Ecological and phylogenetic dimensions of cranial shape diversification in South American caviomorph rodents (Rodentia: Hystricomorpha)

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Caviomorph rodents represent an excellent model to explore morphological diversification on a macroevolutionary scale, as they are ecologically and morphologically diverse. We analysed cranial shape variation using geometric morphometrics and phylogenetic comparative methods. Most variation involved the shape of the rostrum, basicranium, and cranial vault, and clearly matched the phylogenetic structure. At the same time, a strong allometric pattern was associated with the length of the rostrum and cranial vault, size of the auditory bulla, and depth of the zygomatic arch. After accounting for size influence, and taking phylogenetic structure into account, shape variation was significantly associated with habitat. Our results highlight the presence of complex relationships between morphological, phylogenetic, and ecological dimensions in the diversification of the caviomorph cranium. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **110**, 898–913.

ADDITIONAL KEYWORDS: caviomorph rodents – cranial shape – evolutionary diversification – habitat – size.

INTRODUCTION

The factors responsible for morphological diversification on a macroevolutionary scale have been widely discussed recently (Schluter, 2000; Wainwright, 2007; Gavrilets & Losos, 2009; Losos & Mahler, 2010). Ecologically diverse organisms have been considered for the discussion of this topic at different levels of phylogenetic divergence (e.g. Freeman, 2000; Meloro *et al*., 2011; Monteiro & Nogueira, 2011; Perez *et al*., 2011). Extant caviomorphs (South American Hystricomorpha) represent an excellent model to explore this issue, as they are the most ecologically diverse rodents and one of the most abundant living mammalian groups of the Neotropics, with a deep phylogenetic divergence. They display diverse modes of life (Mares & Ojeda, 1982; Elissamburu & Vizcaíno, 2004), and inhabit a wide variety of habitats (Nowak, 1991; Emmons & Feer, 1997; Eisenberg & Redford, 1999). Concurrently, caviomorphs are morphologically diverse, with a wide range of body size (Sánchez-Villagra, Aguilera & Horovitz, 2003; Rinderknecht & Blanco, 2008) and skeletal variation (Vassallo & Verzi, 2001; Morgan, 2009; Álvarez, Perez & Verzi, 2011a). This wide ecological and morphological variation of caviomorphs originated during the last *c*. 41 Myr (Antoine *et al*., 2012).

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Table 1. Caviomorph taxa included in this study and number of specimens examined (N)

Taxa	N	Taxa	N
Cavioidea		Octodontoidea	
Caviidae		Abrocomidae	
Cavia aperea	9	*Abrocoma cinerea* complex	6
Galea leucoblephara	9	Echimyidae	
Microcavia australis	11	*Myocastor coypus*	9
Dolichotis patagonum	12	*Proechimys guyannensis*	3
Pediolagus salinicola	4	*Thrichomys*	6
Hydrochoerus hydrochaeris	9	Octodontidae	
Kerodon rupestris	4	*Aconaemys porteri*	3
Dasyproctidae		*Aconaemys sagei*	3
Dasyprocta	16	*Octodon degus*	3
Cuniculidae		*Octodon bridgesi*	5
Cuniculus paca	8	*Octodontomys gliroides*	11
		Octomys mimax	7
Chinchilloidea		*Pipanacoctomys aureus*	11
Chinchillidae		*Spalacopus cyanus*	4
Chinchilla	5	*Tympanoctomys barrerae*	12
Lagidium viscacia	10	*Ctenomys australis*	1
Lagostomus maximus	10	*Ctenomys talarum*	9

The cranium is particularly interesting for morphological studies, as it is a complex structure that houses the brain and sense organs, and forms the orognathofacial complex together with the jaw. Several factors have been hypothesized to drive cranial diversification in mammalian clades, with size changes being an important source of morphological variation through allometric processes (Emerson & Bramble, 1993). Another important factor is the environment occupied by an organism and the modes of life associated with this occupation, which promote morphological adaptations (Nevo, 1979; Hildebrand, 1985; Stein, 2000).

Likewise, phylogenetic structure is a dimension that underlies every diversification process (Felsenstein, 1985; Rohlf, 2001). The importance of phylogenetic structure for the patterns of cranial variation may vary according to the phylogenetic scale of the analysis: whereas the pattern of morphological variation at lower hierarchical levels would be explained by ecological dimensions and evolutionary processes independent from the phylogeny, at a higher level, a greater influence of evolutionary processes co-varying with or occurring along the phylogeny could be expected (Felsenstein, 1985; Perez *et al*., 2009; Álvarez *et al*., 2011a). Relatively few studies on morphological variation in caviomorphs have been performed within a phylogenetic framework (Morgan, 2009; Perez *et al*., 2009; Álvarez *et al*., 2011a; Álvarez, Perez & Verzi, 2011b; Hautier *et al*., 2011; Hautier, Lebrun & Cox, 2012).

In this study, we analyse cranial shape variation among several caviomorph genera by means of geometric morphometrics and phylogenetic comparative methods. The main goal is to explore this variation and its relationship with phylogeny and ecological variables. Based on previous results, we expect phylogenetic structure to be the most important dimension for explaining cranial shape variation in these rodents (Samuels, 2009; Hautier *et al*., 2011, 2012; Álvarez *et al*., 2011a, b). To meet the primary objective, we assess the presence and strength of the phylogenetic signal in the shape data. At the same time, we determine whether allometric trends are present within cranial shape, as expected for mammalian groups with ample size variation such as caviomorphs. Finally, we analyse the association between cranial shape and ecological (mode of life and habitat) and functional (masticatory mode and bite force exerted by masticatory muscles) variation. As the cranium meets relevant functional requirements, we expect its shape to be highly associated with differences in masticatory modes or bite force. We test the association of cranial shape with size and ecological data using phylogenetic regression analyses to explore this expectation.

MATERIAL AND METHODS

SAMPLE

The total sample included 200 specimens belonging to 24 genera (26 species) and seven families, represent-

ing three of the four monophyletic caviomorph superfamilies (Table 1; a detailed list of specimens is included in Appendix S1): Cavioidea, Chinchilloidea, and Octodontoidea. Only adults, defined by the presence of a functional third molar, were included in the analyses.

PHYLOGENETIC RELATIONSHIPS AMONG CAVIOMORPH GENERA

Phylogenetic relationships and divergence time among genera were estimated through Bayesian inference methods implemented in BEAST 1.6.1 (Drummond & Rambaut, 2007). Sequences from the growth hormone receptor (*GHR*, 823 bp), trans-tyrethin hormone (*TTH*, 987 bp) and mitochondrial subunit *12S* (*12S* rRNA, 949 bp) genes were obtained from GenBank (accession numbers are listed in Appendix S2). jModelTest 0.1 (Posada, 2008) was employed to determine the most appropriate model

