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Geometric morphometrics of the scapula of South American caviomorph rodents (Rodentia: Hystricognathi): Form, function and phylogeny

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Abstract

The scapula of the ecomorphologically diverse South American caviomorph rodents was studied through geometric morphometric techniques, using landmarks and semilandmarks to capture the shape of this complex morphological structure. Representatives of 33 species from all caviomorph superfamilies, as well as *Hystrix cristata* for comparisons, were analyzed. Marked differences in scapular shape were found among the major caviomorph lineages analyzed, particularly in the shape and length of the scapular spine and development of the great scapular notch. Shape differences were not influenced by body size, and only partially influenced by locomotor mode. Thus, at this scale of analysis, phylogenetic history seems to be the strongest factor influencing scapular shape. The scapular shape of erethizontids, chinchillids and *Cuniculus paca* could represent the less specialized state with respect to the highly differentiated scapula of octodontoids and most cavioids. In this sense, the characteristic scapular morphologies of octodontoids and cavioids could reflect particular functional capabilities and constraints associated with the evolution of prevalent locomotor modes within each lineage.

Keywords: Caviomorpha; Functional morphology; Geometric morphometrics; Rodent; Scapula

Introduction

The therian scapula is a morphologically complex structure (Monteiro and Abe 1999) that plays a major role in mammalian locomotion (Fischer et al. 2002). Scapular morphology responds to the combined influence of historical (phylogenetic) and functional factors. The functional requirements include shoulder stabilization and scapular mobility, an essential component of therian mammal locomotion (Fischer et al. 2002), as well as particular requirements linked to specialized locomotor modes; furthermore, body size is expected to entail special biomechanical requirements that could also influence scapular morphology (scaling and allometry, Biewener 2000). At the same time, the evolutionary history of a clade may constrain or channel the morphological changes in the scapula (an influence summarized by the term "phylogenetic constraint", Losos and Miles 1994). Thus, the analysis of scapular shape in an ecomorphologically diverse clade may provide insight about the contribution of these factors to the evolution of scapular features.

The primarily South American hystricognathous "caviomorph" rodents comprise 14 living families and about 250 living species (Woods and Kilpatrick 2005). This diversity encompasses four major lineages with diverse adaptive types in terms of body size, habit and locomotor mode. The Erethizontoidea (porcupines) are semi-terrestrial and scansorial arboreal climbers; the

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Chinchilloidea (viscachas, mountain viscachas, chinchillas and pacaranas) include both primarily epigean ricochetal and fossorial forms; the Cavioidea are mainly epigean generalized and cursorial taxa and the Octodontoidea include arboreal, terrestrial, aquatic, fossorial and completely subterranean species with wide-ranging climbing and digging specializations (Nowak 1991; Kleiman et al. 2003).

The postcranial skeletal anatomy of these rodents is expected to reflect both their adaptive diversity and their shared evolutionary history. Previous works have analyzed characteristics of the long bones and autopodial skeleton of diverse caviomorphs and studied adaptive traits of these postcranial elements (Biknevicius 1993; Casinos et al. 1993; Vassallo 1998; Stein 2000; Elissamburu and Vizcaíno 2004; Weisbecker and Schmid 2007; Candela and Picasso 2008). Although several workers have analyzed the mammalian scapula using morphological and morphofunctional approaches (Lessertiseur and Saban 1967; Oxnard 1968; Hildebrand 1985; Price 1993; Swiderski 1993; Taylor 1997; Sargis 2002; Young 2004 2006), including caviomorph rodents (Lehmann 1963; Fernández et al. 2000; Seckel and Janis 2008), no comprehensive analyses have been made of the shoulder girdle of caviomorphs as a group.

The goal of this work is to apply geometric morphometrics to the analysis of scapular shape, and to assess the effects of body size, functional and historical factors on the scapular morphology of the ecomorphologically diverse South American hystricognath rodents.

Material and methods

Materials

The materials examined include representatives of the major Caviomorpha taxa, as well as the African species *Hystrix cristata* (Old World porcupine; Hystricidae, Hystricognathi), representing the sister group of Thryonomidae + Caviomorpha (Honeycutt et al. 2007; Veniaminova et al. 2007), as outgroup for comparative purposes. Table 1 shows the species and number of specimens examined.

