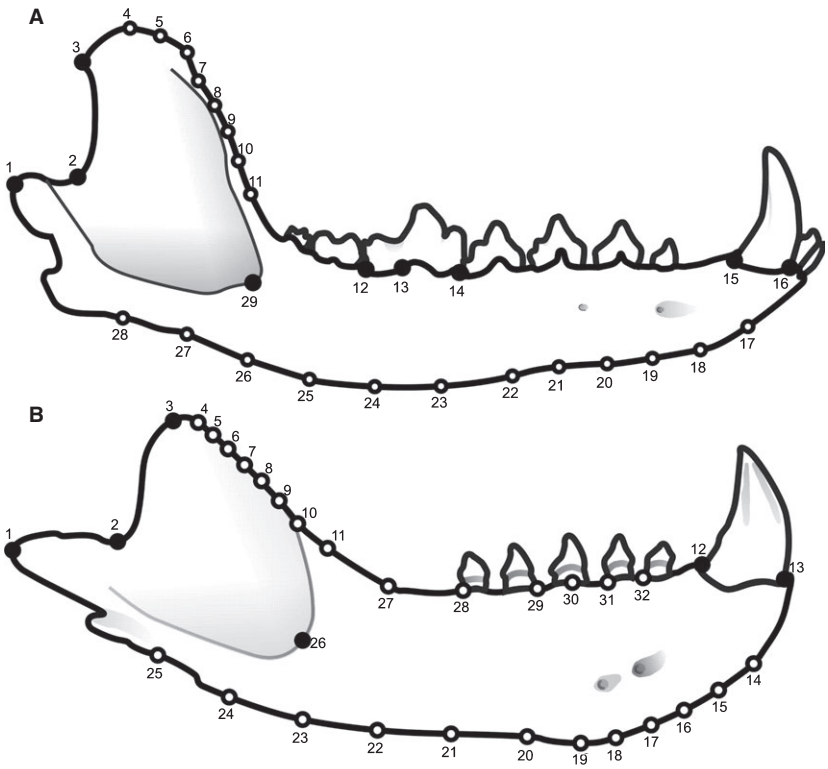

Fig. 1. Configurations of landmarks (●) and semilanmarks (○) used. A, set 1 in *Chrysocyon brachyurus* lower jaw: 1 – distal extreme of the mandibular condile; 2 – most concave point of mandibular notch; 3 – dorso-caudal angle of the coronoid process; 12 – distal Extreme of the lower carnassial; 13 – distal border of the protoconid projected to the base of the crown; 14 – mesial extreme of the lower carnassial; 15 – distal extreme of the lower canine; 16 – mesial extreme of the lower canine; 29 – anterior border of the masseteric fosa; 4–11 and 17–28 – semilandmarks. B, set 2 in *Arctocephalus gazella* lower jaw; 1 – distal extreme of the mandibular condile; 2 – most concave point of mandibular notch; 3 – dorso-caudal angle of the coronoid process; 12 – distal extreme of the lower canine; 13 – mesial extreme of the lower caninne; 26 – anterior border of the masseteric fosa; 4–11; 17–25 and 27–30 – semilandmarks.

Morphological disparity analysis

The specimens were separated in four groups to analyse the morphological disparity between placental and metatherian carnivores and to evaluate the influence of the inclusion of fossil taxa and pinnipeds. The groups are (1) extant placentals and marsupials, excluding pinnipeds; (2) extant placentals and marsupials including pinnipeds; (3) extant and extinct placentals and metatherians, excluding pinnipeds and (4) extant and extinct placentals and metatherians, including pinnipeds.

We explored the variation of the form and the morphological disparity in the PCA for each analysis, and evaluated the distribution in the morphospace of the representatives of Carnivora and Metatheria. To avoid intraspecific variation affecting the disparity comparisons, we averaged Procrustes coordinates and centroid size per species (Klingenberg 2011). As a disparity indicator, we used the sum of the trace of the variance–covariance matrix (see Zelditch *et al.* 2004), which was obtained by summing the variances of the Procrustes coordinates of metatherian and placental mammals for the different data sets. We also used the mean pairwise dissimilarity (MPD) as another disparity indicator (Foote 1993, 1997). To take into account the sample size differences, we compared the variances by randomly reducing the number of taxa from the largest group (placental) to the smallest group (metatherians), resampling the first group ten thousand times. The differences in the disparity between them were calculated for each resample. We mixed each resample with the smallest group to test the significance of the comparisons. This joined dataset was randomly divided into two blocks. The difference in the disparity of them is the expected by random, and it was used for comparing with the difference of disparity obtained in the first step (i.e. if the difference obtained in the 10000 resamples is larger than the obtained by random, in a proportion larger than 95% of the cases, we considered that the difference is significant at a $P < 0.05$). We used the program R 2.9.2 (R Development Core Team 2008) for these analyses.