of sequence evolution for each gene analysed. The best-fit model for *GHR*, *TTH* and *12S* was GTR + G. The analyses were performed using Markov chain Monte Carlo (MCMC) simulations for 50 000 000 generations and a sample frequency of 5000. We used a relaxed molecular clock model, which allows substitution rates to vary across branches according to an uncorrelated lognormal distribution (Drummond *et al*., 2006; Drummond & Rambaut, 2007). Four fossil calibrations were selected following Upham & Patterson (2012). Convergence in the analyses was determined using the program TRACER 1.5 (Rambaut & Drummond, 2007). We computed the maximum credibility tree in TreeAnnotator 1.4.8 (Drummond & Rambaut, 2007), and the first 1250 sampled trees were excluded. The maximum clade credibility phylogenetic tree obtained through Bayesian methods (Fig. 1) is mostly congruent with previous phylogenies (Rowe & Honeycutt, 2002; Spotorno *et al*., 2004; Blanga-Kanfi *et al*., 2009;
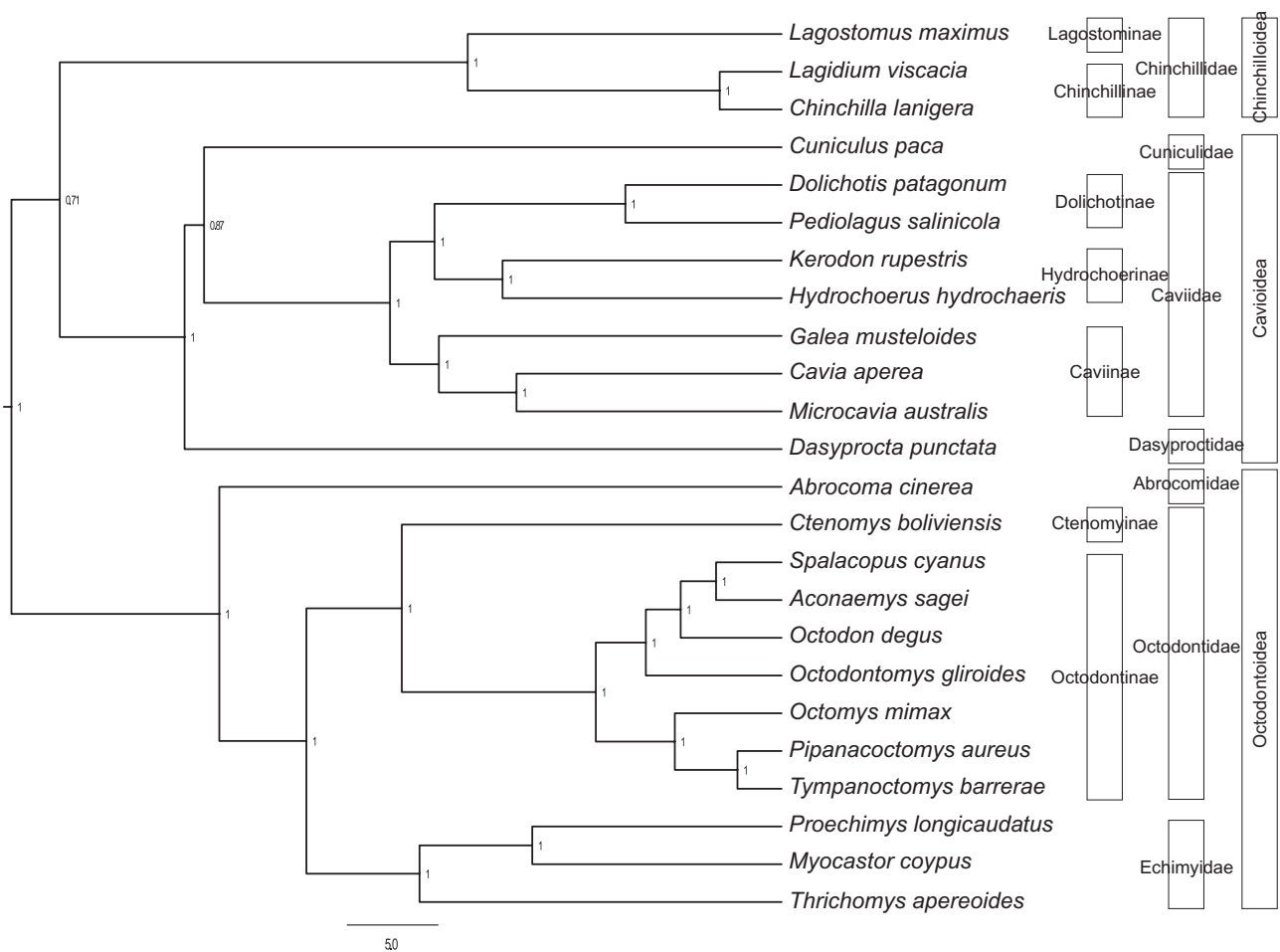

Figure 1. Phylogenetic tree of the caviomorph rodents studied, obtained by Bayesian inference analysis applied to a combined matrix with the sequences for *GHR*, *TTH*, and *12S* genes. Numbers in nodes indicate the posterior probability support for each clade. Node support values were superior to 0.9.

Upham & Patterson, 2012), although with some minor discrepancies probably arising from the use of a partially different set of genes. In addition, relationships among the genera studied were consistent with currently accepted taxonomy.

ECOLOGICAL AND FUNCTIONAL VARIATION

We selected a set of variables that has previously been proposed as significant for understanding the morphological diversification of caviomorphs (Olivares, Verzi & Vassallo, 2004; Verzi & Olivares, 2006; Álvarez, 2012; Becerra, Casinos & Vassallo, 2013; Table 2). Diet was not included in the analyses because we consider our sample of caviomorphs as essentially homogeneous with respect to diet (Nowak, 1991). Before the regression analyses, collinearity of variables was checked by means of correlation analyses. As correlation values among variables were low, all the selected explanatory variables were used.

Chewing modes
The chewing mode variable refers to the direction of the horizontal grinding movement, which may vary among caviomorphs from propalinal (direction angle $\leq 30°$) to oblique ($> 30°$) (Vassallo & Verzi, 2001; Olivares *et al.*, 2004). Chewing direction was assessed by calculating the angles between the enamel tooth scars of upper molariforms and the sagittal skull axis. Angles were measured with a protractor from camera lucida drawings (Fig. S1; Leica MS5 stereomicroscope).

Bite force
The force exerted by the main masticatory muscles (i.e. temporal and masseter muscles; Turnbull, 1970) was calculated using the equilibrium formula $F_o = F_i * L_i/L_o$, where F_o is the external force (i.e. the bite force at the incisors), F_i is the internal force (force exerted by muscles), and L_o and L_i are the external and internal moment arms, respectively. Jaw width was used as an estimator of the development of masseter muscles linked to the production of F_i (Fig. S1; Olivares *et al.*, 2004; Becerra *et al.*, 2013). In addition, the surface area of the site of origin of the main part of the temporal muscle (see Woods, 1972) (Figs S1, S2) was used as an estimator of the size and strength of this muscle (following Kiltie, 1984). This area was defined by the ventral margin of the squamosal bone, the dorsal temporal ridge, and the lambdoidal crest; its anterior limit was defined as the line connecting the anterior extremes of the dorsal and ventral margins of the delimited area. This area was delimitated and estimated from digital images of dry crania using the area demarcation tool in tpsDig 2.12 (Rohlf, 2008).

Habits
Habits were represented by three categories (based on Lessa *et al.*, 2008): epigean, i.e. organisms that perform all their activities above ground, although they may use shallow and simple burrows; fossorial, organisms that build simple to complex burrows, although their activities occur mostly above ground; and subterranean, organisms that build complex burrows and spend most of their time underground. Categories were considered as ordered for analyses. This ordinal variable was normalized to *Z*-scores.

Habitat
We built a variable to reflect the wide range of habitats occupied by caviomorph rodents. We followed the proposal of Ebensperger & Blumstein (2006), who established a ranking according to the vegetation cover of the areas inhabited by each species. We modified this ranking in order to take into account both this feature and the climatic context (i.e. humid to arid conditions; Martin, 1970; Glanz & Anderson, 1990; Woods *et al.*, 1992; Emmons & Feer, 1997; Torres-Mura & Contreras, 1998; Mares *et al.*, 2000; Cortés *et al.*, 2002; Justo, De Santis & Kin, 2003; Sobrero *et al.*, 2010). For this composite variable, low values indicate open and arid environments; higher values indicate an increase in both vegetation cover and humidity.

To summarize the ecological and functional variation displayed by caviomorphs, we conducted a principal component analysis (PC analysis) of the correlation matrix including these four variables. The ordination obtained for the taxa studied was illustrated by means of a biplot graph that allows joint representation of the observations and variables, and provides a visual appraisal of the structure of data. This analysis was carried out using the LABSDV package (Roberts, 2012) for R (R Development Core Team, 2009).

MORPHOMETRIC ANALYSES
Geometric morphometric techniques were employed to study caviomorph crania. Fourty-three tridimensional landmark coordinates were used to represent cranial shape. These coordinates were acquired with a Microscribe G2X digitizer and collected from the left side of each cranium (Fig. 2; Table S1) to avoid redundant information from symmetrical structures (Cardini, Hoffmann & Thorington, 2005). In the case of landmarks that were missing on the left side, all data were collected from the right side. Average configurations for each genus were obtained through generalized Procrustes analysis of raw coordinates. Shape variation among genera was studied through

Table 2.

