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(METATHERIA, DIPROTODONTIA, MACROPODIDAE) AND CAVIIDS (EUTHERIA,
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Artículo

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ABSTRACT. Quantification of morphological diversity among herbivorous mammals and comparisons between herbivorous marsupials and placentals are scarce. In this report we compared morphological variation of the skull and mandible in three representatives of caviid rodents and three species of macropodid marsupials, whose size is comparable, using three-dimensional geometric morphometrics. We applied two levels of comparison, one pointed to a placental-marsupial dichotomy and another pointed to the intra-variation in each group. We also performed an analysis of modularity based on a likelihood approach in order to evaluate different modularity models and analyzing the intra- and inter-module correlation (i.e., morphological integration). Beyond strong morphological differences that split caviids and macropodids along the first axes of the morphospaces of the cranium and mandible, they shared similar allometric shape changes, including the enlargement of muscular attachment areas and lengthening of the diastema. In both clades, the largest value of inter-module correlation (as a measure of modular integration) was found for the oral-nasal and orbit modules. We reported relatively low values of within-module correlation for the oral-nasal and molar modules in macropodids while the opposite was recorded for caviids. Beyond the great differences in cranial structure, one of the factors that influence the patterns of morphological variation and differential integration was the processing of plant matter which seems to induce strong structural changes in both clades, in which the efficiency of the masticatory apparatus is resolved in a similar way.

RESUMEN. Morfología cráneo-mandibular en mamíferos herbívoros: macropódidos (Metatheria, Diprotodontia, Macropodidae) y cávidos (Eutheria, Rodentia, Hystricomorpha) como un caso de estudio. La cuantificación de la diversidad morfológica entre mamíferos herbívoros y las comparaciones entre herbívoros marsupiales y placentarios son escasas. En este reporte, comparamos la variación morfológica del cráneo y mandíbula en representantes de roedores cávidos y marsupiales macropódidos mediante técnicas de morfometría geométrica en 3D. Aplicamos dos niveles de comparación, uno apuntando a una dicotomía placentario-marsupial y el otro a la variación interna en cada grupo. También realizamos un análisis de modularidad basado en un enfoque de verosimilitud para evaluar diferentes modelos y analizar la correlación intra- e inter-módulo (integración morfológica). Cávidos y macropódidos se separaron en los espacios de forma del cráneo y mandíbula, particularmente sobre el primer eje, mientras que se distribuyeron a lo largo del segundo eje principalmente de acuerdo con la variación de tamaño. Los cambios de forma vinculados al tamaño

estuvieron relacionados con la ampliación de las áreas de fijación muscular y el alargamiento del diastema. Los módulos oral-nasal y orbital mostraron los valores más altos de correlación tanto en macropódidos como en cávidos. Se obtuvieron valores de correlación intra-módulo relativamente bajos para los módulos oral-nasal y molar en macropódidos, mientras que se registró lo contrario para los cávidos. Más allá de las grandes diferencias en la estructura craneana, uno de los factores que influye en los patrones de variación morfológica e integración diferencial es el procesamiento de materia vegetal que parece inducir fuertes cambios estructurales que en ambos clados, en los que la eficiencia del aparato masticatorio se resuelve de manera similar.

Key words: Caviidae, functional convergences, herbivory, Macropodidae, modularity, morphological integration.

Palabras clave: Caviidae, convergencias funcionales, herbivoría, integración morfológica, Macropodidae, modularidad.

INTRODUCTION

Mammals have evolved remarkable variability in cranio-mandibular design and many morphological and physiological convergent adaptations are mainly related to feeding ecology (Fritz et al. 2009). Browse-plants and grasses exhibit fundamental differences in their properties, such as cell structure, plant chemistry, architecture, and secondary components (e.g., Short 1971; Freeland & Janzen 1974; Rosenthal & Janzen 1979; Demment & van Soest 1985; Cooper & Owen-smith 1986; Shipley 1999), and herbivorous specializations are highly diverse in mammals (Turnbull 1970; Gordon & Illius 1988; Janis & Ehrhardt 1988; Janis & Fortelius 1988; Clauss et al. 2008). Indeed, eutherian and metatherian mammals have evolved a number of parallelisms in their adaptations to dietary type although they show several completely different life history features related to the strategy of reproduction and developmental processes, such as the Metatheria needing for an earlier development of the jaw to suck very early in postnatal life (e.g., Smith 1997; Sánchez-Villagra et al. 2008; Goswami et al. 2012; Rager et al. 2014, but see, Sánchez-Villagra et al. 2008). Among the similar morphological characters in herbivores, the development of complex occlusal dental surfaces suitable for grinding and crushing and hypsodonty are observed in many grazer taxa among marsupials, rodents, lagomorphs, and ungulates (e.g., Simpson 1953; Fortelius 1985; Janis & Fortelius 1988). Herbivores usually also exhibit relatively large pterygoid and masseteric muscles, contrasting with carnivores that present more developed temporal muscles (Maynard Smith & Savage 1959; Turnbull 1970; Greaves 2008). Among the morphological divergences, a number of differences in relative craniodental proportions between macropodids and ungulates have been observed (see Janis 1990).

On the other hand, comparisons of the occlusion pattern of macropodids and rodents indicate large differences because the occlusion of incisors and molars occurs simultaneously in macropodids but not in rodents (Hiiemae 1971; Weijs & Dantuma 1975; Thorington & Darrow 1996; Lentle et al. 2003).