Table 1. Taxa studied, number of specimens examined (*n*) and locomotor mode (references in the text)

Taxon	*n*	Locomotor mode
Aconaemys sp.	5	Fossorial[1]
Cavia aperea	10	Ambulatory[1]
Chinchilla sp.	1	Ricochetal[6]
Coendou sp.	3	Scansorial[1]
Ctenomys australis	8	Fossorial[1]
Ctenomys rionegrensis	3	Fossorial[1]
Ctenomys talarum	8	Fossorial[1,2]
Cuniculus paca	1	Occasional digger[1,5]
Dasyprocta sp.	2	Cursorial[1]
Dolichotis patagonum	4	Cursorial[1,7]
Erethizon dorsatum	1	Scansorial[4]
Galea musteloides	6	Occasional digger[1]
Hydrochoerus hydrochaeris	2	Cursorial[1]
Hystrix cristata	1	Occasional digger[1]
Lagidium sp.	6	Ricochetal[1,6]
Lagostomus maximus	5	Fossorial[1]
Microcavia australis	7	Occasional digger
Myocastor coypus	5	Occasional digger[1]
Octodon degus	1	Fossorial[1,3]
Octodontomys gliroides	8	Ambulatory[1]
Proechimys poliopus	1	Ambulatory[1]
Spalacopus cyanus	1	Fossorial[1]
Thrichomys apereoides	3	Ambulatory[1]

Sources: 1. Nowak 1991; 2. Justo et al. 2003; 3. Woods and Boraker 1975; 4. Mertz 2004; 5. Pérez 1992; 6. Spotorno et al. 2004; 7. Campos et al. 2001.

The specimens are deposited in the following mammalogical collections: Museo de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia", Argentina (MMPMa); Museo de La Plata, Argentina (MLP); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina (MACN); Laboratorio de Evolución, Facultad de Ciencias, Universidad de la República, Uruguay (CA and EV), Universidade de Brasília, Brazil (UnB); Colección Mamíferos Lillo, Tucumán, Argentina (CML); J. Gelfo's personal collection (JG). Caviidae – *Cavia aperea* MLP 678a, MLP 678b, MLP 2.IV.02.8, MLP 2.IV.02.9, MLP 5.VI.00.8, MLP 15.II.96.49, MLP 29.VII.00.15, MLP 30.V.02.8, MLP 585.4, MLP 678; *Galea musteloides* MLP 5.VI.00.9, MLP 12.IV.99.46, CML 3430, CML 3432, CML 7132, CML 7240; *Microcavia australis* MLP 26.VIII.01.22, MLP 7.IV.99.7, MLP 7.IV.99.8, MLP 7.IV.99.9, CML 7223, CML 7238, CML 7239; *Dolichotis patagonum* MLP 1078, MLP 1079, MLP 1895, MLP 249. Chinchillidae – *Chinchilla* sp. MLP 24.VIII.98.4; *Lagidium* sp. MLP 29.XII.01.22, MLP 534, MACN 4425, CML 5099, CML 7349, CML 7350; *Lagostomus maximus* MLP 1083, MLP 15.V.96.3, MLP 27.IV.95.1, MACN 23.14, MACN 21983. Ctenomyidae – *Ctenomys australis* MLP 1.VII.00.10, MLP 3.XI.95.5, MLP 7.XI.95.1, MLP 7.XI.95.2, MLP 7.XI.95.4, MLP 7.XI.95.6, MLP 7.XI.95.7, MLP 7.XI.95.12; *Ctenomys rionegrensis* N$\underline{\text{o}}$ Prov. 42, CA 393, EV 1137; *Ctenomys talarum* MLP 1.VIII.00.7, MLP 1.VIII.00.13, MLP 1.VIII.00.14, MLP 4.XI.02.3, MLP 23.VIII.01.3, MLP 23.VIII.01.4, MLP 26.VIII.01.12, MLP 26.VIII.01.15. Cuniculidae – *Cuniculus paca* MACN 49396. Dasyproctidae – *Dasyprocta* sp. MLP 1090, MLP 10.VI.98.1. Echimyidae – *Thrichomys apereoides* UnB 188, UnB 190, MMPMa 542; *Proechimys poliopus* MLP 22.II.00.8; *Myocastor coypus* MLP 1089, MACN 15.20, MACN 14058, MACN 30.70, JG1. Erethizontidae – *Coendou* sp. MACN 6.34, MACN 25.22, MLP 1084; *Erethizon* *dorsatum* MLP 1086. Hydrochoeridae – *Hydrochoerus hydrochaeris* MLP 1085, MACN 29865. Hystricidae – *Hystrix cristata* MACN 5.51. Octodontidae – *Aconaemys* sp. MLP 17.II.92.06, MLP 17.II.92.07, MLP 17.II.92.08, MLP 17.II.92.09, MLP 17.II.92.10; *Spalacopus cyanus* MLP 10.XI.96.1; *Octodon degus* MLP 12.XI.02.15; *Octodontomys gliroides* CML 2872, CML 7137, CML 7138; CML 7144, CML 7145, CML 7146, CML 7148, MMPMa 4027.