Taxa	CS	Habit	Habitat	Chewing mode	Bite force	Taxa	CS	Habit	Habitat	Chewing mode	Bite force
Cavioidea						Octodontoidea					
Cavidae						Abrocomidae					
Cavia	4.8958	-0.69655*	1.2528	33.68	0.1486	*Abrocoma*	4.5911	-0.69655*	0.9163[2]	9.45	0.1313
Microcavia	4.6002	0.82320†	0.9163	42.04	0.1284	Octodontidae					
Galea	4.6436	-0.69655*	1.2528	26.46	0.1440	*Aconaemys*	4.4282	0.82320†	1.6094[3]	5.49[10]	0.2177
Pediolagus	5.2419	-0.69655*	0.9163	23.31	0.0881	*Spalacopus*	4.3658	2.34294‡	1.2528[4]	19.82	0.2042
Dolichotis	5.5737	-0.69655*	0.9163	22.03	0.1121	*Octodon*	4.5064	0.82320†	1.2528	55.04	0.2266
Hydrochoerus	6.2010	-0.69655*	1.2528	9.51	0.1482	*Octodontomys*	4.5425	0.82320†	0[3]	56.3	0.1499
Kerodon	4.9888	-0.69655*	1.2528	12.16	0.1235	*Octomys*	4.4803	-0.69655*	0[5]	4.76	0.1501
Cuniculidae						*Pipanacoctomys*	4.4197	0.82320†	0[6]	4.31	0.1619
Cuniculus	5.6989	-0.69655*	1.9459	13.87	0.1072	*Tympanoctomys*	4.3696	0.82320†	0	5.93	0.1703
Dasyproctidae						*Ctenomys*	4.4219	2.34294‡	1.2528[7]	66.57	0.2202
Dasyprocta	5.3843	-0.69655*	1.9459	56.86	0.1511	Echimyidae					
Chinchilloidea						*Myocastor*	5.4569	-0.69655*	1.2528[8]	59.72	0.2553
Chinchillidae						*Proechimys*	4.5870	-0.69655*	1.7918[9],	38.04	0.2113
Chinchilla	4.9174	-0.69655*	0.9163[1]	31.05	0.1316	*Thrichomys*	4.6305	-0.69655*	1.2528	37.17	0.1868
Lagidium	5.2249	-0.69655*	0.9163	44.92	0.1303						
Lagostomus	5.5510	0.82320†	1.2528	43.98	0.1757						

CS, cranial size measured as the centroid size of landmark configurations (ln-transformed); habitat, values for habitat categories assigned to each genera; habitat, composite habitat ranks built to represent features such as tree cover and atmospheric relative humidity (from Ebensperger & Blumstein, 2006, except those indicated) – higher values indicate increased tree cover and humidity; chewing mode, angle (°) formed by tooth (superior molars) scars and the sagittal cranial plane (data for Octodontidae are from Olivares *et al.*, 2004 and unpublished data of D. H. Verzi and A. I. Olivares) – values below 30° indicate a predominance of propalinal movement; bite force, estimated for masseter and temporal masticatory muscles; *epigean, †fossorial, and ‡subterranean.

[1]Cortés *et al.* (2002).
[2]Glanz & Anderson (1990).
[3]IUCN (http://www.iucnredlist.org/).
[4]Torres-Mura & Contreras (1998).
[5]Sobrero *et al.* (2010).
[6]Mares *et al.* (2000).
[7]Justo *et al.* (2003).
[8]Woods *et al.* (1992).
[9]Emmons & Feer (1997); Martin (1970).
[10]Olivares, Verzi & Vassallo (2004); Verzi and Olivares (unpublished data).
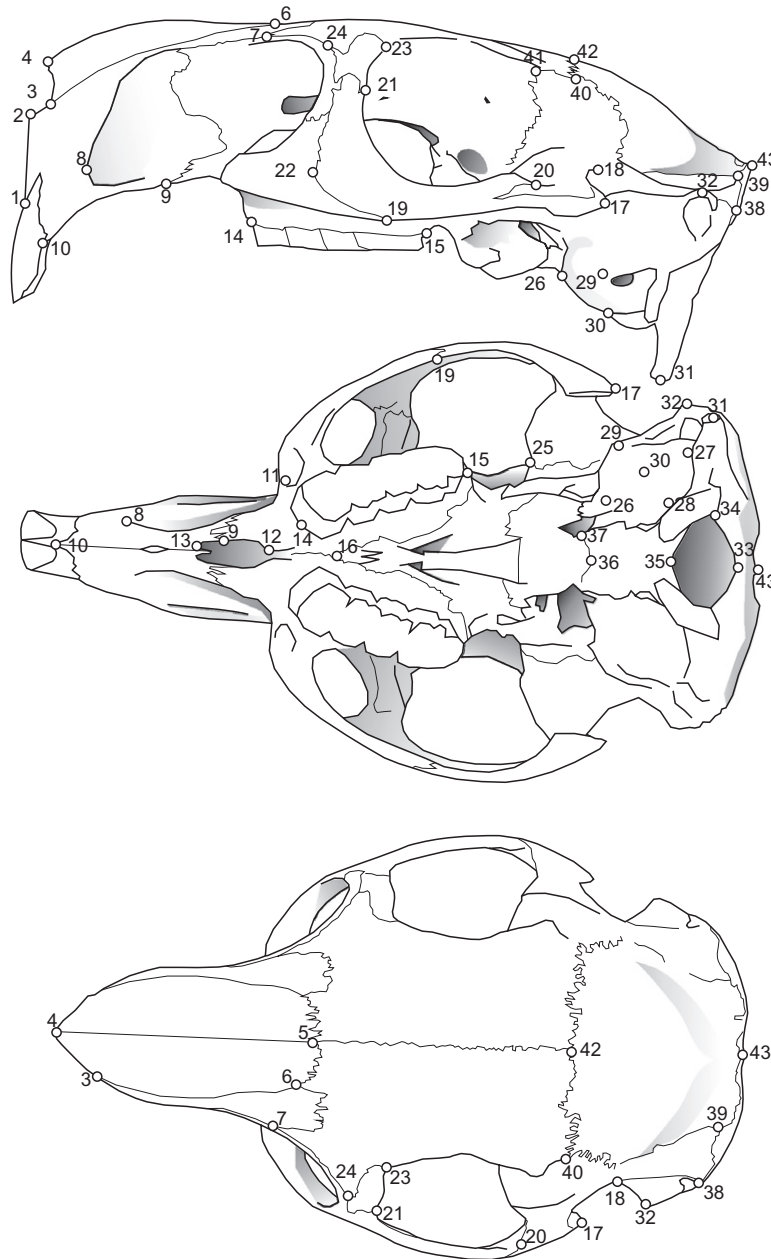
Figure 2. Cranial landmarks used in the present study, recorded using a Microscribe G2X digitizer.

generalized Procrustes analyses and principal component analysis [i.e. relative warp (RW) analysis; Rohlf & Slice, 1990; Rohlf, 1993]. Generalized Procrustes analysis allows the removal of differences in location, orientation, and scaling (i.e. non-shape variation) of the landmark configurations. The principal components (i.e. RWs) summarize the major trends of shape variation in a low-dimensional morphospace. The centroid size (CS) of the cranium (i.e. the square root of the summed squared distances from all landmarks to the configuration centroid) was measured to

explore size variation. The software packages MORPHOLOGIKA 2.5 (O'Higgins & Jones, 2006) and MorphoJ (Klingenberg, 2011) were used for these analyses.

Following Mitteroecker *et al.* (2004) and Drake & Klingenberg (2008), shape variation was decomposed into allometric and non-allometric components. Allometric trends in shape variation were analysed through an ordinary least squares regression analysis between the aligned Procrustes coordinates and the natural logarithm of centroid size (lnCS). This

procedure defines an allometric component (AC) that represents the direction of shape changes among genera when size increases (Mitteroecker *et al*., 2004; Drake & Klingenberg, 2008). The remaining shape variation (i.e. non-allometric component) was analysed by means of a principal component analysis of the residuals of this regression analysis (RSCs; Mitteroecker *et al*., 2004). This method allows us to graphically explore shape changes along the AC axis and the residual shape variation. These analyses were made using the software MorphoJ (Klingenberg, 2011).

STATISTICAL ANALYSES

To analyse the relationships between cranial shape, size, allometric and non-allometric variation, and phylogeny, the phylogenetic signal of the data was measured by calculating the K statistic (Blomberg, Garland & Ives, 2003) for the first two RWs, lnCS, the AC, and the first three RSCs. We also evaluated the phylogenetic signal of the ecological and functional principal components. This statistic provides a univariate measure of the strength of phylogenetic signal in the data: the null hypothesis for this statistic is the lack of signal, i.e. values of K near 0, whereas values near 1 are expected if the character evolved under a Brownian motion model (Blomberg *et al*., 2003). We also estimated the measurement tree length (Laurin, 2004; Klingenberg & Gidaszewski, 2010) for all RWs, lnCS, and all RSCs. This statistic measures the total number of squared changes (of size and shape), summed over all branches of the phylogenetic tree. The null hypothesis for this statistic is that character values are randomly distributed in the tree. The significance of both statistics was assessed via permutation tests with 10 000 replications. These analyses were carried out using the PICANTE package for R (Kembel *et al*., 2010) and MorphoJ (Klingenberg, 2011).