Among mammals, carnivorans (including placentals and marsupials) were frequently used as examples of convergence relating skull morphology and feeding ecology (e.g., Wroe & Milne 2007; Goswami et al. 2011; Prevosti et al. 2012). In these taxa, morphological variation was observed principally in the rostrum and maxilla anatomy, with metatherian carnivores exhibiting a degree of disparity which exceeds that of the more speciose eutherian carnivore radiations (Goswami et al. 2011). However, comparisons considering a more comprehensive sample including herbivore taxa, resulted in an inverse result (Bennett & Goswami 2013), where the extant marsupial taxa occupied a much smaller area of morphospace than the placental taxa, supporting the hypothesis of developmental constraint limiting the evolution of the marsupial skull (e.g., Wroe & Milne 2007; Goswami et al. 2011; Prevosti et al. 2012). Following these results, we wanted to test whether the supposed morphological constraint in marsupials has an impact on herbivore masticatory adaptations. In this sense, we expect that placentals will show higher shape variation because their facial region is not constrained by functional requirements caused by its early development, as occurs in marsupials.

Correlated evolution of traits can impact the morphological evolution of a structure. That correlation could constrain the variation in some features or, conversely, could promote changes in a trait associated to other that is changing (e.g., Olson & Miller 1958; Goswami 2006). Highly correlated, integrated traits may build up a module ("developmental

unit" of Atchley & Hall 1991) since they can share genetic sources, and developmental processes and mechanic demands acting on them (Goswami 2006; Klingenberg 2013) that in turn could be more or less integrated to other modules. Modularity refers to differences in the degree of integration of sets of traits within and between them. Mammalian cranium is a complex, highly integrated structure; but given that the integration is not pervasive, the cranium is structured in modules that are relatively independent (Klingenberg 2013). Various models of modularity have been proposed, and among them the most recognized are those that involve two (neurocranium and face), three (face, cranial base and cranial vault) or six modules (cranial base, cranial vault, orbital, anterior oral-nasal, molar and zygomatic-pterygoid regions, Lieberman et al. 2000; Goswami 2006; Hallgrímsson et al. 2007; Drake & Klingenberg 2010; Goswami & Finarelli 2016). Alterations of developmental pathways can generate differences in the patterns of modularity and/or integration (e.g., Goswami et al. 2014; Koyabu et al. 2014), so it could be expected that marsupial and placental mammals present different patterns.

In this study case, we took some selected species represented by macropodid marsupials and caviid rodents, representing appropriate models for the study of anatomical correlates in herbivore marsupials and placentals. Both groups developed several ecological similarities, such as a mostly grazing feeding habit and the occupation of open and semi-wooded environments in Australia and South America, respectively. They also show a great size variation, ranging between 200 g to 90 kg in caviids (Mones & Ojasti 1986; Nowak 1999), and between 1 kg to 80 kg in macropodids (Hume et al. 1989). Macropodids are Australia's dominant mammalian herbivores, similar to caviomorph rodents in the Neotropics (Osborne 2000; Fabre et al. 2013; Cox & Hautier 2015). Macropodids have a long history of endemism close to 30 Myr in Australia, while caviids are recorded from 12.5 Myr ago in the Neotropics (Kirsch 1977; Hume et al. 1989; Nowak 1999; Pérez & Pol 2012). In the context of comparison between placental and metatherian herbivores, the analyses presented here represent an important step in order to understand the impact of feeding ecology and evolutionary history onto morphological evolution. We expect not only obvious differences between clades, mostly attributed to separate phylogenetic stories, but an intra-clade distribution on the morpho-space, attributed to different patterns associated to size variation or ecology in each group, as well as variations

in the modularity models of both clades through the observation of trait correlations.

MATERIAL AND METHODS

Sample

In order to illustrate shape variation of the skull and mandible of the selected species and to study patterns of cranial modularity, we examined 81 adult specimens representative of each family, Caviidae and Macropodidae (Appendix A). In the case of Caviidae, we included the Brazilian guinea pig, *Cavia aperea* (0.65 kg; Canevari & Vaccaro 2007, N=13), the Patagonian mara, *Dolichotis patagonum* (8 kg; Campos et al. 2001, N=13), and the capybara, *Hydrochoerus hydrochaeris* (50 kg; Mones & Ojasti 1986, N=15). For Macropodidae, we selected the Tasmanian pademelon, *Thylogale billardieri* (9 kg; Watson et al. 2012, N=13), the swamp wallaby, *Wallabia bicolor* (15 kg; Nowak 1999, N=11), and the Eastern gray kangaroo, *Macropus giganteus* (43 kg; Poole 1982, N=16). Although the species selection consists of strict herbivores, differences in food habits exist among them. For instance, *C. aperea* is a generalist grazer, it feeds on seeds, leaves, stems, and in some cases, roots or tubers (Asher et al. 2004; Kraus et al. 2005); *D. patagonum* also shows considerable flexibility in adjusting its diet to different ecosystems, but grasses make up nearly 70% of its diet (Sombra & Mangione 2005); and *H. hydrochaeris* is principally a grazer, also feeding on aquatic plants (Herrera & Macdonald 1989). Among herbivore marsupials it also exists a wide range of feeding types. *Macropus giganteus* is a grazer but eat a wide variety of foliage ranging from grasses to herbs (Strahan 1995); *T. billardierii* eats mainly both short green grasses and occasionally taller woody plants, whereas *W. bicolor* is a browser (Ellis 2000; Di Stefano & Newell 2008).