The disparity of the non-allometric component was studied with the residual shape from a multivariate regression of Procrustes coordinates of the centroid size, with MorphoJ (Klingenberg 2011). A value representing the difference in the disparity between groups was calculated as the disparity of the group with the largest value minus the disparity of the group with the smallest value, divided by the largest, and multiplied by 100.

Results

Geometric morphometrics analysis

In the principal component analysis (PCA), Metatheria overlaps with the distribution of some Carnivora in the first axis, being mandibles with slender bodies and a low coronoid processes in the positive values of the axis, except in the PCA that included all the specimens, in which the polarity of the axis is inverted. The second axis shows the same overlap between carnivorans and metatherians and similar distribution (slender mandibles are in the positive values of the axis, except for the sample that includes extant and extinct specimens excluding pinnipeds, where the polarity of the axis is inverted). Together, both axes explain more of the 50% of the variation (Figs 2, 3). The remaining axes show a pattern similar to the first two.

In the analyses that included the fossils, the distribution of Sparassodonta in the first axis is greater than for Marsupialia and occupies a different morphospace. The sabretooth form a separate group in most of the PCA axes and includes the placental sabretooth cats and the sparassodontan *Thylacosmilus atrox*. The pinniped morphospace overlapped completely with other Carnivora, although in some axes the group is more separated than in others (Figs 2, 3 and S1).

Morphological disparity analysis

Based on the whole sample, we did not find significant differences in shape disparity between groups in the analysis of variance disparity. This is also true when including pinnipeds and the 'allometry free' data, except in the analysis of mean pairwise dissimilarity of Procrustes, in which case only without pinnipeds were not significant. After fossils exclusions significant differences between Carnivora and Marsupialia were detected in all the cases (Table 1). We should note that, even in non-significant cases, the disparity is being conspicuously greater in Carnivora (between 23.3% and 61.3%; Table 1). This difference is greater when the size effect is excluded. When the fossil specimens were included the difference is lower but Carnivora still has a larger disparity even when pinnipeds were excluded.

Discussion

The distribution of specimens in the morphospace (PCA) (Figs 2, 3 and S1) shows a very broad