Finally, we assessed the correspondence between patterns of cranial shape variation and ecological and functional variables through phylogenetic generalized least squares regression analyses (PGLS; Martins & Hansen, 1997). We ran a second PGLS analysis considering lnCS as covariate to account for allometric effects. The PGLS regression model takes the form: $Y = XB + \varepsilon$, where Y is a matrix containing the RW scores describing shape variation (the first three and ten RWs, which explained 70 and 90% of the total shape variation, respectively), X is the matrix containing the ecological, functional, and size variables, B is the matrix of partial regression coefficients, and ε is the error term that contains the phylogenetic covariance matrix derived from the phylogenetic tree (Rohlf, 2001). This matrix was used assuming a Brownian motion model in the first PGLS analysis. It was subsequently modified by multiplying its off-diagonal elements by λ, an estimator of the degree of phylogenetic dependence (Freckleton, Harvey & Pagel, 2002). The value of λ was set at its maximum-likelihood value for the latter analysis, and to a value of 1 for the former. These analyses were performed with the Caper package for R (Orme *et al*., 2011).

RESULTS

ECOLOGICAL AND FUNCTIONAL VARIATION

Estimated chewing directions (Table 2) were partially similar to previously reported values (Vassallo & Verzi, 2001). Overall, cavioids showed propalinal to oblique mastication, and chinchilloids showed oblique mastication. Octodontoids were more diverse, ranging from strongly oblique chewers (e.g. *Ctenomys*) to markedly propalinal ones (e.g. *Pipanacoctomys*).

Estimates of biting force (*BF*, Table 2) were in accordance with results in progress obtained using a force transducer (Becerra *et al*., 2011; F. Becerra, pers. comm.). Most cavioids and chinchilloids showed low bite force values, whereas some octodontoids showed the highest values.

The first two PCs of the principal component analysis of the matrix of ecological and functional variables explained 74% of the total variation. Chewing modes and bite force showed the highest loadings on PC1; taxa located on negative values of this axis show higher bite forces and oblique chewing. The variable 'habitat' loaded on PC2, with taxa located on the highest positive values associated with closed, humid environments (Fig. 3). The ordination of genera also matched the phylogenetic structure of data, as reflected by the K values obtained for the first two PCs (PC1, $K = 0.707$, $P = 0.004$; PC2, $K = 1.075$, $P = 0.0005$).

MORPHOMETRIC VARIATION

Cranial size varied among the caviomorphs studied (Table 2). This variation followed a clear phylogenetic pattern ($K = 1.028$, $P = 0.0005$; tree length = 2.334, $P = 0.00237$). Cavioids, which include several of the largest rodents, such as *Hydrochoerus* and *Cuniculus*, showed the highest values. The octodontoids showed moderate to low values; among them are the octodontids, the smallest caviomorphs.

The first two relative warps explained nearly 60% of the total variation (RW1, 47.04%; RW2, 11.64%). A clear separation of major caviomorph clades was observed in this morphospace (Fig. 4A). The Octodontoidea were located on negative values of RW1, whereas the Cavioidea occupied positive values. The Chinchilloidea were separated from the
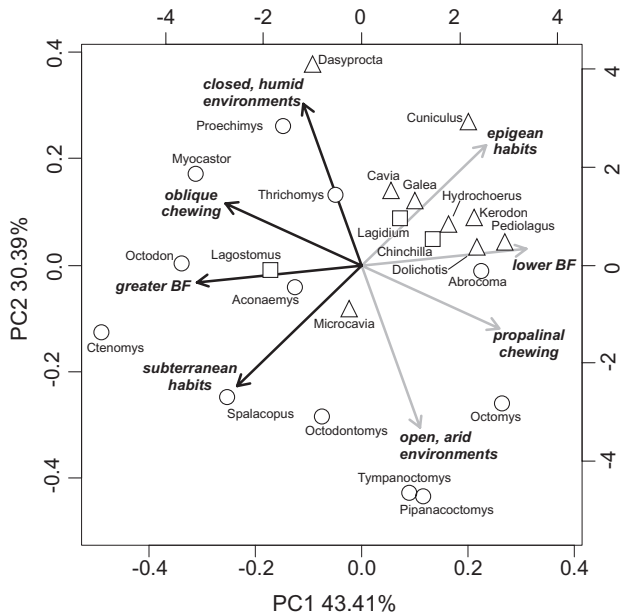
Figure 3. Ordination of the 24 caviomorph genera in the space defined by the ecological and functional variables (see Material and methods for explanation). Arrows indicate the direction of variation in the variables. Opposite tendencies are indicated. Symbols represent caviomorph superfamilies: ○, Octodontoidea; △, Cavioidea; and □, Chinchilloidea.

remaining clades on RW2. Significant phylogenetic signal was found for all RWs (tree length = 0.153, $P \leq 0.0001$) and for the first two RWs (RW1, $K = 0.979$, $P = 0.0001$; RW2, $K = 0.930$, $P = 0.0002$).

Regarding morphological variation, towards negative values of RW1 the rostrum and diastema are relatively shorter, the auditory bulla is larger, and the orbit is smaller and more dorsally placed (Fig. 4A). All changes described from here on are relative, as the descriptions correspond to shape changes that do not include size. In addition, the zygomatic arch is located dorsally with respect to the upper cheek teeth, the cranial vault is anteroposteriorly longer, and the occipital region tends to be vertically oriented. These features are shared by octodontoid genera, especially *Pipanacoctomys* and *Tympanoctomys*. Towards positive values of RW1, the opposite morphological traits are observed in cavioids and *Lagostomus*. Towards positive values of RW2, both rostrum and rostral masseteric fossa are lower and longer, the posterior margin of the orbit is wider, and the cranial vault is shorter and associated with a more ventrally facing occipital region. These traits are present in the chinchillids and *Abrocoma*. Towards negative values of RW2, the cranium is lower, the maxillary and jugal areas of the zygomatic arch are wider, generating a larger anteroventral surface area, and the auditory

bulla is smaller (Fig. 4A). Such morphology is evident in *Cuniculus*. Several interesting issues are worth noting. The chinchillids were clearly split into two locations: *Chinchilla*, situated on negative values of RW1 close to *Abrocoma*, and *Lagidium* and *Lagostomus*, grouped on positive values of RW1. On the other hand, the separation of cavioids into two groups along the RW2 is obvious. Also noteworthy is the departure of *Cuniculus* from the remaining cavioids.

A strong allometric pattern in shape variation was observed in the morphospace of the RWs (Fig. 4A), with the larger cavioids and *Lagostomus* located on one extreme and most of the small octodontoids occupying the opposite extreme. Size explained 38% ($P < 0.0001$) of cranial shape variation. The same distribution of genera was observed within AC/lnCS morphospace (Fig. 4B). This phylogenetic ordination was reflected in the phylogenetic signal value obtained for the AC component ($K = 0.988$, $P < 0.001$). Species with larger crania presented a more elongated rostrum and rostral masseteric fossa, reduced auditory bulla, deeper zygomatic arch, and a relatively shorter vault. Given the strong influence of size on cranial shape variation, we subsequently visualized the variation of the non-allometric component of shape.