Phylogenetic and ecological information

Since no complete phylogeny that includes all the taxa studied was available, a composite tree was constructed (Fig. 4). Overall tree topology was based on Huchon and Douzery (2001) for suprafamilial and higher level relationships; familial and infrafamilial relationships were resolved following Rowe and Honeycutt (2002) for Cavioidea, Spotorno et al. (2004) for Chinchilloidea and Honeycutt et al. (2003), Galewski et al. (2005), Slamovits et al. (2001), Gallardo and Kirsch (2001) and Castillo et al. (2005) for Octodontoidea. Because comparable branch-length data were not available for all the taxa studied, arbitrary branch lengths were used following Grafen's (1989) method. A matrix of phylogenetic distance was constructed from this tree and used for the Mantel test. Information about species' locomotor habits (Table 1) was taken from the literature; since most caviomorphs are not greatly specialized for any particular locomotor mode, assignation to these categories was based on relative involvement of the forelimb in each case. Species with no predominant locomotor mode were assigned to an "ambulatory" category.

Data acquisition and processing

Bookstein's (1991) type 1 biological landmarks (discrete juxtaposition of tissues or structures, e.g. bone sutures) are nearly absent from the scapula of adult caviomorphs; consequently, I used type 2 landmarks (i.e. points situated on local maxima of curvature) as well as semilandmarks (i.e. sliding points placed along outlines and allowed to change their spacing along the curves they describe; Bookstein 1997). Nine landmarks were selected on the basis of a qualitatitive analysis of shape variation in the sample, as well as previous studies (Swiderski 1993; Monteiro and Abe 1999; Young 2004), and digitized from digital photographs of the scapula in external view (Fig. 1, Table 2). I used the application MakeFan6 (Sheets 2003) to place alignment "fans" at equal angular displacements along the curved scapular outline, and nine semilandmarks were extracted along the craniodorsal outline of the scapula between landmarks (5) and (6) to describe the variably convex shape of the cranial border and angle (Fig. 2). Landmark and semilandmark coordinates were recorded and digitized using the software tpsDig2 2.10 (Rohlf 2007). The effects of location, size and orientation ("nonshape variation", Rohlf and Slice 1990) were removed by General Procrustes Analysis (GPA; Gower 1975; Rohlf 1990), and the semilandmarks were slid to minimize variation tangential to the curve (Adams et al. 2004). Shape changes were then analyzed using thin plate splines (Bookstein 1989; Monteiro and dos Reis 1999; Zelditch et al. 2004).

A Relative Warps Analysis (RWA) of the consensus configuration for each species was used to explore the distribution of taxa in the morphospace, and shape changes were visualized by means of deformation grids. The number of principal components (Relative Warps) to be retained for further analysis was determined by the broken-stick model (Frontier 1976), according to which the observed eigenvalues are interpretable if they exceed the values generated by the broken-stick model (total

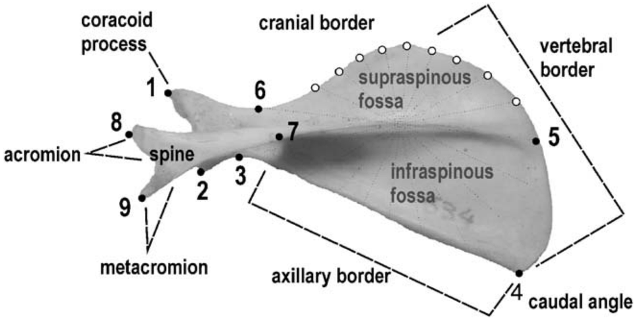

Fig. 1. Left scapula of *Lagidium* sp. showing position of landmarks (full circles, numbered) and semilandmarks (empty circles), and anatomical structures discussed in the text. See Table 2 for definition of landmarks.

Table 2. Description of scapular landmarks used in this work (see Fig. 1)

Landmark	Definition
1	Tip of coracoid process
2	Ventralmost point on lip of glenoid fossa
3	Point of maximum curvature along lower scapular neck margin
4	Caudal angle
5	Intersection between vertebral border and base of scapular spine
6	Point of maximum curvature along upper scapular neck margin
7	Union between spine and blade (point of max. concavity on greater scapular notch)
8	Tip of acromion (cephalic endpoint)
9	Ventral tip of metacromion or ventralmost point along scapular spine tip when no metacromion is evident

