



Ecological and phylogenetic influence on mandible shape variation of South American caviomorph rodents (Rodentia: Hystricomorpha)

ALICIA ÁLVAREZ^{1†}, S. IVAN PEREZ^{2†} and DIEGO H. VERZI^{1*†}

¹*Sección Mastozoología, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Paseo del Bosque s/n, La Plata CP 1900, Argentina*

²*División Antropología, Facultad de Ciencias Naturales y Museo, Paseo del Bosque s/n, La Plata CP 1900, Argentina*

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We analyzed mandible shape variation of 17 genera belonging to three superfamilies (Cavioidea, Chinchilloidea, and Octodontoidea) of South American caviomorph rodents using geometric morphometrics. The relative influence of phylogeny and ecology on this variation was assessed using phylogenetic comparative methods. Most morphological variation was concentrated in condylar, coronoid, and angular processes, as well as the diastema. Features potentially advantageous for digging (i.e. high coronoid and condylar processes, relatively short angular process, and diastema) were present only in octodontoids; cavioids showed opposing trends, which could represent a structural constraint for fossorial habits. Chinchilloids showed intermediate features. Genera were distributed in the morphospace according to their classification into superfamilial clades. The phylogenetic signal for shape components was significant along phylogeny, whereas the relationship between mandibular shape and ecology was nonsignificant when phylogenetic structure was taken into account. An early evolutionary divergence in the mandible shape among major caviomorph clades would explain the observed strong phylogenetic influence on the variation of this structure. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 828–837.

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INTRODUCTION

Patterns and processes of morphological diversification are of great interest in macroecology and evolutionary biology (Schluter, 2000; Wainwright, 2007; Diniz-Filho *et al.*, 2009). Morphological variation among species is mainly shaped by two factors: ecology and evolutionary history (Schluter, 2000; Viguier, 2002; Caumul & Polly, 2005; Wiens & Graham, 2005). Evolutionary history is important because ancestor–descendant relationships make phylogenetically close species more similar to each other with respect to their morphology than would be

expected by chance (Rohlf, 2001; Blomberg, Garland & Ives, 2003; Garland, Bennett & Rezende, 2005). In particular, several studies have shown that evolutionary history is paramount to shape morphological variation at lower taxonomic levels (i.e. species and genera) under conditions of ecological homogeneity (Polly, 2001; Renaud, Chevret & Michaux, 2007; Perez *et al.*, 2009). Conversely, when ecological heterogeneity exists (e.g. great habit variation), as is usual at higher taxonomic levels, ecological factors could be more important with respect to shaping morphological variation (Dumont, 1997; Nogueira *et al.*, 2005; Renaud *et al.*, 2007; Perez *et al.*, 2009). Tests for patterns of morphological variation are more frequently performed at lower taxonomical levels, whereas they remain scarce at higher taxonomical levels that comprise great ecological variation (Goswami, 2006;

*Corresponding author. E-mail: dverzi@fcnym.unlp.edu.ar
†CONICET.

Meloro *et al.*, 2008; Morgan, 2009; Samuels, 2009; Jones & Goswami, 2010).

The rodent mandible is an excellent model for studies of patterns and processes of morphological evolution (Duarte *et al.*, 2000; Cardini, 2003; Klingenberg, Mebus & Auffray, 2003; Renaud & Michaux, 2003; Monteiro & dos Reis, 2005; Barrow & MacLeod, 2008; Zelditch *et al.*, 2008; Hautier, Fabre & Michaux, 2009) because of its complex morphology mainly related to functional demands of feeding and digging activities in fossorial taxa (Hildebrand, 1985; Ubilla & Altuna, 1990; Verzi & Olivares, 2006). Such functional demands can generate great mandible morphological variation among species with wide ecological differences (Thorington & Darrow, 1996; Renaud *et al.*, 2007). Caviomorphs (i.e. South American hystriognaths), in particular, represent a very suitable model for this type of study as a result of their great ecomorphological diversity and long evolutionary history. Caviomorphs are considered to be a monophyletic group, according to phylogenetic estimations using nuclear and extranuclear nucleotide sequences (Huchon & Douzery, 2001; Poux *et al.*, 2006). These rodents probably had an African origin, likely with a single dispersal event into South America, followed by quick radiation in the early Oligocene (31 Mya; Vucetich, Verzi & Hartenberger, 1999; Huchon & Douzery, 2001; Flynn *et al.*, 2003; Opazo, 2005; Vucetich *et al.*, 2010b). Currently, caviomorphs show great ecological diversity (Mares & Ojeda, 1982; Nowak, 1991). In accordance with their wide-ranging habits (arboreal, epigeal, semi-aquatic, fossorial, subterranean; Nowak, 1991; Emmons & Feer, 1997), their skeletal morphology shows remarkable variation (Vassallo & Verzi, 2001; Candela & Picasso, 2008; Morgan, 2009). Previous analyses of craniomandibular morphological disparity have shown that this morphological variation is more related to habit diversity than to masticatory strategies (Vassallo & Verzi, 2001; Olivares, Verzi & Vassallo, 2004; Verzi, 2008).