The ordination of caviomorph genera along the first two components of the morphospace built from the principal component analysis on the RSCs was quite different from that observed for the Procrustes shape data (Fig. 5). The variation explained by these components was only 40%, with the first axis explaining 22% of the total variation. There was no clear segregation of major clades as observed in the Procrustes shape (RWs) morphospace; however, the phylogenetic signal remained significant for all RSCs (tree length = 0.118, $P < 0.0001$), and for the first two residual components (RSC1, $K = 0.642$, $P = 0.007$; RSC2, $K = 0.824$, $P = 0.001$). On the other hand, the ordination obtained for the residual component reflects, at least partially, segregation according to habitat. According to the regression analyses, the latter variable was significant to explain cranial shape variation (see below). Taxa inhabiting open and arid environments were located on positive values of RSC1 and near central values of RSC2, whereas taxa that occupy closer and wetter environments were situated on negative values of both axes. Positive values of RSC1 were associated with a relatively larger auditory bulla (and narrower basicranium), smaller bizygomatic width, and reduced and slightly anteriorly positioned orbits (Fig. 5). The caviomorph genera with such features were the octodontids *Tympanoctomys* and *Pipanacoctomys* and the chinchillid *Chinchilla*. The
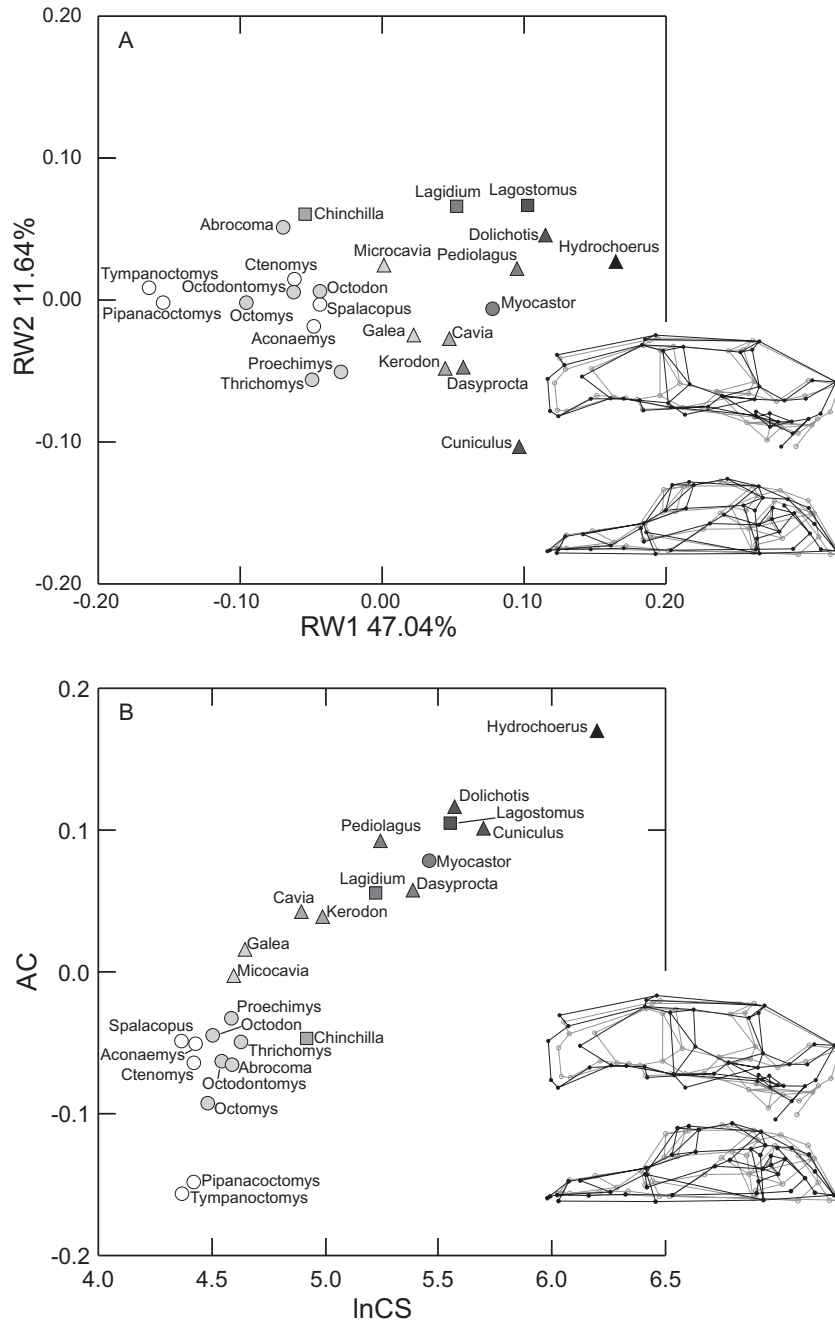
Figure 4. A, ordination of the 24 caviomorph genera in the morphospace defined by the first two relative warps (RWs) of the analysis of cranial shape variation. Cranial shape changes associated with positive values of the first relative warp (RW1) are shown as outline diagrams: black dots and lines indicate shape changes with respect to the mean configuration (indicated with grey dots and lines). B, allometric changes in cranial shape of caviomorphs; the allometric component of cranial shape is plotted against size (ln-transformed centroid size of mean configurations for each genus, lnCS). Shape changes associated with increasing size (per unit) are represented by black dots and lines; grey dots and lines represent the consensus shape. Symbols indicate caviomorph superfamilies: ○, Octodontoidea; △, Cavioidea; and □, Chinchilloidea. The shading gradient indicates size variation, from lower (white) to higher (black) values.
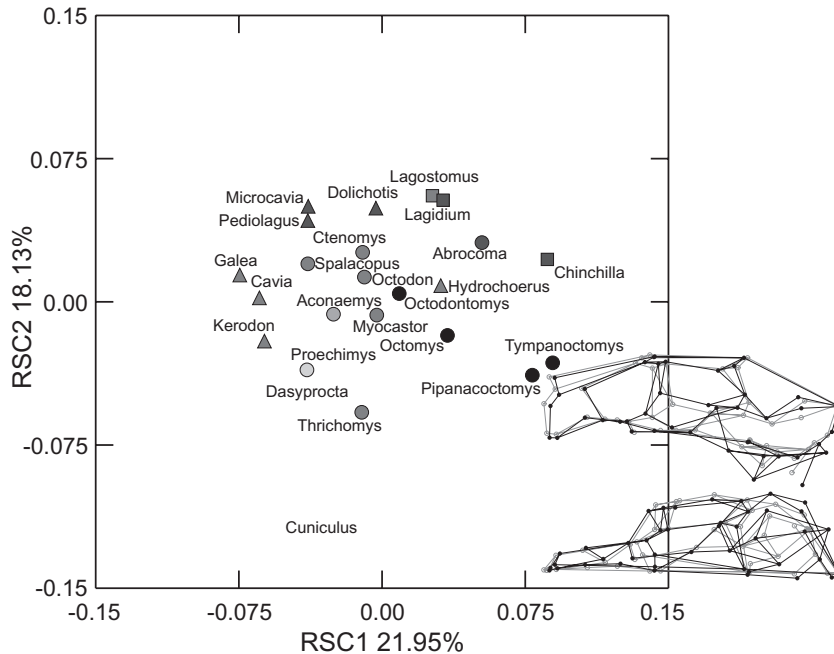
Figure 5. Ordination of the 24 caviomorph genera in the morphospace defined by the first two residual shape components (RSCs) of the analysis of cranial residual shape variation, after taking into account the effect of size. Cranial shape changes associated with positive values of the first residual shape component (RSC1) are shown as outline diagrams. Black dots and lines indicate shape changes with respect to the mean configuration (indicated with grey dots and lines). Symbols indicate caviomorph superfamilies: ○, Octodontoidea; △, Cavioidea; and □, Chinchilloidea. The shading gradient indicates habitat variation, from close and humid environments (white) to open and arid environments (black).

opposite extreme of the first axis was occupied by several caviids with contrasting traits. Increased values of RSC2 implied a relatively elongated and slender rostrum, a shallow zygomatic arch, and longer and convergent tooth rows. These features were present in the chinchillids *Lagostomus* and *Lagidium*, and in the caviids *Microcavia* and *Dolichotis*.

REGRESSION RESULTS

Phylogenetic regressions between cranial shape and the ecological and functional variables were significant only for the first three RWs (Table 3). In this case, shape was significantly related with the habitat variable. On the other hand, when size was included as a covariate, regressions were significant for both three and ten RW data sets (Table 4). Regression models that included size as a covariate explained more of the variance and had a better significance (lower *P* values). In these regressions, shape was significantly related to size and to habitat in the case of three-RW regression. Results for regression models where λ was set to 1 (meeting the assumption of a Brownian model of evolution) were similar to those just described (Tables S2, S3).

DISCUSSION

In accordance with their large ecological diversity, caviomorphs exhibit wide cranial shape variation. This involves marked diversity in the shape of the rostrum, basicranium, and cranial vault. The ordination of taxa in the shape (Procrustes and residual) morphospaces corresponded, to greater or lesser extent, with the major clades recovered in the phylogeny. A strong association between shape and phylogeny has also been observed both in previous studies of masticatory morphology of caviomorphs (Álvarez *et al.*, 2011a, b; Hautier *et al.*, 2012) and in analyses of cranial diversity of other mammals, such as non-caviomorph rodents, carnivores, and monkeys (Caumul & Polly, 2005; Figueirido *et al.*, 2010; Perez *et al.*, 2011).