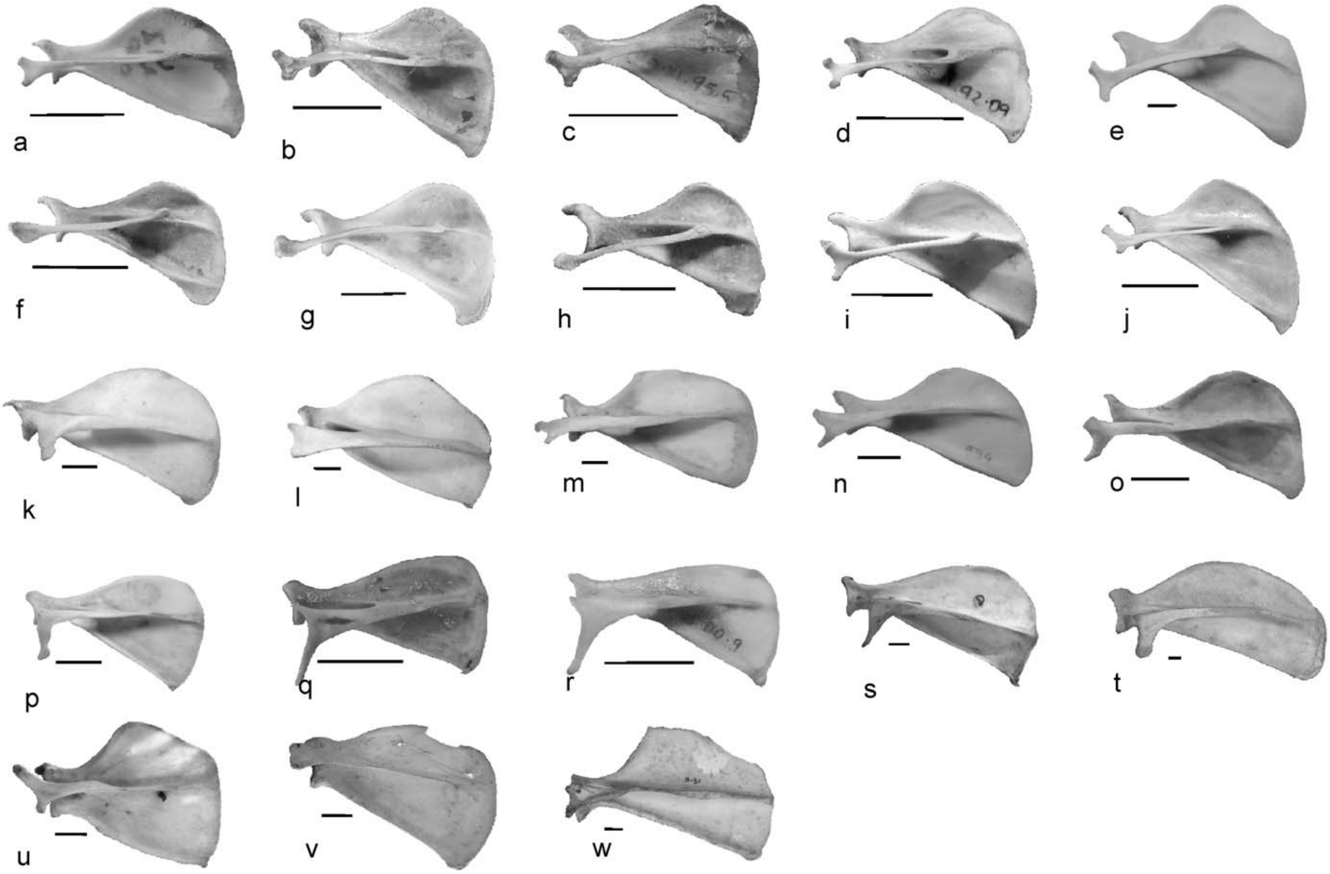

Fig. 2. External view of scapulae of caviomorphs analyzed: (a) *Octodontomys gliroides*, (b) *Octodon* sp., (c) *Spalacopus cyanus*, (d) *Aconaemys sp*., (e) *Myocastor coypus*, (f) *Ctenomys talarum*, (g) *C. australis*, (h) *C. rionegrensis*, (i) *Proechimys poliopus*, (j) *Thrichomys apereoides*, (k) *Dasyprocta* sp., (l) *Cuniculus paca*, (m) *Lagostomus maximus*, (n) *Lagidium* sp., (o) *Chinchilla* sp., (p) *Cavia aperea*, (q) *Microcavia australis*, (r) *Galea musteloides*, (s) *Dolichotis patagonum*, (t) *Hydrochoerus hydrochaeris*, (u) *Coendou prehensilis*, (v) *Erethizon* sp., (*w*) *Hystrix cristata*. Scale bar = 1 cm.

variance randomly divided amongst components, MacArthur 1957).