In the present study, we analyze mandible shape variation in caviomorphs through a wide taxonomic range, from the level of genera through families up to superfamilies, including several species belonging to three of the four caviomorph superfamilies (Cavioidea, Chinchilloidea, and Octodontoidea). The main goal of the study is to test whether mandible shape variation among these rodents is related to phylogenetic and/or habits variation using geometric morphometric techniques (Adams, Rohlf & Slice, 2004; Mitteroecker & Gunz, 2009) and comparative phylogenetic methods (Rohlf, 2001; Garland *et al.*, 2005). On the basis of functional characteristics of the mandible and the habit diversity of caviomorph rodents, we hypothesized that ecology is a key factor in explaining mandible shape variation in these

rodents, whereas phylogenetic relationships, on the other hand, are less important (Caumul & Polly, 2005; Barrow & MacLeod, 2008; Zelditch *et al.*, 2008). In addition, we test the correspondence between shape ordinations generated using two-dimensional landmarks and landmarks plus semi-landmarks datasets, and discuss the extent of functional and phylogenetic information represented in each dataset.

MATERIAL AND METHODS

SAMPLE

One hundred and twenty-six mandibles of 19 living species included in 17 genera and seven families, representing three of the four caviomorph superfamilies (Cavioidea, Chinchilloidea and Octodontoidea), were studied (Table 1; a detailed list of analyzed specimens is provided in the Supporting information, Appendix S1; morphological variation of the mandible in analyzed caviomorph species is provided in the Supporting information, Fig. S1). We follow the systematic scheme described by Woods & Kilpatrick (2005) and Dunnun & Salazar-Bravo (2010). Only adults, defined by the presence of a functional third molar, were included, and males and females were pooled in the analyses.

GEOMETRIC MORPHOMETRICS

Geometric morphometric techniques are an effective tool for analyzing variation in complex structures such as the mandible (Renaud & Michaux, 2003; Monteiro & dos Reis, 2005; Barrow & MacLeod, 2008; Zelditch *et al.*, 2008). The present study follows the long tradition of analyzing mandible shape variation of rodents in lateral view (Duarte *et al.*, 2000; Cardini, 2003; Cheverud, 2004; Perez *et al.*, 2009). Two-dimensional coordinates were captured on digital images of the left hemi-mandible in lateral view; when this side was missing or damaged, the reflected image of the right side was used. Images were standardized for mandible and camera lens plane position, and the distance to camera lens (Zelditch *et al.*, 2004). Two datasets were chosen to represent the two-dimensional geometry of the mandible in lateral view. First, we used a set of thirteen landmarks (L; Fig. 1, Table 2) partially *sensu* Monteiro & dos Reis (2005) and Duarte *et al.* (2000). In a second dataset, we incorporated 31 semi-landmarks (SL; Fig. 1) to the mentioned landmarks to represent the mandible contour in more detail. The x , y coordinates of landmarks and semi-landmarks were digitized using TPSDIG, version 2.12 (Rohlf, 2008). L and SL coordinates have been deposited at <http://datadryad.org/repo>.