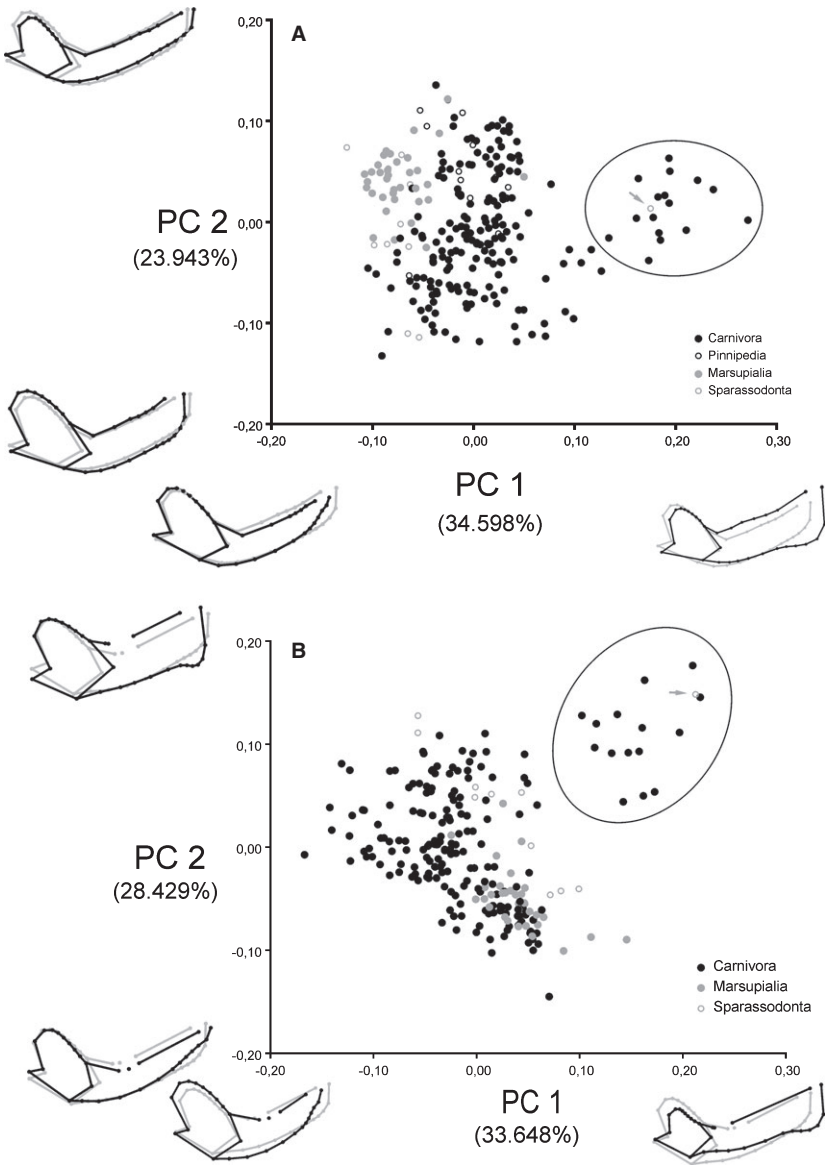

Fig. 2. Dispersion graphics of the PCA for PC2 vs. PC1. A, using the dataset for extant and extinct specimens including pinnipeds. B, using the dataset for extant and extinct specimens excluding pinnipeds. The black mandible shows the form of the extreme of each axis respect of the consensus in grey; filled black circles represent Carnivora except pinnipeds, the open black circles represent Pinnipedia, the filled grey circles represent Marsupialia, the open grey circles represent Sparassodonta; the grey arrow shows *Thylacosmilus atrox* and the black ellipse encloses the sabretooth cats. In parentheses indicates the percentage of variation accounted for each axis.

variation in each group, but it is difficult to determine whether these differences are related to the inclusion of more specimens of Carnivora than of Metatheria. However, for most disparity tests, we found significant differences between both groups, indicating that the observed differences in the PCAs are not a result differences in the sample sizes (Table 1).

The findings of this work confirm earlier work (Prevosti *et al.* 2012) in confirming differences in disparity between extant placental carnivores (Carnivora) and marsupial carnivores (Table 1). Including fossil taxa diminishes the disparities, but the Procrustes distance test index is still significantly greater in Carnivora. The disparity of Carnivora is increased by the inclusion of both fossil and live pinnipeds (e.g. Drake & Klingenberg 2010), confirming that the pinnipeds represent a different morphotype.

It should be noted that the inclusion of the sabretooth *Thylacosmilus* in the metatherian fossil clade distorts the disparity of the metatherian group, and reduces the differences between the Carnivora and Metatheria. Although the placentals include