Shape analysis

Shape variation was examined through geometric morphometric techniques. Twenty-five and 11 three-dimensional landmark coordinates were used to represent the cranium and the mandible, respectively (**Fig. 1**; **Table 1**). Landmark coordinates were collected using a digitizer (Immersion MicroScribe MX; Immersion Corp., San José, CA, USA). We took care in selecting some landmarks with functional homologies among selected species, such as those that represent muscular attachments and the diastema. In such cases, we generated a description of the landmark that is applicable in both families (see **Table 1**). Raw coordinates of each dataset were put through to a generalized Procrustes analysis in order to remove non-shape variation (differences in location, orientation and scaling; Rohlf 1999; Mitteroecker & Gunz 2009). To summarize and describe the major trends of cranial and mandibular shape variation a principal component analysis (PCA) of the aligned Procrustes coordinates were carried out for cranial and mandible datasets. Because we expected a considerable high amount of variation on the first principal component (PC1), as a consequence of the phylogenetic distance between macropodids and caviids, the information on the following components could be especially important in terms of shape changes not associated to phylogeny. We run and report the results of a Jolliffe cut-off analysis (Jolliffe 2002) in order to test whether shape change along
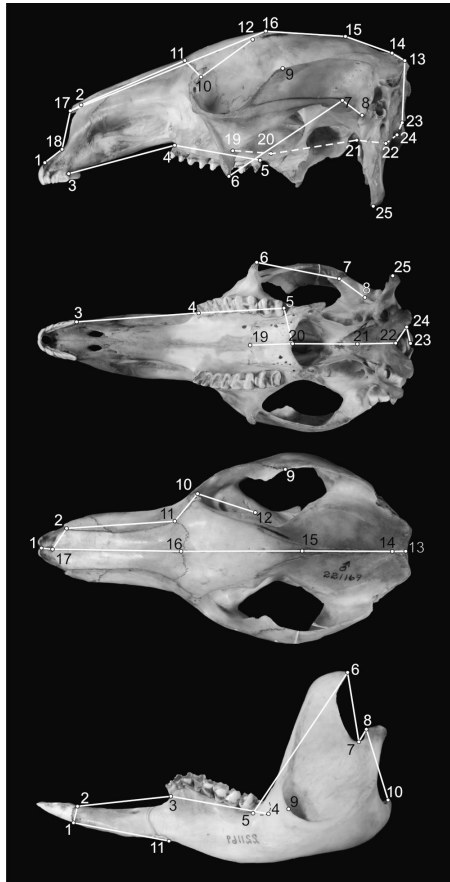
Fig. 1. Landmarks used in this study to represent cranial and mandibular configurations. Definitions in **Table** 1.

the PCs might be considered significant. Allometric trends in shape variation of cranium and mandible in caviids and macropodids were analyzed through separate (by family) ordinary least squares regression analyses between the aligned Procrustes coordinates and the natural logarithm of the centroid size (i.e., the square root of the summed squared distances from all landmarks to the configuration centroid) of each specimen (Klingenberg 2016). These morphometric analyses were performed using MorphoJ 1.05f (Klingenberg 2013) and Jolliffe cut-off analysis was carried out in Past vers. 2.16 (Hammer et al. 2001).

In addition, we applied the recently proposed method EMMLi (Evaluating Modularity with Maximum Likelihood) to study phenotypic modularity (Goswami & Finarelli 2016). It allows for comparison of hypotheses of different modularity models, and selection of the most probable model, through the assessment of the likelihoods of trait correlation matrices (each modularity model) using the corrected Akaike Information Criterion (Goswami & Finarelli 2016). For each clade, we confronted three commonly recognized models of mammalian cranial modularity: the first one divides the cranium into two modules (face and

neurocranium Drake & Klingenberg 2010), the second one divides it into three modules (face, cranial base and vault; see **Table** 1; e.g., Bookstein et al. 2003; Hallgrímsson et al. 2007; Álvarez et al. 2015) and the third one divides the cranium into six modules (anterior oral-nasal, molar, orbit, zygomatic-pterygoid, vault, and basicranium; see **Table** 1; Goswami 2006; Goswami & Polly 2010; Goswami & Finarelli 2016). EMMLi gives the values of inter-module and within-module correlations along the selected model; these values allow comparing, between the analyzed clades, which modules are more correlated with each other and the degree of integration of each module. These analyses were carried out using the package EMMLi (Goswami et al. 2016) for R (R Development Team 2016).

RESULTS

In both cranial and mandibular shape analyses, caviids and macropodids were clearly separated in the morphospace defined by the first two principal components. Both groups were separated along the first PC, whereas species within each family were distributed along the second PC mainly according to size variation (Figs. 2, 3).

In the analysis of the cranium, PC1 explained 69.2% of total variation. The main shape changes contributing to the complete separation of caviids and macropodids on this axis involved the configurations of the rostrum, orbit, and zygomatic arch. Caviids, which were located on positive values of PC1 (**Fig.** 2), present the following features compared with macropodids: the diastema is larger and deeper, the suture between premaxillary and maxillary bones is backward displaced, the orbit has a posterior position, the supraorbital process is more ventrally and posteriorly located, and the postglenoid process is lacking. Also, the zygomatic arch is not laterally expanded (as it is in macropodids), its dorsal margin reaches a lower position with respect to that of macropodids, and its anterior end is at the same level of the anterior end of superior toothrow, whereas in macropodids it is located far, more posteriorly with respect to the anterior end of superior toothrow. Such deep differences are obviously attributed to separate evolutionary history on both groups. PC2 was significant (Jollifee cut-off 0.0036) and explained 13.52% of total shape variation, including flattening of cranium, lengthening of cranial vault, nasals, and tooth rows towards negative values. According to the ordination obtained for both groups, shape changes observed along this axis could be linked with size variation (see below). In the multivariate space of the cranium, caviids showed more dispersion and it occurred mostly following the PC2 direction, whereas macropodids showed more variation on PC1.