According to our results, part of the shape divergence in caviomorphs seems to have progressed at the same time as the phylogenetic divergence of size. The correspondence between size and phylogeny is evidenced by the distribution of size among clades: the largest extant rodents, the capybara *Hydrochoerus* and the paca *Cuniculus*, belong to Cavioidea, whereas all South American Octodontoidea are medium- to small-sized caviomorphs, excepting *Myocastor*. The

Table 3. Phylogenetic regression analyses (PGLS) among the first three and ten relative warps (RWs; 70 and 90% of variation, respectively) and four ecological and functional variables (habit, chewing mode, bite force, habitat; see the Material and methods section for explanation)

Shape data	λ	R^2	$F_{5,19}$	P				
Three RWs	**0.000***	**0.410**	**4.988**	**0.004**				
					Variables	Partial coefficients	t	P
					Habit	0.011	0.549	0.589
					Chewing mode	−0.011	−0.208	0.837
					Bite force	0.082	0.171	0.866
					Habitat	**−0.125**	**−3.891**	**0.001**
Ten RWs	0.781†	0.153	2.040	0.119				
					Habit	0.019	0.816	0.424
					Chewing mode	−0.020	−0.324	0.749
					Bite force	−1.174	−1.444	0.164
					Habitat	−0.049	−1.054	0.305

Parameters for the regression models are given in the first line of each block. Partial regression coefficients for explanatory variables are shown. Subscripts indicate freedom degrees in parameter estimation. The value of λ was set at its maximum likelihood value. Bold letters denote that the parameter/model is significant at the 0.05 probability threshold.
*The maximum likelihood estimate of λ is not significantly different from zero.
†The maximum likelihood estimate of λ is not significantly different from 1.

Table 4. Phylogenetic regression analyses (PGLS) among the first three and ten relative warps (RWs; 70 and 90% of variation, respectively) and four ecological and functional variables (habit, chewing mode, bite force, habitat; see the Material and methods section for explanation)

Shape data	λ	R^2	$F_{6,18}$	P				
Three RWs	**0.495***	**0.679**	**10.72**	**< 0.0001**				
					Variables	Partial coefficients	t	P
					Habit	−0.009	−0.649	0.524
					Chewing mode	−0.006	−0.174	0.964
					BF	−0.379	−0.904	0.378
					Habitat	**−0.077**	**−3.121**	**0.006**
					lnCS	**−0.137**	**−4.842**	**0.000**
Ten RWs	**0.837†**	**0.458**	**4.88**	**0.004**				
					Habit	−0.001	−0.046	0.964
					Chewing mode	−0.007	−0.147	0.885
					Bite force	−0.886	−1.341	0.197
					Habitat	−0.041	−1.085	0.292
					lnCS	**−0.145**	**−3.487**	**0.003**

Size is included as a covariate. Parameters for the regression models are given in the first line of each block. Partial regression coefficients for explanatory variables are shown. Subscripts indicate number of degrees of freedom in parameter estimation. The value of λ was set at its maximum-likelihood value. Bold letters denote that the parameter/model is significant at the 0.05 probability threshold.
*The maximum likelihood estimate of λ is not significantly different from zero.
†The maximum likelihood estimate of λ is not significantly different from 1.

Chinchilloidea include medium- to large-sized representatives. At least part of the variation found in the rostrum, cranial vault, and basicranium could have evolved accompanying changes in size (see Radinsky, 1985; Emerson & Bramble, 1993). Accordingly, in our analysis, the larger caviomorphs show more elongated faces, whereas some of the smaller ones have shorter rostra. Additionally, larger caviomorphs are

also characterized by the reduction of the auditory bullae and the shortening of the cranial vault. Hautier *et al*. (2012) tentatively associated variation in the auditory system with differential predation pressure, which in turn is associated with habitat variation (see below). The implications of cranial vault shortening and the concurrent modifications of brain structure are at present difficult to interpret.

Similarly to previous analyses made for a more restricted clade of caviomorphs (octodontids; Olivares *et al*., 2004), castorimorphs (geomyids; Wilkins & Woods, 1983), and sciurids (Michaux *et al*., 2008), our results failed to associate gross cranial morphology with chewing modes; thus, taxa with very divergent morphologies show similar masticatory directions. Phylogenetic regressions also showed that the habit variable used here (i.e. ranging from epigean to subterranean modes of life) is not relevant to explain cranial shape variation in the context of this analysis.

On the other hand, we detected significant association between shape variation and habitat characteristics, an association that is independent of size variation. Major shape changes involving the size of the auditory bullae (and associated development of basicranium) and position of the orbits were found between species inhabiting open environments and those from forested habitats. Similar features were described by Hautier *et al*. (2012), who highlighted the position of the eyes and the position and convergence of the orbits as key features to understand the morphological evolution of rodents. Changes in these traits are thought to promote changes in the arrangement of masticatory muscles and associated cranial and mandibular morphology (Hautier *et al*., 2012). The relative size of the auditory bullae showed a clear distribution along the first axis of the residuals representing non-allometric shape. Caviomorphs with enlarged auditory bullae are adapted to semi-arid/arid environments (Braun & Mares, 1996; Cortés, Tirado & Rosenmann, 2003; Ebensperger *et al*., 2006, 2008; Gallardo *et al*., 2009; Traba *et al*., 2010). Bullar hypertrophy is especially marked in the desert-adapted octodontids *Tympanoctomys* and *Pipanacoctomys* (Ojeda *et al*., 1999; Mares *et al*., 2000; Verzi, 2001). Such an increase of bullar size occurs in rodents inhabiting arid biomes worldwide (Mares, 1980; Randall, 1994). The adaptive meaning of this pattern is not clear, and the hypothesis of increasing sensitivity to low-frequency sounds as a strategy to detect predators in open environments is controversial (Lay, 1993). From an ontogenetic perspective, large bullae in rodents have been interpreted as a result of heterochronic evolution (Hafner & Hafner, 1988). The relevance of environment and ecological traits as sources of the variation found in this study add to previous works that have already supported similar ideas regarding rodent evolution (Samuels, 2009; Hautier *et al*., 2012).

The evolution of morphological variation of the mammalian cranium is influenced by functional, structural, and developmental demands (Emerson & Bramble, 1993). Our results contribute to the understanding of the complex relationships among the morphological, phylogenetic, and ecological dimensions in the diversification of the caviomorph cranium. Caviomorphs have a long-standing evolutionary history in South America, which began as early as the middle Eocene (Antoine *et al*., 2012). Before the end of the Oligocene, they experienced a wide radiation (Vucetich, Verzi & Hartenberger, 1999; Verzi, Olivares & Morgan, 2013), probably accompanied by early morphological divergence, which would explain the strong phylogenetic signal detected in shape variation. Additionally, this study detected a marked influence of size over cranial shape variation, as could be expected given the existence of such a wide size range in these mammals. This result was quite different from previous works in which geometric morphometric shape data showed little or no dependence on size (Swiderski, 2003; Perez *et al*., 2011), although it should be remembered that caviomorphs have greater size variation among themselves than occurs among several other groups of mammals. Nevertheless, even though caviomorphs display an allometric trajectory for large-scale variation, it does not follow from this result that the same pattern holds for lower clades: indeed, Wilson & Sánchez-Villagra (2010) found that many rodents, including hystricognaths, display high allometric disparity, that is to say varied allometric patterns. On the other hand, a persistent relationship between shape changes and occupied environments, even after taking into account the phylogenetic structure and the effect of size, could be indicating that size would not have been the only factor affecting the pathways of cranial diversification.

Further studies, covering a comprehensive range of variation within each major caviomorph lineage, are required to improve the knowledge of the evolutionary patterns of cranial morphology in these rodents.

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REFERENCES

Álvarez A. 2012. Diversidad morfológica cráneo-mandibular de roedores caviomorfos en un contexto filogenético comparativo. Unpublished D. Phil. Thesis, Universidad Nacional de La Plata, Argentina.

Álvarez A, Perez SI, Verzi DH. 2011a. Ecological and phylogenetic influences on mandible shape variation of South American caviomorph rodents (Rodentia: Hystricomorpha). *Biological Journal of the Linnean Society* **102:** 828–837.

Álvarez A, Perez SI, Verzi DH. 2011b. Early differentiation of morphological variation in the mandible of South American caviomorph rodents (Rodentia, Caviomorpha). *Journal of Evolutionary Biology* **24:** 2687–2695.

Álvarez A, Perez SI, Verzi DH. 2013. Data from: Ecological and phylogenetic dimensions of cranial shape diversification in South American caviomorph rodents (Rodentia: Hystricomorpha). *Dryad Digital Repository*. doi:10.5061/dryad.qg67c

Antoine P-O, Marivaux L, Croft DA, Billet G, Ganerød M, Jaramillo C, Martin T, Orliac MJ, Tejada J, Altamirano AJ, Duranthon F, Fanjat G, Rousse S, Gismondi RS. 2012. Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. *Proceedings of the Royal Society B* **279:** 1319–1326.

Becerra F, Casinos A, Vassallo AI. 2013. Biting performance and skull biomechanics of a chisel tooth digging rodent (Ctenomys tuconax; Caviomorpha; Octodontoidea). *Journal of Experimental Zoology* **319:** 74–85.

Becerra F, Echeverría A, Vassallo AI, Casinos A. 2011. Bite force and jaw biomechanics in the subterranean rodent Talas tuco-tuco (Ctenomys talarum) (Caviomorpha: Octodontoidea). *Canadian Journal of Zoology* **89:** 334–342.

