Locomotion in Rodents and Small Carnivorans: Are they So Different?

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Abstract

Rodents and carnivorans constitute two diverse clades with variable life habits. To analyze the common ecomorphological aspects of their limbs in relation to their different substrate uses, the shape of humerus and femur was explored using 3-D geometric morphometrics. The principal components and MANOVA analyses show that the shape of the humerus is similarly related to the substrate use and taxonomy, and the shape of the femur is heavily influenced by taxonomic differences. Nevertheless, beneath those differences in the latter, a relation with the proposed ecological categories is also found. The stronger ecomorphological correlation of the humerus with respect to the femur may indicate a differential selective pressure on each limb. This could be reflecting the greater involvement of the forelimb over the hind limb in several activities performed with the limbs such as digging and climbing. The combined analysis of two distantly related groups with diverse ecological characteristics allows a recognition of similar biological patterns hidden under taxonomic differences. Furthermore, the study of morphological similarities and differences underlying taxonomic variability may led to a more profound understanding of the evolution of the locomotor apparatus.

Keywords Functional morphology · Geometric morphometrics · Comparative morphology · Small mammals · Humerus · Femur · Ecomorphology

Introduction

This work is part of a tribute to Leonard B. Radinsky centered on the form-function correlation in recent mammals. Radinsky's greatest contributions were on the systematics and evolution of early perissodactyls, on the evolution of the mammalian brain, and on the functional morphology of the mammalian skull (Hopson 1989; Kay 2019). He dedicated his academic work to study the morphological patterns of evolution and his book "Evolution of Vertebrate Design" (Radinsky 1987), oriented to undergraduate students, is an excellent introduction to functional morphology and biomechanics (Vizcaíno and Bargo 2019).

This textbook not only explores skull morphology but also post-cranial morphology. The latter is often studied in functional analyses regarding the different substrate uses/preferences and types of locomotion. There are several works that examine the morphology of different elements of the fore- and hind limbs of small mammals. Some of them focus on a particular systematic group such as rodents (Elissamburu and Vizcaíno 2004; Samuels and Van Valkenburgh 2008; Morgan 2009; Candela et al. 2017; Muñoz et al. 2019) and carnivorans (Van Valkenburgh 1987; Samuels et al. 2013; Martín-Serra et al. 2014a, 2014b). Nevertheless, others analyze a combination of different mammalian orders (Seckel and Janis 2008; Álvarez et al. 2013; Muñoz et al. 2017), and therefore help to understand the common underlying morphological features among dissimilar sets of organisms.

Rodents and carnivorans are a good example of two distinct and diverse clades with various specializations to different life habits (e.g., cursorial, arboreal, and semi-aquatic). Rodents are the most diverse order among placental mammals representing almost half of the diversity of Mammalia with approximately 32 extant families and 2552 species (Burgin et al. 2018). They are present nearly worldwide and are characterized by ever-growing incisor teeth, most of them being herbivorous (Nowak and Paradiso 1983). Carnivora is also a diverse set of mammals and contains approximately 16 extant

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families and 305 living species (Burgin et al. 2018). They have a nearly worldwide distribution, as the rodents, and are mostly carnivorous (Nowak and Paradiso 1983).

Although these two clades have been analyzed individually and together with other mammalian orders in previous works, to date there has not been an exhaustive analysis centered in both groups comparing this biological aspect. The main goal of this work is to analyze the morphology of the limb in rodents and carnivorans in search of a common morphological pattern and its possible relation with its function.

Materials and Methods

Institutional Acronyms: AMNH, American Museum of Natural History, New York, USA; CNP, Centro Nacional Patagónico, Puerto Madryn, Argentina; FMNH, Field Museum of Natural History, Chicago, USA; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCN, Museu de Ciencias Naturais, Porto Alegre, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina; and YPM, Yale Peabody Museum, New Haven, USA.