In the analysis of the mandible, PC1 explained 78.06% of the total variation. As occurred in the analysis of the cranium, caviids and macropodids were placed in opposite ends of the first axis, showing contrasting features (**Fig.** 3). Caviids bear a lower coronoid process, higher condyle, and a posteriorly extended angular process compared to macropodids, in which it is shorter and medially reflected. PC2 was also significant (Jollifee cut-off 0.0008) and explained 6.51% of the total variation. Association between shape changes and size, as observed in the cranium, was not as clear for caviids as it was for macropodids. While the latter maintained a similar ordination pattern, in caviids, the largest genus, *Hydrochoerus*, showed a mandibular shape more similar to that of the smallest, *Cavia*. Toward
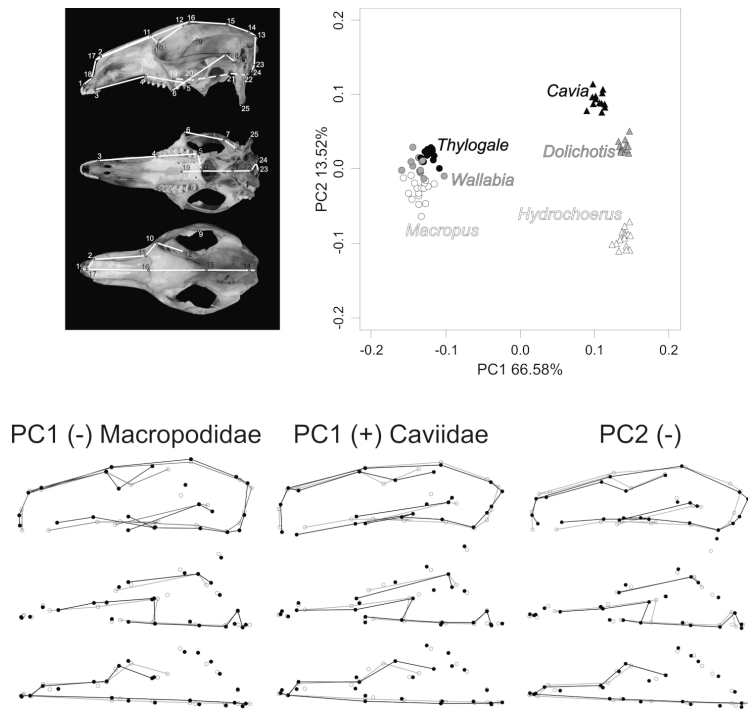
Fig. 2. Ordination of caviids and macropodids in the cranial morphospace defined by the first two principal components (PCs). Shape changes are shown as wireframes: black dots and lines indicate shape changes with respect to the mean configuration (indicated with grey dots and lines).

Fig. 3. Ordination of caviids and macropodids in the mandibular morphospace defined by the first two principal components (PCs). Shape changes are shown as wireframes: black dots and lines indicate shape changes with respect to the mean configuration (indicated with grey dots and lines).
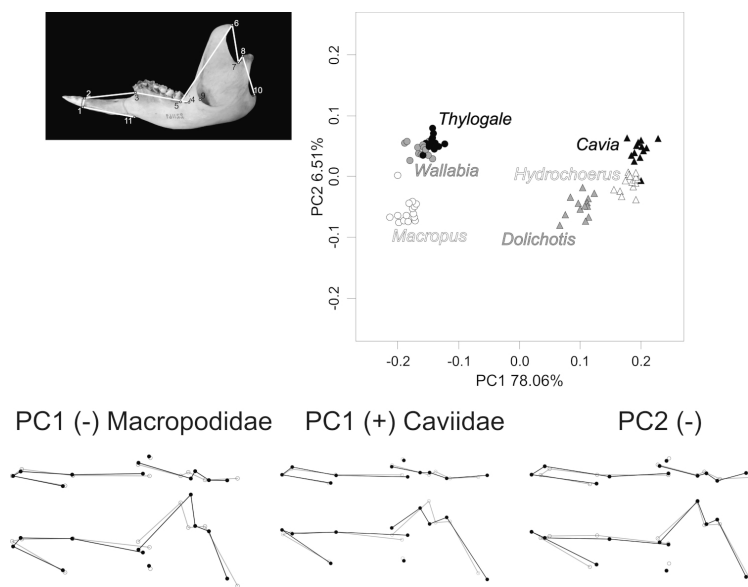
Table 1

Definition of landmarks used to represent cranial and mandibular shape of macropodids and caviids. Numbers correspond to those depicted in **Fig.** 1. Three cranial-modules models were confronted through an EMMLi analysis: a two-module model that includes facial (f) and neurocranial (n) modules, a three-module model that includes face (F), cranial base (CB), and cranial vault (CV), and a six-module model that involves anterior oral-nasal (AON), molar (M), orbit (O), zygomatic-pterygoid (ZP), vault (V), and basicranium (B) modules.

Landmark number (cranial modules)	Definition
Cranium	
1 (f, F, AON)	Anterior tip of premaxillary bone (Prostheon)
2 (f, F, AON)	Anterior tip of suture between nasal and premaxillary bones
3 (f, F, AON)	Posterior border of the last incisor alveolus. In caviids, it is the posterior border of the alveolus on the unique incisive
4 and 5 (f, F, M)	Extremities of upper tooth row (anterior and posterior, respectively)
6 (f, F, ZP)	Antero-ventral zygomatic root. In macropodids, it is placed on the ventral tip of the maxillary process
7 (f, F, ZP)	Posterior tip of the zygomatic arch. In macropodids, it is placed at the contact between squamosal and jugal bones. This landmark corresponds to the posteriormost point of the origin of the masseter
8 (f, CB, ZP)	Posterior end of cranial glenoid fossa. In macropodids, it is the ventral tip of the posglenoid process
9 (f, F, ZP)	Dorsal meeting between jugal and squamosal bones on the zygomatic arch. This landmark is posteriorly displaced in caviids.
10 (f, CV, O)	Anterior end of the orbit, placed on the lacrimal bone
11 (f, F, O)	Most external point of the posterior margin of the nasals. In macropodids this it coincides with the tripartite point maxillary-nasal-frontal, whereas in caviids it coincides with the tripartite point premaxillary-nasal-frontal
12 (f, CV, O)	Supraorbital process
13 (n, CV, V)	Inion
14 (n, CV, V)	Lambda
15 (n, CV, V)	Bregma
16 (f, F, O)	Nasion
17 (f, F, AON)	Rhinium
18 (f, F, AON)	Nasospinale. In macropodids, the distance of this landmark to landmark 1 is notably short
19 (f, F, M)	Middle point on the junction between maxillary and palatine bones.
20 (f, F, M)	Middle point of the palatine torus
21 (n, CB, B)	Middle point of basisphenoid-basioccipital suture
22 (n, CB, B)	Most ventral point of the foramen magnum
23 (n, CB, B)	Most dorsal point of the foramen magnum
24 (n, CB, B)	Most lateral point of the foramen magnum
25 (n, CB, B)	Tip of paraoccipital process
Mandible	
1	Antero-ventral border of incisor alveolus
2	Antero-dorsal border of incisor alveolus
3 and 4	Extremities of inferior tooth row (anterior and posterior, respectively)
5	Anterior end of base of coronoid process
6	Coronion
7	Maximum curvature of incisura mandibulae
8	Condylion
9	Anterior end of masseteric fossa. In caviids it is placed on the ventral masseteric fossa (insertion of the lateral masseter muscle)
10	Tip of angular process
11	Posterior extremity of mandibular symphysis