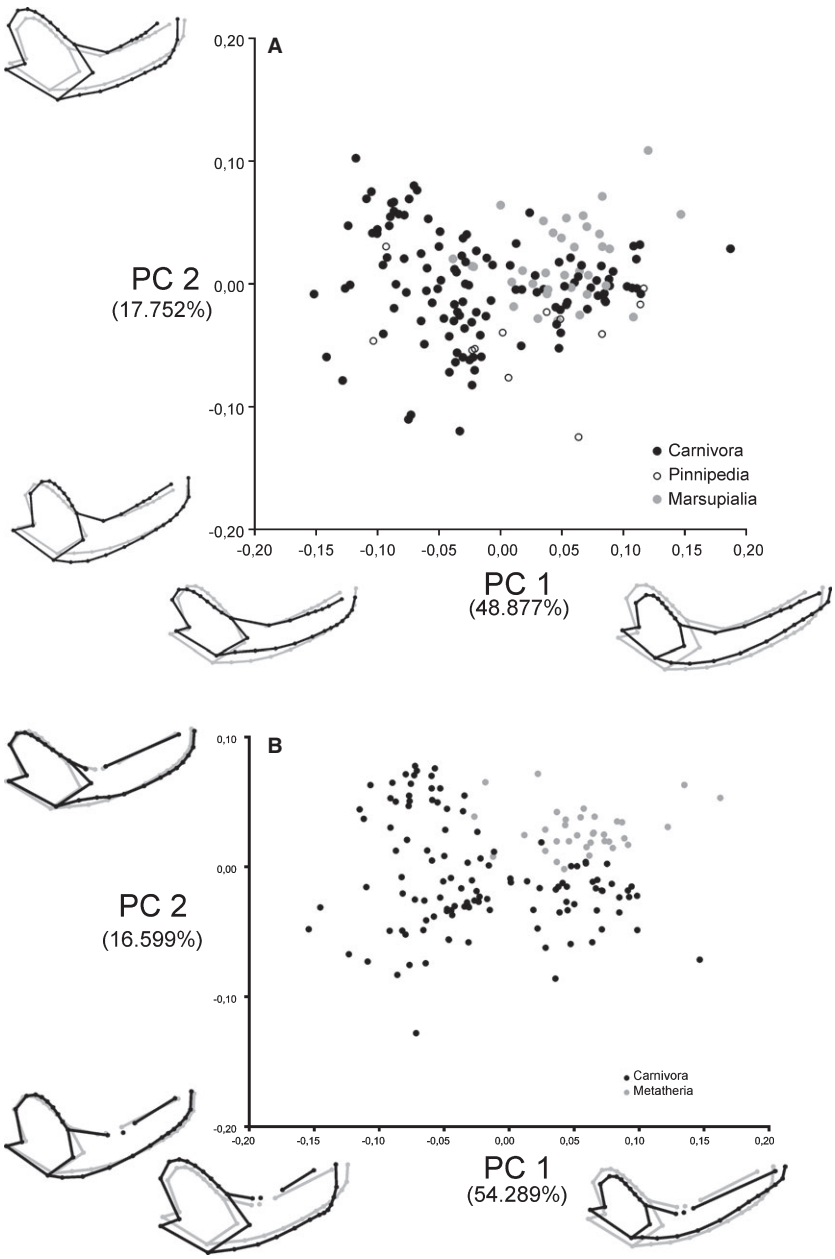

Fig. 3. Dispersion graphics of the PCA for PC2 vs. PC1. A, using the dataset for only extant specimens including pinnipeds. B, using the dataset for only extant specimens excluding pinnipeds. The black mandible shows the form of the extreme of each axis respect of the consensus in grey; filled black circles represent Carnivora except pinnipeds, the open black circles represent Pinnipedia, the filled grey circles represent Marsupialia, In parentheses indicates the percentage of variation accounted for each axis.

sabretooth forms, inclusion of *Thylacosmilus* raises the disparity of the metatherians to a similar level to the Carnivora. Excluding these forms from both groups leaves the Carnivora with significantly larger disparity. This indicates that few specimens with a very different morphology could act as outliers and mask disparity difference of the rest of the sample, biasing the variance test, but the Procrustes distance test was mainly robust to this bias with our data. An examination of the cranial disparity in living and extinct Carnivora and Marsupialia, including extinct Creodonta (Eutheria) and Sparassodonta (Metatheria) using geometric morphometry was inconclusive, with no significant differences, even with the inclusion of *Thylacosmilus* (Goswami *et al.* 2011). These results were contradicted by a recent study (Bennett & Goswami 2013), which presented a different sample across most living orders of placentals and marsupials (and some fossils of Metatheria), that found a significantly larger disparity in placentals using the

Table 1. Results of the disparity analyses for the four datasets including allometrict component (Procrustes) or not (Residuals).

	Analysis	Pinnipeds	Fossils	Dis M	Dis C	Relative diff	Diff	*P*
Variance disparity								
1	Procrustes	No	No	0.0051288	0.0096543	46.87558685	0.00453	0.0068*
	Residuals	No	No	0.0042905	0.0095252	54.95661183	0.00523	5.00E−04*
2	Procrustes	Yes	No	0.004097	0.0102567	60.05533938	0.00616	7.00E−04*
	Residuals	Yes	No	0.0038825	0.0100366	61.31662719	0.00615	4.00E−04*
3	Procrustes	No	Yes	0.009455	0.012821	26.25408411	0.00337	0.1725
	Residuals	No	Yes	0.007479	0.0121754	38.57263827	0.00470	0.0604
4	Procrustes	Yes	Yes	0.0092462	0.0134406	31.20674582	0.00419	0.1493
	Residuals	Yes	Yes	0.0080147	0.0128623	37.68825351	0.00485	0.0748
Mean pairwise dissimilarity								
1	Procrustes	No	No	0.0931	0.1310523	28.95963673	0.03795	0.0015*
	Residuals	No	No	0.0858484	0.1305398	34.23586523	0.04469	1.00E−04*
2	Procrustes	Yes	No	0.0838554	0.1334964	37.18529488	0.04964	1.00E−04*
	Residuals	Yes	No	0.0814047	0.1319525	38.30758796	0.05055	1.00E−04*
3	Procrustes	No	Yes	0.120437	0.14806	18.65662569	0.02762	0.0578
	Residuals	No	Yes	0.1079419	0.1451456	25.63198609	0.03720	0.0065*
4	Procrustes	Yes	Yes	0.1166505	0.1520492	23.2810827	0.03540	0.0262*
	Residuals	Yes	Yes	0.109469	0.1495667	26.80924297	0.04010	0.0083*