With the aim to analyze the morphology of the stylopodium (proximal element of forelimb and hind limb) in relation to substrate use, a sample 37 specimens of small- to medium-sized Rodentia (18 genera; 16 Hystricognati, two Sciuridae, and no members of the mouse-related clade) and Carnivora (19 genera; no pinnipeds included) was gathered (Table 1). The size categories used here are based on the three size groups of base-10 logarithmic scale ranges proposed by Cassini et al. (2012), in which each log unit corresponds to one order of magnitude: small-sized (1–10 kg), medium-sized (10–100 kg), and large-sized (100–1000 kg). Some species in the present sample (e.g., *Ctenomys australis*, *Sciurus carolinensis*) would correspond to a new smaller category of less than 1 Kg, but are considered small-sized for simplicity. All species in the chosen sample are above 100 g and they are no larger than medium-sized. This selection was made in order to minimize the influence of size-based morphological differences and focus on the remaining shape changes.

The humeri and femora were digitized with a NextEngine Desktop 3-D Scanner and the raw 3-D meshes were created with its associated software Scanstudio v2.0.2. The MeshLab v1.3.3 software (Cignoni et al. 2008) was used for further post-processing until obtaining clean meshes of right laterality (mirroring the left elements). To improve the visualization of the elements on the figures, the Radiance scaling complement (Granier et al. 2012) for MeshLab was used.

The landmark coordinates were taken on the meshes using the Landmark Editor software v3.0 (Wiley 2006). Fifteen landmarks were digitized on the humerus and fifteen on the femur (Fig. 1 and Table 2). The configuration of only a few landmarks in each epiphysis was oriented to preserve the basic shape of the bones, mainly the proportions between the two epiphyses including their relative sizes, relative rotation, and general shape of the articular surfaces and the protrusion and position of tuberosities, trochanters, and epicondyles.

In order to evaluate the ecomorphological relationship between the morphology of the osteological elements and substrate use, seven ecological categories were defined following the classification proposed by Muñoz et al. (2017) as a baseline: (1) climber; (2) occasional digger; (3) digger; (4) swimmer; (5) runner; (6) jumper; and (7) ambulatory. This is a mixed classification for the substrate use, and is a result of the combination of five locomotor categories (climber, swimmer, runner, jumper, and ambulatory) and three associated with digging (not-digger, occasional digger, and digger). Digging is an activity that requires great forces to be applied to the substrate and is expected to have a morphological counterpart. For that reason, the digging habit was incorporated in the classification. Substrate use assignation was based on information available in the literature (Taylor 1974; Nowak and Paradiso 1983; Morgan 2009; Ercoli et al. 2012 and references therein) (Table 1).

All statistical analyses were performed using R software v3.1.5 (R Development Core Team 2015). The geometric morphometrics analyses and 3-D graphics, based in TPS methods with color patterns associated with the shape changes, were made using the R packages Morpho v2.3.1.1 (Schlager 2013) and geomorph v2.1.3 (Adams and Otárola-Castillo 2013). These shape changes are shown in the figures after warping osteological elements of *Leopardus*. Each landmark configuration was superimposed using the generalized Procrustes analysis (GPA). A regression between the $\log_{10}$ of centroid size (CS) and the shape variable (aligned Procrustes coordinates) for each bone was used to test for allometry. In this regression the CS of the analyzed element was considered a proxy for the body size of the animal. A principal component analysis (PCA) was performed to identify major components of shape variation, and morphospaces were evaluated in terms of ecological and taxonomic categories. Two PCAs were undertaken, one for the humerus (PCAH) and one for the femur (PCAF). The number of principal components (PCs) that were analyzed was selected to sum a correlation of at least 0.95 between the Euclidean distances matrix in the reduced shape space and the Procrustes shape distances matrix in the full shape space (Cardini et al. 2010). To compare the morphological range of each taxonomic group as a hypervolume, the convex hull that minimally encloses the data was calculated using the R package hypervolume v2.0.12 (Blonder et al. 2014). To quantify magnitude of morphological variation or morphological diversity (disparity) as a Procrustes variance (Zelditch et al. 2012), the partial disparity of each taxonomic group and its contribution to the total disparity was calculated using the R package geomorph v2.1.3 (Adams and Otárola-

Table 1 Mammalian species in the sample, numerical code used in the PCAs, taxonomic group (order), category of substrate use and specimen number