ANOVA and post-hoc tests were used to explore the relationship between shape and locomotor mode, and multiple regressions of partial warp scores of the mean shapes onto log-transformed centroid size (Zelditch et al. 2004), to analyze the influence of body size on scapular shape. Multiple regressions were made using tpsRegr 1.33 (Rohlf 2007); other statistical analyses were made using the statistical software package PAST 1.68 (Hammer et al. 2001). Phylogenetic inertia was estimated from the Mantel test of correlation between morphometric (Procrustes) distance and phylogenetic distance. To control for phylogenetic influence, the data were reanalyzed using Generalized Estimating Equations (GEE); this approach is an extension of the Phylogenetic Generalized Least Squares (PGLS) regression model (Martins and Hansen 1997), which allows for the inclusion of multiple discrete or continuous variables (Paradis and Claude 2002). The matrix of partial warp scores (W) of each species was regressed onto the log-transformed centroid size and locomotory habit categories. GEE were executed in (R Development Core Team 2005) using the Analysis of Phylogenetics and Evolution (APE) package (Paradis and Strimmer 2004).

Results

All the specimens were included in a Relative Warps Analysis (RWA); subsequently, the average species configurations (consensus) were used for other analyses, after confirming the existence of significant interspecific differences (MANOVA of partial warp scores classified by species: Wilks' lambda 0.00, $F = 4.78$, $p < 0.0001$; canonical discriminant analysis: only two misclassified specimens out of 85; $p < 0.001$). For certain species (*Spalacopus cyanus*, *Proechimys poliopus*, *Erethizon dorsatum* and *Hystrix cristata*) only one specimen was available; these taxa were nevertheless included in the analyses because even small samples can provide

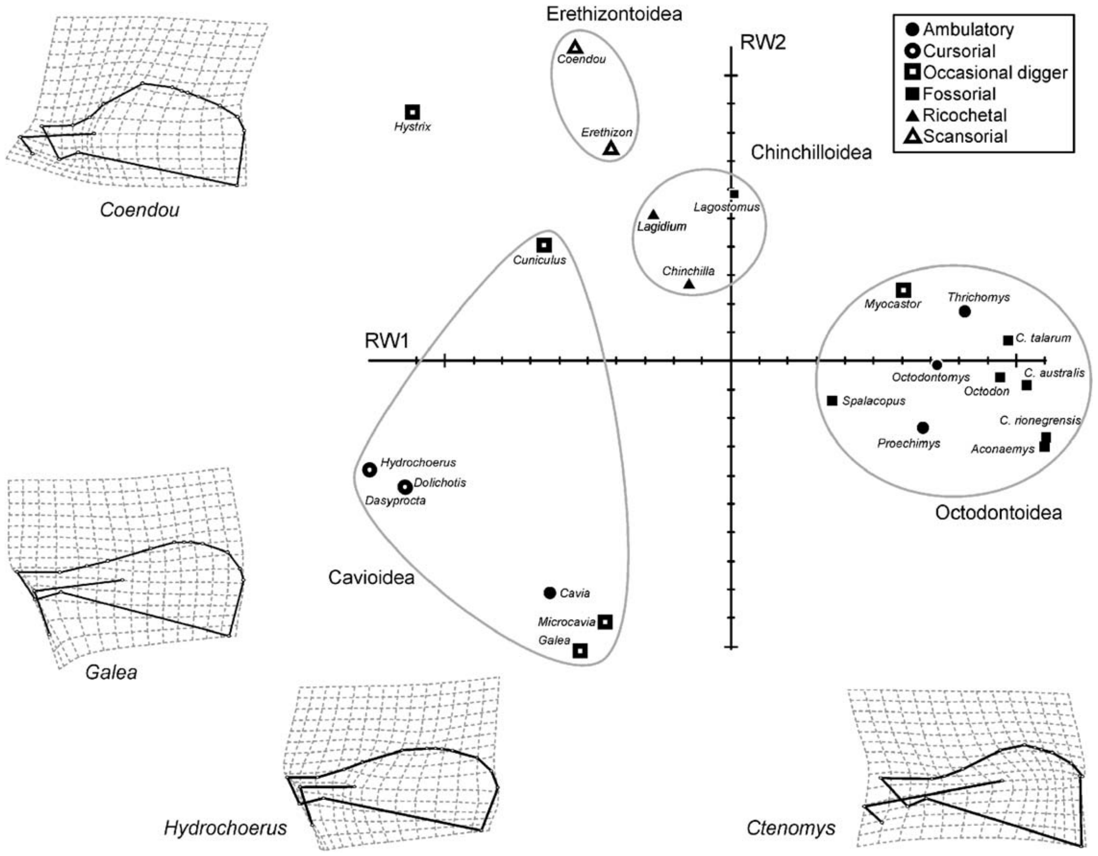

Fig. 3. Mean species scores for the first two Relative Warps; locomotor habit for each studied species is indicated. Ellipses enclose all members of each superfamily. Deformation grids included for visualization of scapular shape changes.

valuable morphological information for this first analytical approach.