negative values, the main changes correspond to the relative shortening of the tooth row, lengthening of diastema, rising of the condyle, and a ventrally wider angular process.

The allometric analysis showed that the cranium of caviids presented the strongest allometric influence, with size explaining more than half of variation, although the mandible showed the weakest pattern of allometric vari-

Table 2

Percentage of cranial and mandibular shape (aligned Procrustes coordinates) variation explained by size (natural logarithm of centroid size).

	%predicted	p-value
Caviidae		
Cranium	54.77	<0.0001
Mandible	27.35	<0.0001
Macropodidae		
Cranium	42.36	<0.0001
Mandible	47.42	<0.0001

ation. Macropodids also displayed high proportions of shape explained by size, for both the cranium and mandible (**Table** 2; Figs. 4, 5). Overall, cranial shape changes follow similar tendencies in caviids and macropodids; for increasing size, these changes involved shortening of the cranial vault, advancement of the upper incisor alveolus and the enlargement of the diastema, and lengthening of the paracondylar process. In particular for macropodids, there is a notable dorsal flexion of the rostrum (in its dorsal margin) and a dorsal flattening of the braincase in the larger species. In addition, the zygomatic arch is more dorsally placed, and the maxillary process is more ventrally extended and posteriorly positioned in larger species. In the orbital region, the supraorbital process and the anterior margin of the orbit (i.e., lacrimal bone) are more posteriorly positioned in *Macropus*, determining a proportionally shorter braincase respect to *Wallabia* and *Thylogale*. On the other side, the ventral flexion of the palatine torus (as occurs with the ventral extension of the pterygoid hamulus and the already mentioned maxillary process) is notable in the larger species. Among caviids, larger species show a markedly posteriorly tilted occipital plane and a broad rostrum that is widened in its anterior end. In the orbital region, the supraorbital process is more dorsally located. Mandible shape changes associated with size increase were less obvious in caviids than in macropodids. As a common pattern, changes involved a slightly larger diastema and shortening of the angular process. In macropodids, a higher coronoid process is present in *Macropus* with respect to *Wallabia* and *Thylogale*.

The cranial modularity model selected by the EMMLi analysis was that involving a six-module structure for the cranium (**Table** 3). Both inter-module and within-module correlations resulted in similar values between caviids and macropodids (**Table** 4) although in caviids the anterior oral-nasal and molar modules are relatively highly integrated while the zygomatic-pterygoid module is the most integrated module among macropodids. Moderate values were recovered for inter-module correlations; the largest values for caviids were obtained for the correlation between molar and zygomatic-pterygoid modules and the oral-nasal and orbit modules, while these last two modules were the most correlated among macropodids (**Table** 4).

DISCUSSION

The basic bauplan of the mammalian masticatory apparatus is usually characterized as bearing a full dentition specialized to omnivory/carnivory, with a generalized masticatory muscular system in which the temporalis muscle is predominant over the masseteric and pterygoid muscle groups (e.g., Turnbull 1970; O'Lleary et al. 2013). Herbivory, in turn, is linked to specialized morphologies that have been achieved by several mammalian groups in a convergent way. Likewise, rodents (and artiodactyls) represent highly specialized morphologies among mammals that departure far from what is considered to represent the generalized skull morphology among basal placentals (O'Lleary et al. 2013), and macropodids (and the remaining diprotodonts) also represent a specialized morphology respect to basal marsupials (e.g., Russell 1974; Horovitz & Sánchez-Villagra 2003).

In our inter-group comparison (i.e., marsupials and placentals) the divergent morphological configurations between both groups (expected by the phylogenetic legacy) suggest that herbivory can be achieved through different morphological pathways although this specialization could lead to some similarities (see below). Indeed, selection for herbivory may be strong enough to overcome the marsupial constraint on trophic apparatus during early development. Alternatively, even if distant taxa such as marsupials and placentals may present similar developmental processes that rule morphological changes, morphological evolution of their species could show similar directions and thus generate convergence; either due to selection or random drift (see Losos 2011).

However, despite the separate evolutionary history between both groups, and probably responding to overall tendencies in mammals and even vertebrates, there is a similar tendency in cranial shape changes when increasing size (e.g., shortening of the vault, position of the upper incisor alveolus and diastema, and paracondylar process development; e.g., Harvey & Pagel 1988). Caviids and macropodids (as well as artiodactyls) share several traits that are linked to their herbivore habits, such as the presence of a marked diastema that separates the molariform teeth from incisors and their cropping and shearing/grinding functions, respectively (Crompton et al. 2008). At the same time, the superficial part of the masseter muscle is usually enlarged, a condition that has been suggested as facilitating manipulation of food items with the incisors (Woods 1972; Warburton 2009).