To remove differences in location, orientation, and scaling (i.e. nonshape variation) of the landmark and

Table 1. Taxa studied, number of specimens examined (*N*), and habits

Taxon	<i>N</i>	Habits
Cavioidea		
Caviidae		
<i>Cavia aperea</i>	8	Epigean*
<i>Microcavia australis</i>	11	Fossorial*
<i>Galea leucoblephara</i>	8	Epigean*
<i>Galea</i> sp.	2	Epigean*
<i>Dolichotis patagonum</i>	10	Epigean*
<i>Pediolagus salinicola</i>	4	Epigean*
<i>Hydrochoerus hydrochaeris</i>	4	Epigean*
Dasyproctidae		
<i>Dasyprocta</i> sp.	10	Epigean*
Chinchilloidea		
Chinchillidae		
<i>Chinchilla</i> sp.	5	Epigean†
<i>Lagidium viscacia</i>	10	Epigean†
<i>Lagostomus maximus</i>	10	Fossorial*
Octodontoidea		
Ctenomyidae		
<i>Ctenomys australis</i>	9	Subterranean‡
Echimyidae		
<i>Myocastor coypus</i>	10	Epigean*
<i>Proechimys guyannensis</i>	4	Epigean‡
Octodontidae		
<i>Aconaemys porteri</i>	3	Fossorial‡
<i>Aconaemys sagei</i>	1	Fossorial‡
<i>Octodontomys gliroides</i>	7	Fossorial‡
<i>Octodon degus</i>	2	Fossorial‡
<i>Octodon bridgesi</i>	4	Fossorial‡
<i>Spalacopus cyanus</i>	4	Subterranean‡

Systematics *sensu* Woods & Kilpatrick (2005) and Dunnun & Salazar-Bravo (2010). Definition of habit categories *sensu* Lessa *et al.* (2008).

*Nowak (1991).

†Spotorno *et al.* (2004).

‡Lessa *et al.* (2008).

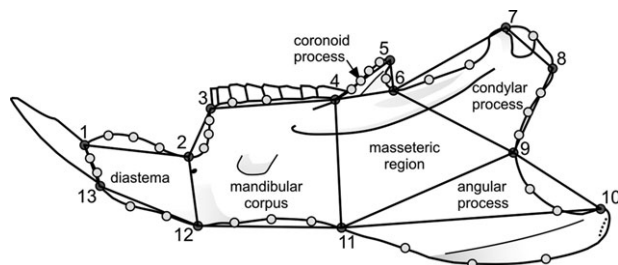


Figure 1. Landmarks (dark gray points) and semi-landmarks (light gray points) used in the present study (for description, see Table 2).

Table 2. Description of mandible landmarks

Landmark	Definition
1	Antero-dorsal border of incisor alveolus
2	Extreme of diastema invagination
3	Anterior end of mandibular toothrow
4	Anterior end of base of coronoid process
5	Tip of coronoid process
6	Maximum curvature of incisura mandibulae
7	Anterior edge of condylar process
8	Posterior-most edge of postcondylar process
9	Maximum curvature of curve between postcondylar process and angular process
10	Tip of angular process
11	Posterior-most point on ventral border of mandibular corpus
12	Posterior extremity of mandibular symphysis
13	Antero-ventral border of incisor alveolus

Definitions taken from Monteiro & dos Reis (2005), except for the landmarks 4 and 8 (this work), and for the landmark 11 (Duarte *et al.*, 2000).

semi-landmark coordinates we performed generalized Procrustes analyses (Rohlf & Slice, 1990; Mitteroecker & Gunz, 2009) for both L and SL. Semi-landmarks were slid along vectors tangent to the respective curves using the minimum bending energy criterion (Bookstein, 1997; Mitteroecker & Gunz, 2009). Sliding semi-landmarks represent an extension of the generalized Procrustes analyses: after removing nonshape variation, the semi-landmarks are aligned to diminish the variation tangential to the represented curve.

MULTIVARIATE ANALYSIS

Principal component analyses [relative warps (RW) analyses] of consensus configurations of both L and SL for each genus were performed (RW scores are available at <http://datadryad.org/repo>). The principal components (i.e. RW) summarize and describe the major trends in mandible shape variation among genera and facilitate the visualization of shape ordination in a low-dimensional morphospace. Differences in shape among caviomorph genera were described in terms of the variation in deformation grids (Bookstein, 1991). The morphometric analyses were performed using TPSRELW, version 1.46 (Rohlf, 2008).