Dis M, index of disparity for Metatheria; Dis C, index of disparity for Carnivora; Relative diff, relative difference between both disparities; Diff, difference between both disparities; *P*, *P*-value.
*Significant difference at 5%.

whole cranium and the vicerocranium, but not in neurocranium. Using only the carnivore/insectivore subset and the Bonferroni correction, the work of Bennett & Goswami (2013) is more congruent Goswami *et al.* (2011) because there is not a significant difference in the neurocranium nor in disparity of the whole cranium between these clades. The viscerocranium continues to be significantly more diverse in placentals (Bennett & Goswami 2013; Table 1).

The study of Bennett & Goswami (2013) shows results that link the results of Goswami *et al.* (2012) and the results obtained in this paper (see also Prevosti *et al.* 2012). Sample size and taxonomic scope could explain some of the observed differences between these works, but the differences among them are probably due to differences in variability between the skull and the lower jaw and also in different regions of the skull (e.g. Bennett & Goswami 2013). The cranium and the lower jaw are composed of different modules and have different integration patterns (Goswami 2006; Goswami *et al.* 2009; Marroig *et al.* 2009; Goswami & Polly 2010; Meloro *et al.* 2011; Bennett & Goswami 2013), which could result in different of evolutionary constraints. The degrees of modularity and integration of the cranium and lower jaw could be a result of functional constraints, with the jaw more related to food intake and processing, while the cranium also has to support and protect the brain and sensitive organs, for the same reason, it is expected that the mandible and the viscerocranium portion of the cranium was less constrained during the evolution of these clades and more correlated with feeding habits than the neurocranium (Radinsky 1981; Slater & Van Valkenburgh 2009; Figueirido *et al.* 2011; Prevosti *et al.* 2012; Goswami *et al.* 2012.

The metatherians display less disparity in the mandible and in the viscerocranium, and this promotes the hypothesis of a biomechanical constraint that limited the evolution of the shape of these components. Marsupials display a singular tooth eruption and teeth are replaced as the animal grows, so the dentition is incapable of adapting to any specialized function (Werdelin 1987; Van Valkenburgh 1999; Wroe & Milne 2007). Placentals show eruption and replacement tooth patterns that allows specialization of the dentition to particular diet. This specialization would increases the disparity of lower jaw in the eutherian group. Other factors may contribute, as for example, marsupials suckle earlier and for longer than placentals, thus influencing the development of the snout (Bennett & Goswami 2013).

The inclusion of the metatherian carnivore Sparassodonta reduces the difference of disparity between Metatheria and Carnivora, but this clade is the sister taxa of the crown group Marsupialia (Forasiepi 2009), which separated 70–80 Ma. Ago (Beck 2008; Meredith *et al.* 2008; Nilsson *et al.* 2010) While the only placental order (Carnivora) originated in the early Palaeocene (50–55 Ma., see Meredith *et al.* 2011; O'Leary *et al.* 2013).

The different biogeographical histories of both groups (see Lillegraven 1974; Sánchez-Villagra 2013) could contribute to the greater disparity of the

placentals. The Carnivora originated in northern continents (Flynn & Wesley-Hunt 2005; Werdelin & Wesley-Hunt 2010) and occupied large continental areas with more chances of intercontinental migrations during the Cenozoic Era. In contrast, the metatherian clades studied (Sparassodonta, Didelphimorphia, Dasyuromorphia) were mostly confined to unconnected southern continents during almost the whole Cenozoic period, and occupy smaller areas with little chance of migration from their 'continent islands' (Lillegraven 1974). This is a plausible cause that could contribute to the difference of disparity between these groups, but it is difficult to test it with the available data.

The metatherians studied share part of the morphospace occupied by the carnivorans (Figs 2, 3 and S1), and in at least one case (*Thylacosmilus*), Metatheria evolved an extreme morphotype that broke the conservative pattern observed in the cranial, mandible shape and dentition (Forasiepi & Sánchez-Villagra 2014) in the rest of the group. Other carnivorous metatherians (e.g. *Thylacoleo*) may show similar excursions into carnivoran territory.

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