Code	Order	Species	Substrate use	Specimen
1	Rodentia	*Hystrix cristata*	occasional digger	MACN 5.51
2	Rodentia	*Lagidium viscacia*	jumper	MLP 29.XII.00.3
3	Rodentia	*Chinchilla chinchilla*	jumper	MACN 13037
4	Rodentia	*Lagostomus maximus*	digger	MLP 27.IV.95.1
5	Rodentia	*Capromys pilorides*	climber	AMNH 35768
6	Rodentia	*Myocastor coypus*	ambulatory	MLP 1172
7	Rodentia	*Dactylomys dactylinus*	climber	YPM 1391
8	Rodentia	*Ctenomys australis*	digger	MLP 7.XI.95.7
9	Rodentia	*Dasyprocta azarae*	runner	CNP 896
10	Rodentia	*Cuniculus paca*	occasional digger	MACN 49396
11	Rodentia	*Hydrochoerus hydrochaeris*	ambulatory	MACN 43.43
12	Rodentia	*Pediolagus salinicola*	runner	MLP 1081
13	Rodentia	*Dolichotis patagonum*	runner	MLP 252
14	Rodentia	*Cavia aperea*	ambulatory	MLP 15.II.96.49
15	Rodentia	*Microcavia australis*	occasional digger	MACN 34.7
16	Rodentia	*Coendou spinosus*	climber	MCN 2681
17	Rodentia	*Cynomys ludovicianus*	digger	FMNH 58998
18	Rodentia	*Sciurus carolinensis*	climber	YPM 10991
19	Carnivora	*Leopardus geoffroyi*	ambulatory	MLP 27.XII.01.15
20	Carnivora	*Arctictis binturong*	climber	MACN 43.67
21	Carnivora	*Civettictis civetta*	ambulatory	FMNH 108174
22	Carnivora	*Genetta genetta*	climber	FMNH 57396
23	Carnivora	*Ichneumia albicauda*	runner	YPM 10417
24	Carnivora	*Suricata suricatta*	digger	FMNH 101744
25	Carnivora	*Cryptoprocta ferox*	climber	FMNH 161707
26	Carnivora	*Crocuta crocuta*	runner	MACN 6.12
27	Carnivora	*Nandinia binotata*	climber	AMNH 35440
28	Carnivora	*Ailurus fulgens*	climber	AMNH 119474
29	Carnivora	*Lontra longicaudis*	swimmer	MLP 1959
30	Carnivora	*Galictis cuja*	ambulatory	MLP 2020
31	Carnivora	*Gulo gulo*	ambulatory	FMNH 151027
32	Carnivora	*Meles meles*	digger	MACN 5.36
33	Carnivora	*Nasua nasua*	climber	MACN 5.12
34	Carnivora	*Procyon cancrivorus*	ambulatory	MLP 2110
35	Carnivora	*Potos flavus*	climber	MLP 1740
36	Carnivora	*Conepatus chinga*	occasional digger	MLP 1.II.95.1
37	Carnivora	*Lycalopex gymnocercus*	runner	MLP 1896

Castillo 2013). Differences in mean shapes of femora and humeri between taxonomic and ecological categories were analyzed by MANOVA procedures, and post-hoc Tukey's test allowed to determine which ecological categories are significantly different. Two taxonomic categories are considered: Rodentia and Carnivora. The swimmer and the two jumpers were excluded from the MANOVA due to the low sample size.

Data Availability. The data generated during the current study are available from the corresponding author on reasonable request.

Results

The regressions of the $\log_{10}$ of CS and the shape change testing the presence of allometry were non-significant in the humerus and the femur analyses, with p values of 0.1336 and 0.2361, respectively. Therefore, neither of the morphological trends seen on the following PCA was explained by the change in size.