The ordinations produced by the two datasets, L and SL, were compared using Procrustes analysis (PROTEST; Gower, 1971; Peres-Neto & Jackson,

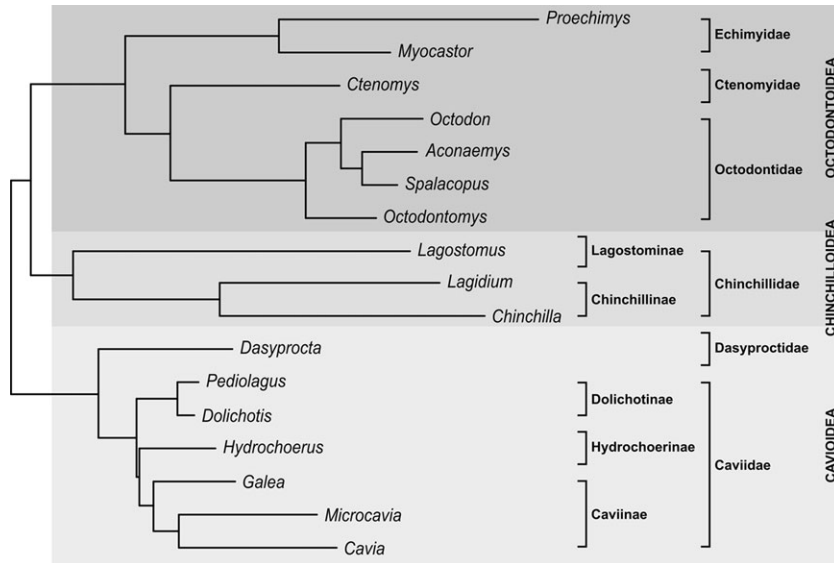


Figure 2. Phylogenetic relationships of South American caviomorph rodents included in the present study. Superfamilial to subfamilial clades are indicated. Topology *sensu* Huchon & Douzery (2001), Rowe & Honeycutt (2002), Honeycutt *et al.* (2003), and Ledesma *et al.* (2009).

2001). We scaled and rotated the ordinations for all RW and for the first two RW, using a minimum squared differences criterion. A permutation procedure (PROTEST; 10 000 permutations) was used to assess the statistical significance of the Procrustean fit (Peres-Neto & Jackson, 2001). This analysis was carried out using VEGAN (Oksanen *et al.*, 2010) for R 2.9.1 (R Development Core Team, 2009).

PHYLOGENETIC COMPARATIVE METHODS

The influence of phylogeny on patterns of shape variation was evaluated by calculating the phylogenetic signal of the first three RW obtained for L and SL. We calculated the commonly used *K*-statistic proposed by Blomberg *et al.* (2003). Blomberg's *K* provides a measure of the strength of phylogenetic signal of the data: values near 0 indicate a lack of signal, and values around 1 are expected for a character evolved under the Brownian motion model (Blomberg *et al.*, 2003). Statistical significance of *K* was assessed via permutation tests with 9999 replications. Phylogenetic relationships among genera were obtained from the maximum-likelihood trees generated by Huchon & Douzery (2001), Rowe & Honeycutt (2002), Honeycutt, Rowe & Gallardo (2003), and Ledesma *et al.* (2009) using von Willebrand Factor, growth hormone receptor, transthyretin, mitochondrial 12S rRNA and cytochrome *b* gene markers (Fig. 2). Analyses were conducted using PICANTE package for R (Kembel *et al.*, 2010).

To evaluate the influence of ecology on mandible shape variation, we fitted a habit dummy variable (i.e. subterranean, fossorial, and epigeal habits; *sensu* Lessa *et al.*, 2008) to the first three RW scores together (approximately 75% of total variance) and to each one separately, using a phylogenetic generalized least square regression model (Martins & Hansen, 1997; Rohlf, 2001), which is suitable for dealing with phylogenetic non-independence in comparative data (Rohlf, 2001; Garland *et al.*, 2005). This regression model takes the form: $Y = XB + \epsilon$, where *Y* is the dependent variable (i.e. RW scores describing shape variation), *X* is the predictor variable (i.e. habits), *B* is the matrix of partial regression coefficients, and ϵ is the error term that has a covariance matrix derived from the phylogenetic tree (Rohlf, 2001). This analysis was carried out using the APE for R (Paradis, Claude & Strimmer, 2004).