Relative Warps Analysis (RWA, Fig. 3)

The first two Relative Warps (RW) explained 72.14% of the observed variation (RW1: 49.57% and RW2: 22.57%). The octodontoids occupied the extreme positive field along the RW1 axis, and the remaining taxa were arranged in a gradient from near zero scores for the chinchillids (chinchilla, mountain viscacha and plains viscacha), through more negative scores for the erethizontids (New World porcupines), *Cuniculus paca* (paca), the caviines (cavies) and *Hystrix cristata*, and extreme negative scores for *Dolichotis patagonum* (Patagonian cavy), *Dasyprocta* sp. (agouti) and *Hydrochoerus hydrochaeris* (capybara). Analysis of the deformation grids shows that RW1 summarizes shape changes of the scapular spine (length of spine and metacromion), as well as extension of the coracoid process, development of the great scapular notch, and blade shape (particularly at the cranial angle and vertebral border). Along RW2, the scores ranged from most positive for the erethizontoids and *Hystrix*, through the chinchilloids and *Cuniculus paca* with positive scores, the octodontoids and the cavioids *Dolichotis*, *Dasyprocta* and *Hydrochoerus* with intermediate values, and the caviines with extreme negative values. RW2 summarized mainly changes in the shape of the scapular neck and the suprascapular fossa, the latter associated with the shape of the cranial margin.

This analysis showed large differences in scapular shape among the major caviomorph lineages (Figs. 2 and 3). The scapula of octodontoids is approximately triangular, with a long spine, large great scapular notch and well-developed coracoid process. In contrast, cavioids (with the exception of *C. paca*, discussed below) have a short scapular spine with well-developed metacromion. The shape of the scapular spine of chinchillids and erethizontids is intermediate between that of cavioids and octodontoids, with subequal acromion and metacromion and moderately developed great scapular notch. As noted above, the scapula of *C. paca* differs from that of other cavioids by having a relatively longer scapular spine and shorter metacromion, and is more similar to the chinchillid–erethizontid morphology (Fig. 3). The outgroup taxon, *Hystrix*

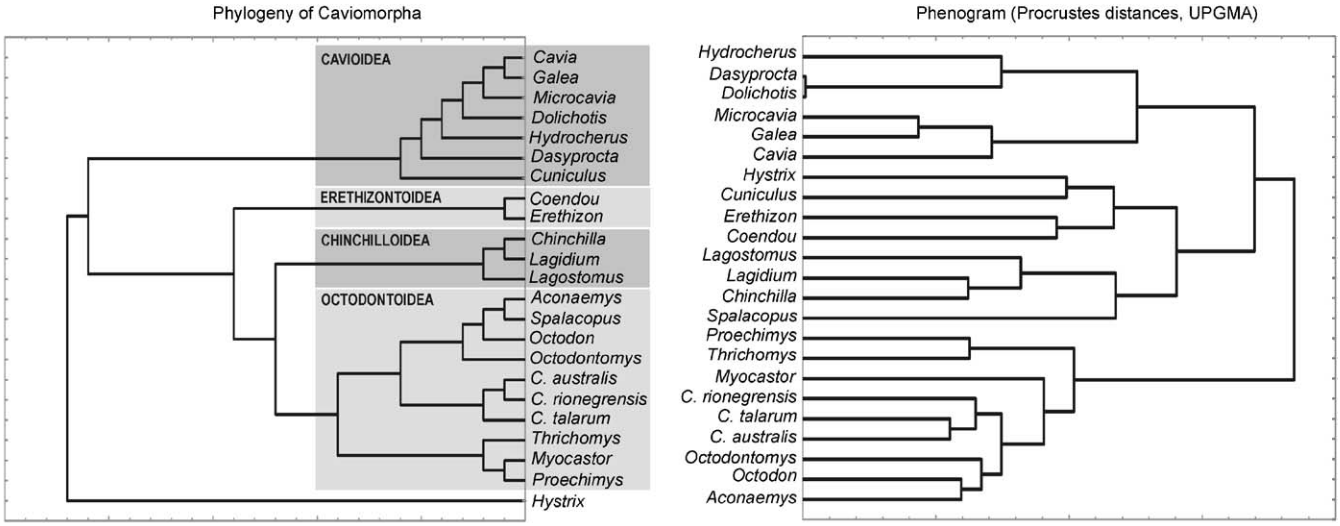

Fig. 4. Arrangement of taxa according to current phylogenetic hypotheses (composite from several sources, see text for references) compared with morphological phenogram of same taxa based on Procrustes distances (UPGMA clustering).

cristata, was also more similar to Erethizontidae + Chinchillidae + *C. paca* in scapular shape.