Blanga-Kanfi S, Miranda H, Penn O, Pupko T, DeBry RW, Huchon D. 2009. Rodent phylogeny revised: analysis of six nuclear genes from all major rodent clades. *BMC Evolutionary Biology* **9:** 71.

Blomberg SP, Garland JT, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57:** 171–745.

Braun JK, Mares MA. 1996. Unusual morphological and behavioral traits in Abrocoma (Rodentia: Abrocomidae) from Argentina. *Journal of Mammalogy* **77:** 891–897.

Cardini A, Hoffmann RS, Thorington Jr RW. 2005. Morphological evolution in marmots (Rodentia, Sciuridae): size and shape of the dorsal and lateral surfaces of the cranium. *Journal of Zoological Systematics and Evolutionary Research* **43:** 258–268.

Caumul R, Polly PD. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). *Evolution* **59:** 2460–2472.

Cortés A, Rau J, Miranda E, Jiménez JE. 2002. Hábitos alimenticios de *Lagidium viscacia* y *Abrocoma cinerea*: roedores sintópicos en ambientes altoandinos del norte de Chile. *Revista Chilena de Historia Natural* **75:** 583–593.

Cortés A, Tirado C, Rosenmann M. 2003. Energy metabolism and thermoregulation in Chinchilla brevicaudata. *Journal of Thermal Biology* **28:** 489–495.

Drake AG, Klingenberg CP. 2008. The pace of morphological change: historical transformation of skull shape in St Bernard dogs. *Proceedings of the Royal Society B* **275:** 71–76.

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4:** e88.

Drummond AJ, Rambaut A. 2007. BEAST: bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7:** 214.

Ebensperger LA, Blumstein DT. 2006. Sociality in New World hystricognath rodents is linked to predators and burrow digging. *Behavioral Ecology* **17:** 410–418.

Ebensperger LA, Sobrero R, Campos V, Giannoni SM. 2008. Activity, range areas, and nesting patterns in the viscacha rat, Octomys mimax. *Journal of Arid Environments* **72:** 1174–1183.

Ebensperger LA, Taraborelli P, Giannoni SM, Hurtado MJ, León C, Bozinovic F. 2006. Nest and space use in a highland population of the southern mountain cavy (Microcavia australis). *Journal of Mammalogy* **87:** 834–840.

Eisenberg JF, Redford KH. 1999. *Mammals of the neotropics. Vol. 3: the central neotropics – Ecuador, Peru, Bolivia, Brazil*. Chicago: University of Chicago Press.

Elissamburu A, Vizcaíno SF. 2004. Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). *Journal of Zoology, London* **262:** 145–159.

Emerson SB, Bramble DM. 1993. Scaling, allometry, and skull design. In: Hanken J, Hall BK, eds. *The skull: functional and evolutionary mechanisms*. Chicago: University of Chicago Press, 384–421.

Emmons L, Feer F. 1997. *Neotropical rainforest mammals: a field guide, 2nd edn*. Chicago: University of Chicago Press.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125:** 1–15.

Figueirido B, Serrano-Alarcón FJ, Slater GJ, Palmqvist P. 2010. Shape at the cross-roads: homoplasy and history in the evolution of the carnivoran skull towards herbivory. *Journal of Evolutionary Biology* **23:** 2579–2594.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* **160:** 712–726.

Freeman PW. 2000. Macroevolution in Microchiroptera: recoupling morphology and ecology with phylogeny. University of Nebraska State Museum, Mammalogy Papers 8.

Gallardo MH, Udrizar-Sauthier DE, Ojeda AA, Pardiñas UFJ. 2009. Discovery of desert-adapted Tympanoctomys barrerae in Central Patagonia, Argentina. *Mammalia* **73:** 158–161.

Gavrilets S, Losos JB. 2009. Adaptive radiation: contrasting theory with data. *Science* **323:** 732–737.

Glanz WE, Anderson S. 1990. Notes on Bolivian Mammals. 7. A new species of *Abrocoma* (Rodentia) and relationships of the Abrocomidae. *American Museum Novitates* **2991:** 1–32.

Hafner JC, Hafner MS. 1988. Heterochrony in rodents. In: McKinney ML, ed. *Heterochrony in evolution: a multidisciplinary approach*. New York, NY: Plenum, 217–235.

Hautier L, Lebrun R, Cox PG. 2012. Patterns of covariation in the masticatory apparatus of hystricognathous rodents: implications for evolution and diversification. *Journal of Morphology* **273:** 1319–1337.

Hautier L, Lebrun R, Saksiri S, Michaux J, Vianey-Liaud M, Marivaux L. 2011. Hystricognathy vs sciurognathy in the rodent jaw: a new morphometric assessment of hystricognathy applied to the living fossil Laonastes (Diatomyidae). *PLoS ONE* **6:** e18698.

Hildebrand M. 1985. Digging in quadrupeds. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, eds. *Functional Vertebrate Morphology*. Cambridge: Harvard University Press, 89–109.

Justo ER, De Santis LJM, Kin MS. 2003. *Ctenomys talarum. Mammalian Species* **730:** 1–5.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **6:** 1463–1464.

Kiltie RA. 1984. Size ratios among sympatric neotropical cats. *Oecologia* **61:** 411–416.

Klingenberg CP. 2011. MorphoJ. Faculty of Life Sciences, University of Manchester, Manchester. Available at: http://www.flywings.org.uk/MorphoJ_page.htm

Klingenberg CP, Gidaszewski NA. 2010. Testing and quantifying phylogenetic signals and homoplasy in morphometric data. *Systematic Biology* **59:** 245–261.

Laurin M. 2004. The evolution of body size, Cope's rule and the origin of Amniotes. *Systematic Biology* **53:** 594–622.

Lay DM. 1993. Anatomy of the heteromyid ear. In: Genoways HH, Brown JH, eds. *Biology of the Heteromyidae*. Provo: American Society of Mammalogists, Special Publication No. 10, 270–290.

Lessa EP, Vassallo AI, Verzi DH, Mora MS. 2008. Evolution of morphological adaptations for digging in living and extinct ctenomyid and octodontid rodents. *Biological Journal of the Linnean Society* **95:** 267–283.

Losos JB, Mahler DL. 2010. Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In: Bell MA, Futuyma DJ, Eanes WF, Levinton JS, eds. *Evolution since Darwin: the first 150 years*. Sunderland: Sinauer Associates, 381–420.

Mares MA. 1980. Convergent evolution among desert rodents: a global perspective. *Bulletin of Carnegie Museum of Natural History* **16:** 1–51.

Mares MA, Braun JK, Bárquez RM, Díaz MM. 2000. Two new genera and species of halophytic desert mammals from isolated salt flats in Argentina. *Occasional Papers of the Museum, Texas Tech University* **203:** 1–27.

Mares MA, Ojeda RA. 1982. Patterns of diversity and adaptation in South American hystricognath rodents. In: Mares MA, Genoways HH, eds. *Mammalian biology in South America*. Linesville: Special Publication Pymatuning Laboratory of Ecology, 393–432.

Martin RE. 1970. Cranial and bacular variation in population of spiny rats of the genus *Proechimys* (Rodentia: Echimyidae) from South America. *Smithsonian Contributions to Zoology* **35:** 1–19.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* **149:** 646–667.

Meloro C, Raia P, Carotenuto F, Cobb SN. 2011. Phylogenetic signal, function and integration in the subunits of the carnivoran mandible. *Evolutionary Biology* **38:** 465–475.

Michaux J, Hautier L, Simonin T, Vianey-Liaud M. 2008. Phylogeny, adaptation and mandible shape in Sciuridae (Rodentia, Mammalia). *Mammalia* **72:** 286–296.

Mitteroecker P, Gunz P, Bernhard M, Schaefer K, Bookstein FL. 2004. Comparison of cranial ontogenetic trajectories among great apes and humans. *Journal of Human Evolution* **46:** 679–698.

Monteiro LR, Nogueira MR. 2011. Evolutionary patterns and processes in the radiation of phyllostomid bats. *BMC Evolutionary Biology* **11:** 137.

Morgan CC. 2009. Geometric morphometrics of the scapula of South American caviomorph rodents (Rodentia: Hystricognathi): form, function and phylogeny. *Mammalian Biology* **74:** 497–506.

Nevo E. 1979. Adaptive convergence and divergence of subterranean mammals. *Annual Review of Ecology and Systematics* **10:** 269–308.

Nowak RM. 1991. *Walker's mammals of the world, 5th edn*. Baltimore: Johns Hopkins University Press.