RESULTS

The percentage of variation explained by the first three relative warps was similar for L and SL datasets (approximately 45%, 18%, and 11% for RW1, RW2 and RW3, respectively). The PROTEST analyses showed high and significant correlations between these datasets, both for all RW and for the first two RW ($r = 0.99$; $P < 0.001$ for both analyses). We obtained similar ordinations using L (Fig. 3A) and SL (Fig. 3B). Most cavioids (except for *Dasyprocta*) were located on the right side of the graph, whereas

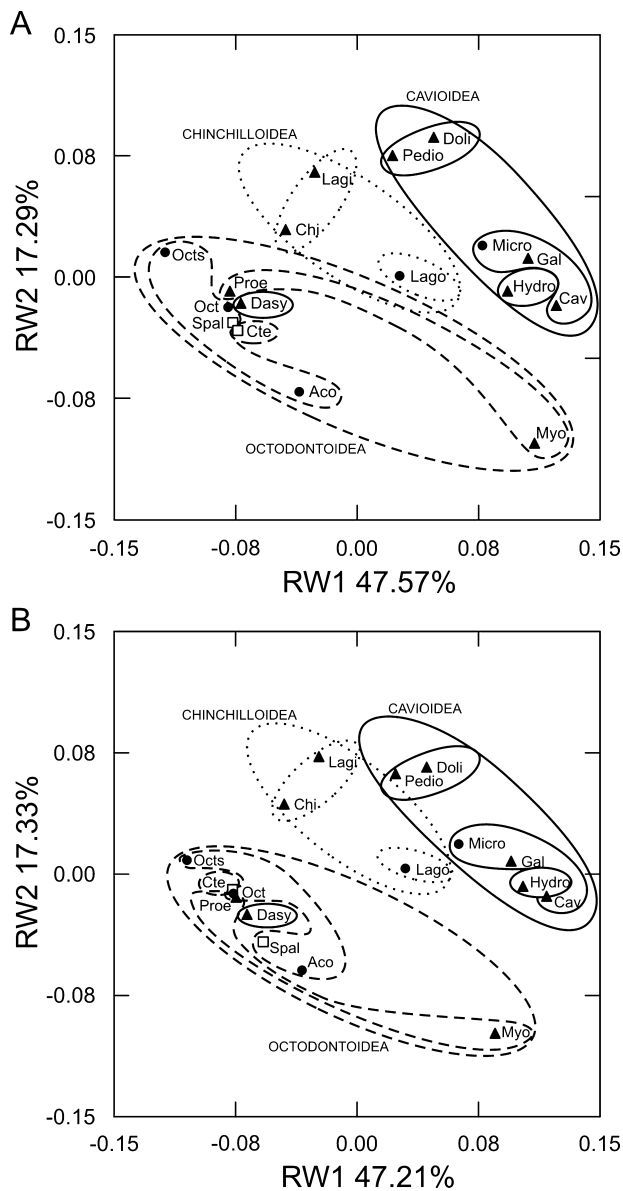


Figure 3. Ordination of the 17 caviomorph genera in the morphospace defined by the first two relative warps (RWs). Landmark analysis (A) and semi-landmark analysis (B). Cav, *Cavia aperea*; Micro, *Microcavia australis*; Gal, *Galea*; Hydro, *Hydrochoerus hydrochaeris*; Dol, *Dolichotis patagonum*; Pedio, *Pediolagus salinicola*; Chi, *Chinchilla*; Lagi, *Lagidium viscacia*; Lago, *Lagostomus maximus*; Octs, *Octodontomys gliroides*; Spal, *Spalacopus cyanus*; Aco, *Aconaemys*; Oct, *Octodon*; Cte, *Ctenomys australis*; Myo, *Myocastor coypus*; Proe, *Proechimys guyannensis*. Triangles, epigean habits; circles, fossorial habits; squares, subterranean habits.

octodontoids (except for *Myocastor*) were situated mainly on the left side of the morphospace. Chinchilloids showed intermediate positions. In addition, within cavioids, *Dolichotis* and *Pediolagus* (Caviidae,

Table 3. Blomberg's *K* statistic indicating phylogenetic signal for the first three relative warps (RW) for landmark (L) and landmark plus semi-landmark (SL) datasets

Dataset		<i>K</i>	<i>P</i>
L	RW1	0.944	0.005
	RW2	0.719	0.073
	RW3	0.529	0.260
SL	RW1	1.021	0.003
	RW2	0.854	0.011
	RW3	0.614	0.127