Beyond sharing these convergent features, the deep differences between both taxonomic groups, principally summarized in PC1, may not have a single explanation related to the phylogenetic legacy, but also with functional aspects or developmental constraints. Macropodids differentiate from caviids by having a shorter diastema related to a greater number of incisive teeth and a different dynamic of tooth replacement (i.e., new cheek teeth erupt, the molars move forward relative to the remainder of the skull; (e.g., Kirkpatrick 1964; Russell 1974; Woods 1982; Lentle et al. 2003), the zygomatic arch expands posteriorly giving space to a well-developed temporalis muscle that attaches to a high coronoid process in the mandible, and an anteriorly positioned orbit that locates it above the anterior root of the zygomatic arch (Figs. 2, 3). Conversely, in rodents, the orbit locates posteriorly in comparison with macropodids, which has been linked to the level of hypsodonty of molariform

Table 3

Results of the EMMLi analysis. Columns show the models confronted by the analysis, the number of model parameters (K), raw log-likelihood (MaxL), AICc and dAICc scores, model log-likelihoods (LogL), and the posterior probability of each model (Post Prob). Sample size used to calculate AICc was 300. Bolds indicate the selected model. 2-mod: two-modules model; 3-mod: three-modules model; 6-mod: six-modules model. SameMod: same within-module correlation for all modules; sameBetw = same within-module for all modules; sepMod: separate within-module for each module; sepBetw: separate between-module correlations for each module.

Caviids	K	MaxL	AICc	dAICc	LogL	Post.Prob
No modules	2	53.2662	-102.492	168.1276	0.0000	0.0000
2-mod.sameMod+sameBetw	3	81.3429	-156.6046	114.0149	0.0000	0.0000
2-mod.sepMod+sameBetw	4	83.0375	-157.9393	112.6802	0.0000	0.0000
3-mod.sameMod+sameBetw	3	91.2281	-176.375	94.2445	0.0000	0.0000
3-mod.sepMod+sameBetw	5	107.2706	-204.3371	66.2825	0.0000	0.0000
3-mod.sameMod+sepBetw	5	92.964	-175.7239	94.8956	0.0000	0.0000
3-mod.sepMod+sepBetw	7	109.0065	-203.6295	66.99	0.0000	0.0000
6-mod.sameMod+sameBetw	3	80.4025	-154.724	115.8956	0.0000	0.0000
6-mod.sepMod+sameBetw	8	112.5502	-208.6056	62.0139	0.0000	0.0000
6-mod.sameMod+sepBetw	17	126.9888	-217.8073	52.8122	0.0000	0.0000
6-mod.sepMod+sepBetw	**22**	**159.1365**	**-270.6195**	**0.0000**	**1**	**1**
Macropodids	K	MaxL	AICc	dAICc	Model_L	Post_Pob
No modules	2	244.1531	-484.2658	34.9784	0.0000	0.0000
2-mod.sameMod+sameBetw	3	244.8338	-483.5865	35.6577	0.0000	0.0000
2-mod.sepMod+sameBetw	4	245.7812	-483.4268	35.8173	0.0000	0.0000
3-mod.sameMod+sameBetw	3	244.3937	-482.7064	36.5378	0.0000	0.0000
3-mod.sepMod+sameBetw	5	245.0999	-479.9958	39.2484	0.0000	0.0000
3-mod.sameMod+sepBetw	5	248.3141	-486.4241	32.82	0.0000	0.0000
3-mod.sepMod+sepBetw	7	249.0203	-483.657	35.5871	0.0000	0.0000
6-mod.sameMod+sameBetw	3	245.6778	-485.2745	33.9697	0.0000	0.0000
6-mod.sepMod+sameBetw	8	256.2859	-496.077	23.1671	0.0000	0.0000
6-mod.sameMod+sepBetw	17	272.8406	-509.511	9.7331	0.0077	0.0076
6-mod.sepMod+sepBetw	**22**	**283.4488**	**-519.2442**	**0.0000**	**1**	**0.9923**

teeth that requires an increased space for rooting or to the necessity of larger panoramic visual fields to avoid predation (e.g. Solounias et al. 1995; Hautier et al. 2012). In fact, considering that macropodids do not show tooth hypsodonty, differences in the orbit position observed in **Figs.** 2 and 3 would support this hypothesis. The achievement of an enlarged superficial masseter muscle (which also presents a proper orientation of its fibers for antero-posterior movements, necessary to separate the functions of incisor and molariform teeth) is accomplished in macropodids by the presence of a characteristic maxillary process in the anterior extreme of the zygomatic arch that extends ventrally, whereas in caviids there is a marked posterior extension of the angular process of the mandible and the zygomatic arch is anteriorly displaced (Figs. 2, 3).

The described patterns of shape variation in both clades (i.e., intra-group variation) allowed analyzing morphological diversification related to size variation into each group, considering that both samples show comparable interspecific size variation. Some variation on PC2 of cranial and mandibular morphospaces was size-dependent, and related, among other features, to a tendency to the lengthening of the rostrum. The propensity for small species to be short-faced and large species to be long-faced) seems to