O'Higgins P, Jones N. 2006. Morphologika 2.5, tools for shape analysis. Hull York Medical School, University of York, York. Avalaible at: http://www.york.ac.uk/res/fme/

Ojeda RA, Borghi CE, Diaz GB, Giannonni SM, Mares MA, Braun JK. 1999. Evolutionary convergence of the highly adapted desert rodent Tympanoctomys barrerae (Octodontidae). *Journal of Arid Environments* **41:** 443–452.

Olivares AI, Verzi DH, Vassallo AI. 2004. Masticatory morphological diversity and chewing modes in octodontid rodents (Rodentia, Octodontidae). *Journal of Zoology, London* **263:** 167–177.

Orme CDL, Freckleton RP, Thomas G, Petzoldt T, Fritz SA. 2011. Caper: Comparative Analysis of Phylogenetics and Evolution in R. Available at: http://CRAN.R-project.org/package=caper

Perez SI, Diniz-Filho JAF, Rohlf FJ, dos Reis SF. 2009. Ecological and evolutionary factors in the morphological diversification of South American spiny rats. *Biological Journal of the Linnean Society* **98:** 646–660.

Perez SI, Klaczko J, Rocatti G, dos Reis SF. 2011. Patterns of cranial shape diversification during the phylogenetic branching process of New World monkeys (Primates: Platyrrhini). *Journal of Evolutionary Biology* **24:** 1826–1835.

Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* **25:** 1253–1256.

R Development Core Team. 2009. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, Available at: http://www.r-project.org

Radinsky LB. 1985. Approaches in evolutionary morphology: a search for patterns. *Annual Review in Ecology and Systematics* **16:** 1–14.

Rambaut A, Drummond AJ. 2007. Tracer v1.4: MCMC trace analyses tool. Available at: http://beast.bio.ed.ac.uk/Tracer

Randall JA. 1994. Convergences and divergences in communication and social organization of desert rodents. *Australian Journal of Zoology* **42:** 405–433.

Rinderknecht A, Blanco RE. 2008. The largest fossil rodent. *Proceedings of the Royal Society B* **275:** 923–928.

Roberts DW. 2012. Labdsv: ordination and multivariate analysis for ecology. R package version 1.5-2. http://ecology.msu.montana.edu/labdsv/R

Rohlf FJ. 1993. Relative warps analysis and an example of its application to Mosquito wings. In: Marcus LF, Bello E, García-Valdecasas A, eds. *Contributions to morphometrics*. Madrid: Monografías del Museo Nacional de Ciencias Naturales, 132–159.

Rohlf FJ. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* **55:** 2143–2160.

Rohlf FJ. 2008. *Tpsdig*, version 2.12; *tpsrelw*, version 1.46. Stony Brook, NY: State University of New York at Stony Brook, Available at: http://life.bio.sunysb.edu/morph/

Rohlf FJ, Slice DE. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39:** 40–59.

Rowe DL, Honeycutt RL. 2002. Phylogenetic relationships, ecological correlates, and molecular evolution within the Cavioidea (Mammalia:Rodentia). *Molecular Biology and Evolution* **19:** 263–277.

Samuels JX. 2009. Cranial morphology and dietary habits of rodents. *Zoological Journal of the Linnean Society* **502:** 864–888.

Sánchez-Villagra MR, Aguilera O, Horovitz I. 2003. The anatomy of the world's largest extinct rodent. *Science* **301:** 1708–1710.

Schluter D. 2000. *The ecology of adaptive radiation*. Oxford: Oxford University Press.

Sobrero R, Campos VE, Giannoni SM, Ebensperger LA. 2010. *Octomys mimax* (Rodentia: Octodontidae). *Mammalian Species* **42:** 49–57.

Spotorno AE, Valladares JP, Marin JC, Palma E, Zuleta CR. 2004. Molecular divergence and phylogenetic relationships of chinchillids (Rodentia: Chinchillidae). *Journal of Mammalogy* **85:** 384–388.

Stein BR. 2000. Morphology of subterranean rodents. In: Lacey AE, Patton JL, Cameron GN, eds. *Life underground, the biology of subterranean rodents*. Chicago: The University of Chicago Press, 19–61.

Swiderski DL. 2003. Separating size from allometry: analysis of lower jaw morphology in the Fox Squirrel, Sciurus niger. *Journal of Mammalogy* **84:** 861–876.

Torres-Mura JC, Contreras LC. 1998. *Spalacopus cyanus*. *Mammalian Species* **594:** 1–5.

Traba J, Acebes P, Campos VE, Giannoni SM. 2010. Habitat selection by two sympatric rodent species in the Monte desert, Argentina. First data for Eligmodontia moreni and Octomys mimax. *Journal of Arid Environments* **74:** 179–185.

Turnbull WD. 1970. Mammalian masticatory apparatus. *Fieldiana: Geology* **18:** 149–356.

Upham NS, Patterson BD. 2012. Diversification and biogeography of the Neotropical caviomorph lineage Octodontoidea (Rodentia: Hystricognathi). *Molecular Phylogenetic Evolution* **63:** 417–429.

Vassallo AI, Verzi DH. 2001. Patrones craneanos y modalidades de masticación en roedores caviomorfos (Rodentia, Caviomorpha). *Boletín de la Sociedad de Biología de Concepción, Chile* **72:** 145–151.

Verzi DH. 2001. Phylogenetic position of Abalosia and the evolution of the extant Octodontinae (Rodentia, Caviomorpha, Octodontidae). *Acta Theriologica* **46:** 243–268.

Verzi DH, Olivares AI. 2006. Craniomandibular joint in South American burrowing rodents (Ctenomyidae): adaptations and constraints related to a specialised mandibular position in digging. *Journal of Zoology, London* **270:** 488–501.

Verzi DH, Olivares AI, Morgan CC. 2013. Phylogeny, evolutionary patterns and timescale of South American octodontoid rodents: the importance of recognising morphological differentiation in the fossil record. *Acta Palaeontologica Polonica* doi:10.4202/app.2012.0135

Vucetich MG, Verzi DH, Hartenberger J-L. 1999. Review and analysis of the radiation of South American Hystricognathi (Mammalia, Rodentia). *Comptes Rendus de l'Académie des Sciences, Paris* **329:** 763–769.

Wainwright PC. 2007. Functional versus morphological diversity in macroevolution. *Annual Review of Ecology, Evolution and Systematics* **38:** 381–401.

Wilkins KT, Woods CA. 1983. Modes of mastication in pocket gophers. *Journal of Mammalogy* **64:** 636–641.

Wilson LAB, Sánchez-Villagra MR. 2010. Diversity trends and their ontogenetic basis: an exploration of allometric disparity in rodents. *Proceedings of the Royal Society of London B* **277:** 1227–1234.

Woods CA. 1972. Comparative myology of jaw, hyoid and pectoral appendicular regions of New and Old World hystricomorph rodents. *Bulletin of the American Museum of Natural History* **147:** 115–198.

Woods CA, Contreras L, Willner-Chapman G, Whidden HP. 1992. *Myocastor coypus*. *Mammalian Species* **398:** 1–8.

ARCHIVED DATA

Data deposited at Dryad (Álvarez, Perez & Verzi, 2013).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Measurements used to estimate the bite force and chew variables.
Figure S2. Surface area of origin estimated for the main part of the temporalis muscle. From top to bottom and left to right for each row: *Cuniculus*, *Dasyprocta*, *Dolichotis*, *Pediolagus*, *Kerodon*, *Hydrochoerus*, *Galea*, *Microcavia*, *Cavia*, *Lagostomus*, *Lagidium*, *Chinchilla*, *Thrichomys*, *Proechimys*, *Myocastor*, *Ctenomys*, *Tympanoctomys*, *Pipanacoctomys*, *Octomys*, *Octodontomys*, *Octodon*, *Spalacopus*, *Aconaemys*, and *Abrocoma*.
Table S1. Definition of landmarks used to represent cranial shape. Numbers correspond to those depicted in Figure 1 of the main text.
Table S2. Phylogenetic regression analyses (PGLS) among the first three and ten relative warps (RWs; 70 and 90% of variation, respectively) and four ecological and functional variables (habit, chewing mode, bite force, and habitat; see Material and methods section for explanation).
Table S3. Phylogenetic regression analyses (PGLS) among the first three and ten relative warps (RWs; 70% and 90% of variation, respectively) and four ecological and functional variables (habits, chewing mode, bite force, and habitat; see Material and methods section for explanation). Size is included as a covariate.
Appendix S1. Detailed list of specimens included in the present study.
Appendix S2. GenBank accession numbers for the sequences of *12S*, *GHR* and *TTH* genes of the caviomorph rodents included in this study.