The gaps between the major taxa (Fig. 3) are noteworthy because they show the absence of certain scapular morphologies in the sample. In particular, a scapula with both a long spine and a long metacromion (intermediate between the shapes typical of Octodontoidea and Cavioidea) was not found among the caviomorphs studied, and such a combination of characters has not been recorded in other mammals either (Lessertiseur and Saban 1967; Seckel and Janis 2008). A long scapular spine might be incompatible with a long metacromion process due to biomechanical constraints (as suggested by Seckel and Janis 2008); but both a larger sample and a detailed biomechanical analysis are needed to test this hypothesis.

Phylogeny and scapular shape

The Mantel test of Procrustes distances vs. phylogenetic distances among species showed high correlation (Pearson's $r = 0.75$, $p < 0.001$). Fig. 4 illustrates the good fit between phylogenetic and Procrustes distances among the species analyzed. The major caviomorph groups (namely the superfamilies Octodontoidea, Chinchilloidea, Cavioidea and Erethizontoidea) are mostly recovered from the phenogram, with some exceptions: the octodontid *Spalacopus* is clustered with the chinchillids, and the cavioid *Cuniculus paca* is closest to the outgroup taxon *Hystrix*. The octodontoids (except *Spalacopus*) are morphologically more distant from the remaining taxa, in contrast with the phylogenetic scheme in which the cavioids are most divergent.

Table 3. Coefficients and standard error (S.E.) within parentheses of linear models relating partial warp scores (‘*W*’ matrix) of mean species configurations with size (estimated as logCS) and habit (six locomotory categories)

Variables	Coefficient (S.E)	t	$P\ (T>\|t\|)$
Intercept	−0.041 (0.076)	−0.541	0.614
logCS	0.086 (0.046)	1.878	0.126
Habit			
Cursorial	0.127 (0.058)	2.193	0.427
Fossorial	−0.058 (0.057)	−1.015	0.599
Ambulatory	0.011 (0.052)	0.205	0.891
Occasional digger	0.088 (0.052)	1.704	0.480
Ricochetal	−0.081 (0.065)	−1.24	0.552
Scansorial	0.009 (0.089)	0.098	0.947

Body size and scapular shape

The multiple regression of the *W* matrix onto log-transformed centroid size (logCS) resulted in only 2.81% of the variation explained by size. The Generalized Goodall *F*-test suggested a non-significant effect of size on shape ($F_{32,678} = 0.61$, $p < 0.95$); 66.10% of the Goodall *F* values were larger or equal to the ones observed after 1000 permutations. This regression was also non-significant under the phylogenetically corrected GEE (Table 3).

Locomotor modes and scapular shape

Scapular shape differences related to locomotor mode were assessed using ANOVAs of species scores (mean RW score for each species) classified by locomotor mode; the first two RW were retained for analysis according to the broken-stick model. The analysis of raw scores with locomotor mode as categorization variable revealed significant differences among all groups (Wilks' lambda $= 0.18$, $F_{10,32} = 4.40$, $p < 0.001$). Post-hoc pairwise analyses (Scheffe's test) showed significant differences between only some locomotor modes for RW1 ("occasional digger" vs. "fossorial", "cursorial" vs. "fossorial" and "ambulatory" vs. "cursorial") and no significant differences for RW2. The analysis of phylogenetically corrected data (GEE) also indicated non-significant effects of locomotory habit on scapular shape (Table 3). However, these results should be interpreted with caution, given the small sample sizes (species assigned to each locomotor mode).

Discussion

In order to assess the relative importance of causal factors of morphological disparity, an estimation of phenotypical differences, a phylogenetic framework and at least a gross description of the environment of each species are required (Straney and Patton 1980). Here, phenotypical variation was quantified in terms of Procrustes distances, and these were contrasted with the phylogenetic relationships and major locomotor modes of South American hystricognaths.

The morphological characterization indicates that, at least at this scale of analysis, the similarities and differences in the scapular shape of caviomorphs are strongly linked to the common evolutionary history of the major lineages, as opposed to more immediate biomechanical or ecological factors. In this sense, the regression analyses confirmed the low influence of body size on scapular shape, which is evident in the marked morphological similarity of scapular shape between closely related caviomorphs with very different body size (e.g. *Cavia* and *Hydrochoerus*; *Ctenomys talarum* and *Myocastor coypus*; Figs. 2 and 3). Furthermore, the multiple comparisons revealed that most of the functional categories are not associated with a distinct scapular morphology. The significant differences found between the cursorial and fossorial taxa could be explained by the close phylogenetic relationship between the cursors on one hand, and most of the diggers on the other; and indeed, the phylogenetically corrected analysis showed no significant correlation between habit and scapular shape. This does not rule out the influence of adaptation, but suggests an agreement between habit and phylogeny in these rodents, similar to the high correlation found by Young (2004) between phylogenetic distance and locomotor similarity in primates. Thus, it is possible that the major features of scapular shape, and possibly the predominant locomotory modes, were established early on during the evolution of each caviomorph superfamily, and have since both facilitated and constrained the ecomorphological evolution within each lineage (Losos and Miles 1994).