be a 'rule' which has been reported in vertebrates (see Emerson & Bramble 1993; Wilson & Sánchez-Villagra 2011) and in a large number of mammalian clades including rodents (Hautier et al. 2012; Álvarez et al. 2013, results presented here), antelopes, fruit-bats, mongooses, tree squirrels (Cardini 2013), deer (Merino et al. 2005), monkeys (Singleton 2005; Cardini & Elton 2008), carnivorans (Segura et al. 2013) and large kangaroos (Milne & O'Higgins 2002; Cardini et al. 2015, results presented here). Beyond the strongly different pattern of development in marsupials and placentals (e.g., Goswami et al. 2009), both clades would present a common pattern of allometric variation of the rostrum because there is a conserved relative timing of cranial ossification patterns in early mammalian evolution (Sánchez-Villagra et al. 2008) and there are no specific differences in the postnatal allometric growth in marsupials and placentals (Flores et al. 2013, 2015, 2018). Cardini (2013) proposed the need for a well-developed trophic apparatus in large mammals, in order to maintain function and efficiency, beyond their belonging to marsupial or placental clades. However, size increasing (and rostrum increasing) can bring a cascade of metabolic consequences referred to, for instance, the volume of processed food, the size of the dental occlusal surface, etc, which were not deeply
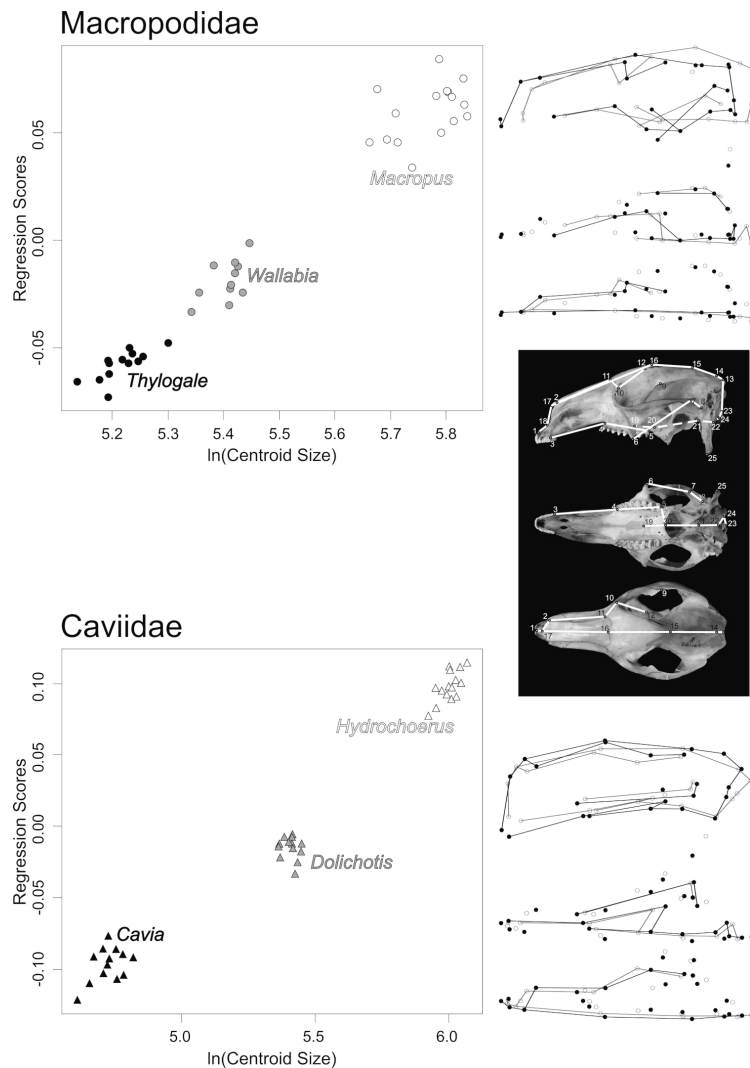
Fig. 4. Allometric changes of cranial shape for macropodids and caviids. Regression scores correspond to the aligned Procrustes coordinates projected onto the regression vector. Shape changes associated with increasing size (lnCentroid Size) are represented by black dots and lines; grey dots and lines represent the consensus shape.

discussed. A large component of the facial variation in mammals was associated with their diversity of size. Facial shape can respond to selection by a simple change in body size (e.g., Schluter 1996; Marroig & Cheverud 2005; Álvarez et al. 2013). A large proportion of the facial variation in both herbivore groups may be associated with size diversification (as was proposed for caviomorph rodents in Álvarez et al. 2013).

These comparable allometric (and developmental) patterns observed among rodents and macropodids may have a correlate with the integration patterns depicted by these groups. It has been shown that the large functional differences between placentals and marsupials regarding the oral apparatus during early developmental stages (i.e., differing feeding strategies of neonates), clearly influences on the amount of morphological integration among cranium parts in both groups (e.g., Goswami et al. 2009, 2012) and it is also associated to the distinct levels of disparity found between placentals and marsupials (e.g., Bennett & Goswami 2013). Both in caviids and macropodids, the largest value of inter-module correlation was found for the oral-nasal and orbit modules that include anatomical landmarks belonging to the viscerocranium that shows common developmental patterns across marsupials (e.g.; Flores et al. 2013, 2015, 2018). However, the intra-module correlation values obtained in the present report were somewhat variable between both groups. Interestingly, we reported relatively low values of within-module correlation for the oral-nasal and molar
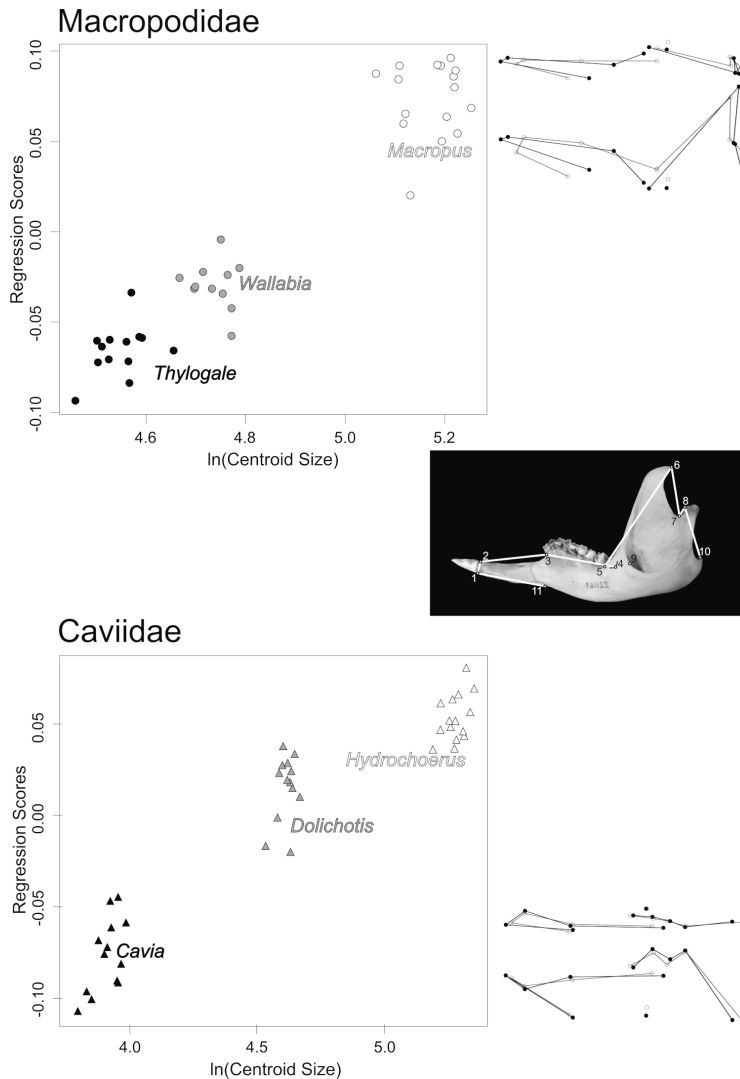
Macropodidae