The expected correlation of 0.95 between the PCs and the full shape space distance matrices was obtained from the first four PC's in both PCAs. Thus, the first four PC's were
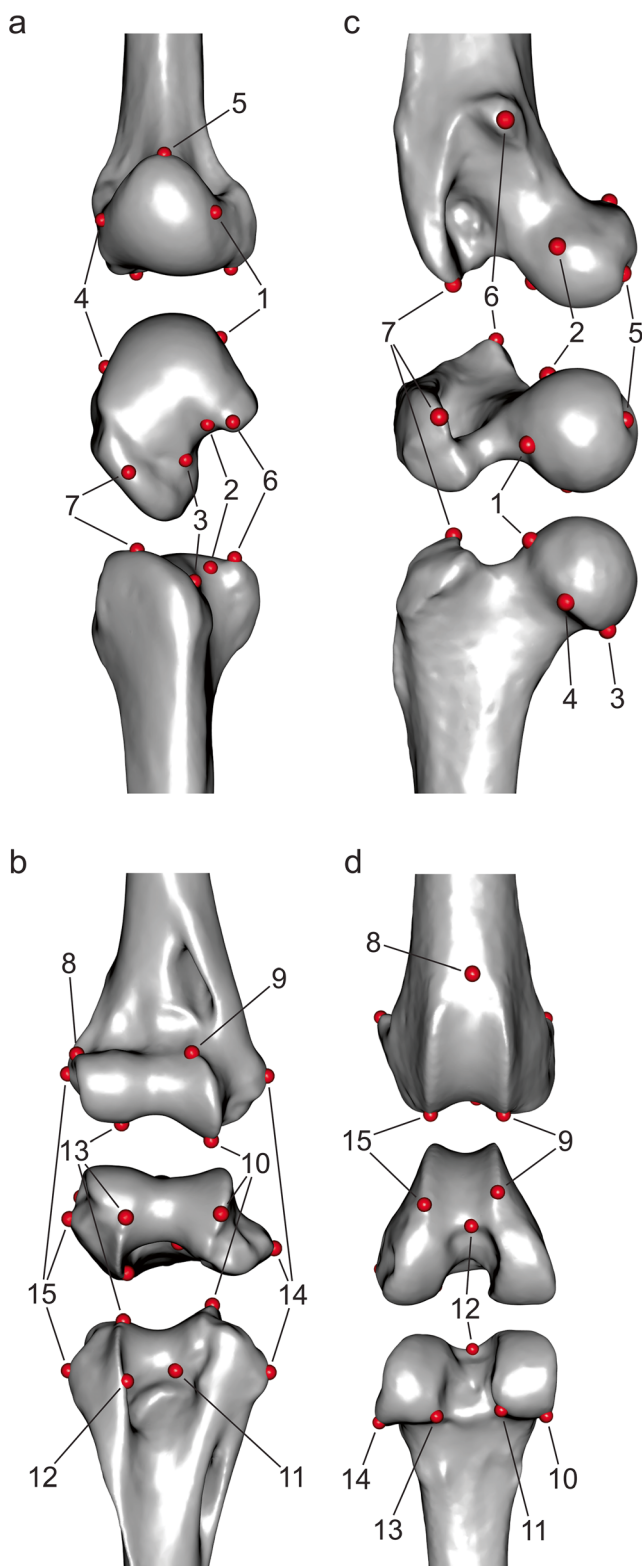
Fig. 1 Landmarks used in this study. **a** Proximal epiphysis of the humerus. **b** Distal epiphysis of the humerus. **c** Proximal epiphysis of the femur. **d** Distal epiphysis of the femur. Proximal epiphyses in posterior, proximal, and anterior views. Distal epiphyses in anterior, distal, and posterior views

explored in each analysis, explaining ~73–75% of the total variance.

In the hyperspace constructed with the first four PCs of PCAH, the hypervolume occupied by rodents (2.605×10^{-6}) is larger than the one occupied by carnivorans (6.364×10^{-7}). In addition, although no statistically significant difference was found, rodents have a greater contribution to the total disparity (54.89%; partial disparity = 0.001481) than carnivorans (45.11%; partial disparity = 0.001217).

The first four PCs of the PCAH (Fig. 2) account for ~73% of the cumulative variance, and the first two PCs account for ~59% of the total variance. The principal differences (PC1; ~43%) are related to the robustness of the bone: from a robust humerus on the negative side to a slender one on the positive side. Along with this change, the proportion of each tuberosity and condyle is maintained. The changes in robustness shown along the PC1 of PCAH are not clearly related to any of the chosen categories. Nevertheless, most diggers and the swimmer are towards the robust-like morphospace and most runners and jumpers are towards the slender-like one. Rodents and carnivorans occupy the whole range of values.