Although locomotor habit did not appear to be a major determinant of scapular shape at species level, the shape differences detected between major caviomorph groups may be associated with mechanical capabilities and constraints of the scapula at higher (suprafamilial) taxonomical level, and consequently some functional aspects are worthy of discussion. Large-scale changes of the scapular blade shape are closely related to the size and position of attached muscles, as well as the magnitude and direction of the forces they exert (Hildebrand 1985; Szalay and Sargis 2001; Sargis 2002), and the differences observed between octodontoids and cavioids probably reflect such myological differences. Because a relatively long vertebral margin provides ample attachment for the muscles involved in rotation and translation of the scapula (Woods 1972; Fischer 1994; Fischer et al. 2002) and because the large great scapular notch allows greater development of the shoulder stabilizer *M. infraspinatus*, the scapular shape of octodontoids might be advantageous for digging, although not a fossorial specialization. In contrast, the short vertebral margin of cavioids could represent a constraint against fossorial locomotor activity, especially in the case of the cursorial cavioids whose elongate scapular blade is convergent with that of cursorial ungulates (Lessertiseur and Saban 1967). In addition, the well-developed coracoid process and long scapular spine of octodontoids restrict lateral movements of the forelimb (Lehmann 1963), whereas the relatively short spine of cavioids is associated with a reduced clavicle, linked to greater anteroposterior mobility at the shoulder in cursorial mammals (Rocha-Barbosa et al. 2002). The shape and relative development of the acromion and metacromion also show striking differences among the caviomorphs: the metacromion of most cavioids is relatively long and caudally directed, contrasting with the other taxa. With respect to this feature, a recent analysis by Seckel and Janis (2008) has shown that a long, narrow and caudally directed metacromion is a feature common to many small cursorial mammals, including lagomorphs, macroscelideans and some Caviomorpha. In agreement with the present results, these authors found long metacromia in *Microcavia*, *Galea*, *Cavia*, *Dasyprocta*, *Dolichotis* and *Lagidium*, whereas *Agouti*, *Chinchilla* and *Proechimys* had a relatively shorter metacromion. The metacromion is the site of attachment of *M. acromiotrapezius* and *M. omocervicalis* (Woods 1972), and an elongated metacromion lengthens the lever arm of these muscles, an arrangement that would be biomechanically advantageous for small cursorial mammals (Seckel and Janis 2008). This interpretation of the long narrow metacromion as an osteomorphological correlate of cursorial half-bounding habits is very useful to analyze the origin of such specializations in caviomorph rodents, especially within the Cavioidea.

Previous morphofunctional analyses of the postcranial skeleton of caviomorphs have shown that most taxa are not highly specialized for any single locomotor mode, but often combine two or more of them (Elissamburu and Vizcaíno 2004; Weisbecker and Schmid 2007); however, if each of the characteristic derived morphologies described above for octodontoids and cavioids represents particular functional capabilities and constraints, they could be closely associated with the evolution of prevalent locomotor modes within each caviomorph lineage. In contrast with these distinct scapular shapes, the scapulae of the chinchilloids, erethizontids and *C. paca* are morphologically more similar to each other and to that of the non-caviomorph hystricognath *Hystrix*. This similarity suggests that a roughly rectangular blade, moderate great scapular notch, intermediate spine length and subequal acromion and metacromion could be plesiomorphic for the scapula of caviomorphs. In contrast, Seckel and Janis (2008) have suggested that a moderate-sized, caudally directed metacromion process is a primitive caviomorph feature. This discrepancy may be due to a certain phylogenetic bias given the greater proportion of cavioid taxa in Seckel and Janis' (2008) sample; in any case, I agree with these authors that a narrow elongated metacromion represents a derived feature among caviomorphs. The inclusion of additional living and extinct caviomorph taxa in future analyses, as well as a reliable estimation of the phylogeny of the group, will permit further testing of these hypotheses by means of the reconstruction of ancestral states (Losos and Miles 1994; Omland 1999; Crisp and Cook 2005).

Because this study is limited to a single structure whose components are probably highly correlated, the shape space represents only a few independent characters (Rohlf 1998). Nevertheless, it provides interesting results that contribute to our understanding of the evolutionary history of the South American Hystricognathi. The inclusion of additional taxa in a more resolved phylogenetic framework, as well as the future availability of more accurate data on their behavior and ecology, will allow a more detailed assessment of the influence of these factors on the evolution of scapular shape and associated functional characteristics in these rodents.

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