Caviidae

Fig. 5. Allometric changes of mandibular (b) shape for macropodids and caviids. Regression scores correspond to the aligned Procrustes coordinates projected onto the regression vector. Shape changes associated with increasing size (ln Centroid Size) are represented by black dots and lines; grey dots and lines represent the consensus shape.

modules in macropodids. This gives support to the finding of Goswami et al. (2012) that in the marsupial analyzed by them (*Monodelphis*) the levels of integration of the oral region decreases along the growth of individuals. In addition, Goswami et al. (2011) showed that carnivorous marsupials exhibited higher morphological disparity of the oral region compared with placentals, which could be supported herein because the shape variation on the PC1 is higher in macropodids, although our sample is still exploratory for a more general conclusion. In contrast, in caviids, the oral-nasal and molar modules are highly integrated. Such result could suggest some constraints related to the presence of the diastema and the development

of incisors, or a probable allometric effect, as the cranial shape variation in caviids was explained by size in high proportion (>50%; **Table** 2). However, it is interesting to note that the amount of shape variation of the mandible on PC1 was higher in caviids than in macropodids. In general terms, and in agreement with previous studies (e.g., Prevosti et al. 2012; Bennett & Goswami 2013), much lower morphospace occupation was found among macropodids compared to that observed for caviids. Thus, although the study case reported here focused on an exploratory inter-generic variation within two families, these results also give some support to the statement that marsupials evolved through a constrained morphological repertoire

Table 4

Intra-module and inter-module correlation values. Values were estimated for the six-modules model selected by the EMMLi analysis, for caviids and macropodids. Bolds indicate the highest values for each group. Module 1, anterior oral-nasal; module 2, molar; module 3, orbit; module 4, zygomatic-pterygoid; module 5, vault; module 6, basicranium.

	Caviids	Macropodids
Module 1	**0.65**	0.29
Module 2	**0.65**	0.38
Module 3	0.33	0.22
Module 4	0.44	**0.54**
Module 5	0.44	0.40
Module 6	0.30	0.30
1 to 2	0.41	0.34
1 to 4	0.27	0.21
1 to 3	**0.47**	**0.45**
1 to 5	0.21	0.32
1 to 6	0.33	0.25
2 to 4	**0.50**	0.29
2 to 3	0.28	0.28
2 to 5	0.27	0.38
2 to 6	0.25	0.29
4 to 3	0.25	0.17
4 to 5	0.33	0.36
4 to 6	0.25	0.28
3 to 5	0.21	0.25
3 to 6	0.31	0.29
5 to 6	0.37	0.37

(Sears 2004; Goswami et al. 2011; Prevosti et al. 2012; Bennett & Goswami 2013). However, to be quite sure of this pattern, most members, both extant and extinct, of these families should be included in further studies since there are some macropodid taxa that could potentially increase shape variation (e.g., †*Halmaturus*, †*Protemnodon*, †*Sthenurus*), considering previous reports (Bennett & Goswami 2013). In a broader taxonomic context, remarkable amplitude of the morpho-space of herbivorous marsupials (possibly comparable to placental) could be expected, considering highly modified forms such as Phalangeriformes or Vombatiformes (Wilson & Mittermeier 2015).

In order to reach a better understanding of the evolution of specializations in the herbivore guilds, it is necessary to conduct comprehensive studies on a wider range of mammalian clades focusing on shape variation analyses and estimation of morphological disparities among herbivore mammals, and its comparison with carnivores. Studies on a wider range of species may reveal cases of morphological or functional convergences, which may aid the understanding of the evolution and specializations to particular feeding niches.

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APPENDIX A

List of specimens examined included in this study. Acronyms: AMNH, American Museum of Natural History, New York; CFA, Colección Fundación Félix de Azara, Buenos Aires, Argentina; FMNH, Field Museum of Natural History, Chicago; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; USMNH, United States Museum of Natural History, Smithsonian Institution, Washington DC.

Cavia aperea: MACN 22587, 22586, 14165, 54.168, 15362, 29.878, 40.186, 15384, 18811, 13291, 14170, 14171, 14177.

Dolichotis patagonum: CFA s/n, 4228; MACN 14532, 30.224, 9.17, 49.59, 13755, 42.117, 29.894, 28.19, 15533, 25.16, 26.65.

Hydrochoerus hydrochaeris: MACN 49302, 50309, 47220, 14039, 49.303, 38.248, 16259, 2.14, 16487, 31.18, 39.954, 3.78, 24495, 14038, 42.43.

Macropus giganteus: AMNH 66175, 66179, 107375 194031 194003 194154, 183401 194002; USMNH 221169, 582054, 151726, 49481; FMNH 160060, 160059, 64427, 83536.

Thylogale billarderi: USMNH 268918, 582036, 582044, 582041, 582032, 582049, 582043, 582048, 582035, 241367, 238337, 449426, 174748.

Wallabia bicolor: AMNH 274443, 160432, 70264, 65126, 65127, 107386, 65125; FMNH 64354; USMNH 238333, 238332, 221194.