Dolichotinae) were separated from the rest of cavioids (Caviinae and Hydrochoerinae), which is consistent with previous hypotheses on the phylogenetic relationships among these clades (Vieytes, Verzi & Vucetich, 2001; Woods & Kilpatrick, 2005; Pérez, 2010). Similarly, the chinchillids *Chinchilla* and *Lagidium* clustered apart from *Lagostomus*, which is in agreement with the recognition of the Chinchillinae and Lagostominae subfamilial clades within Chinchillidae (McKenna & Bell, 1997; Spotorno *et al.*, 2004).

RW1 was associated with the general robustness of the mandible (Fig. 4). The genera on the left side of the graph (i.e. most of the octodontoids) presented high coronoid process (relative height of landmark 5 with respect to the occlusal plane defined by landmarks 3 and 4) and mandibular condyle (idem for landmark 7), along with well developed areas for insertion of masseteric muscles (defined by landmarks 4, 6, 9, and 11), shorter and deeper diastema (defined by landmarks 1, 2, 12, and 13), and deeper horizontal mandibular ramus (depth of landmark 12 with respect to the occlusal plane defined by landmarks 3 and 4). The genera on the right side of the graph (i.e. most of the cavioids) showed opposing characteristics, as well as a more enlarged, backward and ventrally directed angular process. RW2 was associated with differences in the development of the coronoid process and angular process (see Supporting information, Fig. S2).

The shape of the caviomorph mandible showed a clear phylogenetic signal (Fig. 3, Table 3). RW1 showed a statistically significant phylogenetic signal for both L and SL, whereas RW2 showed a phylogenetic signal only for SL. RW3 did not show any significant signal. The L dataset showed the weakest phylogenetic signal, reflected in its having significant signal for RW1 only, with a value of *K* below of 1, indicating lower phylogenetic dependence.

Regressions of mandible shape (first three RWs for L and SL; Table 4) on the habit dummy variable (i.e. subterranean, fossorial, and epigean habits) yielded

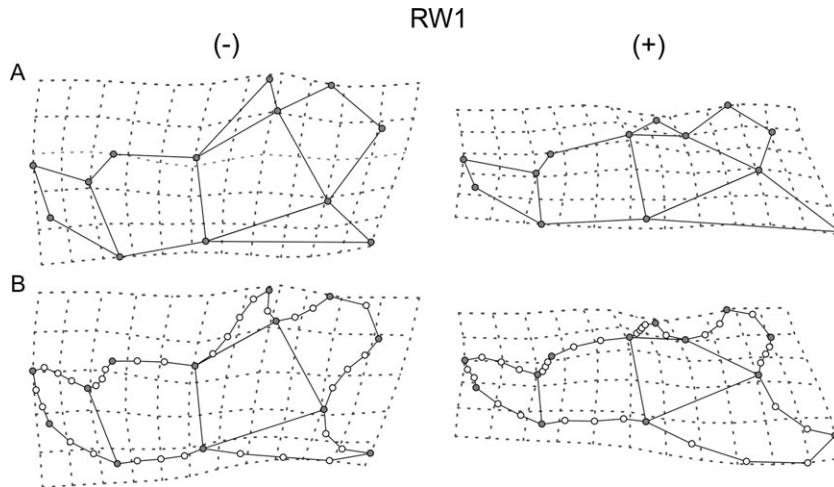


Figure 4. Mandible shape changes along the first relative warp (RW1), from negative (–) to positive (+) values, shown as deformation grids. A, analysis of landmarks. B, analysis of landmarks plus semi-landmarks.

Table 4. Statistics for the relationship between mandible shape [first three relative warps for both landmark (L) and landmark plus semi-landmark (SL) datasets] and habits assessed through a phylogenetic generalized least square regression model

Dataset	Univariate			Multivariate			
	R^2	F	P	λ	F	P	
L	0.062	0.463	0.639	0.866	0.198	0.993	
SL	0.055	0.410	0.671	0.256	2.433	0.033	

some interesting results. The regression analysis of L indicated a lack of significance of habit to explain shape variation. Alternatively, the regression analysis of SL showed marginally significant relationship between mandible shape and habit (Table 4).

DISCUSSION

One of the major advantages of geometric morphometric techniques is the possibility of analyzing, in a detailed manner, the shape of complex structures and their variation. In the present work, we used two geometric morphometric datasets: one comprising landmark coordinates and a second one formed by landmark plus semi-landmark coordinates. Although no large differences could be observed among ordination scatterplots of caviomorph genera, the incorporation of a greater amount of shape information in the landmarks plus semi-landmarks dataset allowed the recovery of a significant relationship between RWs and the habit variable (i.e. between mandible shape and ecology), which appeared as nonsignificant when

the landmark dataset was used. Thus, variation in habits would be reflected by both the relative position of anatomical points, and by the functional information contained in the curves delimited by semi-landmarks, which is lost in landmark analyses.

As expected given the high taxonomic levels analyzed, the main morphological differences that could be observed among caviomorph genera corresponded to variation in the most conspicuous traits of the mandible. The ordination of genera showed clear phylogenetic signal given that representatives from each caviomorph superfamilies, and even lower-level clades (i.e. subfamilies), clustered together in the morphospaces, rather than with other genera that share similar habits, as would be expected (Samuels, 2009). Each clade exhibited a particular combination of morphological features: most cavioids had a shallow mandible, long and slender distema, low coronoid and condylar processes, and backward and ventrally projected angular process. Most octodontoids showed opposing features, whereas chinchilloids exhibited intermediate morphologies (i.e. shallow mandible in combination with high coronoid and

condylar processes). *Myocastor* and *Dasyprocta* were exceptions to this pattern. *Myocastor* is an octodontoid (Echimyidae) that differed from the remaining octodontoid genera because of its very deep anterior mandibular corpus, highly reduced coronoid process, and backward extended angular process. *Dasyprocta* is a basal cavioid (Dasyproctidae) that showed deeper mandible and diastema than the other cavioids, in conjunction with high coronoid and condylar processes. Condylar and coronoid processes rising above the level of the tooth row represent a generalized condition for caviomorphs and even for rodents (Wood, 1949; Korth, 1994). Beyond this, adaptive or phylogenetic causes leading to morphological divergence of these taxa are still unclear.

By contrast to our expectation, phylogenetic constraints were more important than ecological factors for explaining morphological variation. This result contrasts with previous studies performed at specific and generic levels within the octodontoid family Echimyidae (Perez *et al.*, 2009), where a significant association between craniomandibular morphology and ecological heterogeneity was detected. South American caviomorphs are ecologically diverse, and so we would have expected ecological factors to be more relevant than the phylogenetic pattern for explaining morphological variation, as observed at low phylogenetic hierarchies (Polly, 2001; Perez *et al.*, 2009). The strong association between morphological variation and phylogenetic relationships could be explained by the long evolutionary history of caviomorphs, and the early divergence of superfamilial clades (early Oligocene; Flynn *et al.*, 2003; Opazo, 2005; Sallam *et al.*, 2009; Vilela *et al.*, 2009; Vucetich *et al.*, 1999, 2010b). The oldest fossils representing such divergence are fragmentary. Nevertheless, distinctive mandibular traits of each superfamily, as for those examined in the present study, are recorded at least since the early Miocene (Scott, 1905; Vucetich & Verzi, 1996; Pérez, 2010; Vucetich, Kramarz & Candela, 2010a). This pattern of early establishment of the major pathways of specialization in the mandible of caviomorphs would explain the observed strong phylogenetic influence on the morphological variation of this structure.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Lateral view of mandible of caviomorph rodents analyzed. A, *Lagostomus*; B, *Lagidium*; C, *Chinchilla*; D, *Dasyprocta*; E, *Dolichotis*; F, *Pediolagus*; G, *Aconaemys*; H, *Octodon*; I, *Ctenomys*; J, *Cavia*; K, *Microcavia*; L, *Galea*; M, *Octodontomys*; N, *Spalacopus*; O, *Proechimys*; P, *Myocastor*; Q, *Hydrochoerus*. Scale bar = 1 cm.

Figure S2. Mandible shape changes along the second relative warp (RW2), from negative (–) to positive (+) values, shown as deformation grids. A, analysis of landmarks; B, analysis of landmarks plus semi-landmarks.

Appendix S1. Detailed list of specimens included in the present study.

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