The changes in PC2 (~15%) are related to the relative mediolateral width of both epiphyses and the greater tuberosity. Towards the negative values the humerus has mediolaterally narrower proximal epiphysis with respect to the distal one and a proximodistally lower greater tuberosity with respect to the head. These changes are accompanied by a medially extended entepicondyle, a slightly laterally extended ectepicondyle, and a proximodistally and anteroposteriorly compressed distal articular surface elongated mediolaterally. Towards the positive values, the humerus has a proximal epiphysis mediolaterally wider than the distal one and a proximally extended greater tuberosity. On the distal epiphysis there is a slight development of both epicondyles and a proximodistally and anteroposteriorly expanded distal articular surface shortened mediolaterally. On the PC2, climbers and diggers tend to lie on negative values, while runners tend to lie on the positive ones. The carnivorans present mostly low values of PC2 and are included inside the distribution of rodents.

On PC3 (~9%) the principal changes are seen in the anteroposterior compression of the epiphyses, the development of the entepicondyle, and the orientation of the trochlea. Towards the negative values both epiphyses are anteroposteriorly extended, the distal one presents no internal rotation with respect to the proximal one and has slightly more medial protrusion of the entepicondyle. Towards the positive values, both epiphyses are anteroposteriorly compressed, the distal epiphysis presents an internal rotation on the proximodistal plane and a less medially protruded entepicondyle. On this PC there is no clear ecomorphological pattern of the chosen categories but regarding the taxonomic differences, most carnivorans lie towards the negative values

Table 2 Definition of landmarks used in this study

| Number	Definition
	Humerus
1	Most posterior contact between the lesser tuberosity and the proximal articular facet
2	Contact between the bicipital groove, the lesser tuberosity and the proximal articular facet
3	Contact between the bicipital groove, the greater tuberosity and the proximal articular facet
4	Most posterior contact between the greater tuberosity and the proximal articular facet
5	Most posterodistal point on the border of the proximal articular facet
6	Most proximal point of lesser tuberosity
7	Most proximal point of greater tuberosity
8	Most proximolateral point on the anterior portion of the distal articular facet
9	Most proximal point on the anterior portion of the medial lip of the trochlea
10	Most distal point of the medial lip of the trochlea
11	Most proximal point on the posterior portion of the medial lip of the trochlea
12	Most proximal point on the posterior portion of the lateral lip of the trochlea
13	Most distal point of the lateral lip of the trochlea
14	Most medial point of entepicondyle
15	Most lateral point of ectepicondyle
	Femur
1	Most proximal point on the border of the proximal articular facet
2	Most anterior point on the border of the proximal articular facet
3	Most distal point on the border of the proximal articular facet
4	Most posterior point on the border of the proximal articular facet
5	Center of the *Fovea capitis*
6	Most posterior point on the lesser trochanter
7	Most proximal point on the greater trochanter
8	Most proximal point on the union of the medial and lateral lips of the patellar groove
9	Contact between the medial lip of the patellar groove and the medial border of the medial condyle
10	Most proximomedial point on the border of the medial condyle
11	Most proximolateral point on the border of the medial condyle
12	Maximum inflection on the posterior border of the distal articular facet between the condyles
13	Most proximomedial point on the border of the lateral condyle
14	Most proximolateral point on the border of the lateral condyle
15	Contact between the lateral lip of the patellar groove and the lateral border of the lateral condyle

and most rodents towards the positive ones, although the latter occupy all the range.

Finally, on the PC4 (~5%) the shape associated with the negative values shows a slightly proximodistally higher greater tuberosity with respect to the head, with its most proximal portion anteriorly located, and a relatively wider distal epiphysis, with the whole configuration mediolaterally elongated and anteroposteriorly compressed. The shape associated with the positive values shows epiphyses of sub-equal mediolateral width, a slightly lower greater tuberosity with its most proximal portion posteriorly located, and a distal epiphysis mediolaterally compressed. It should be noted that it is not possible to identify a clear ecomorphological or taxonomic pattern on this PC.

The MANOVA performed on PCAH (Table 3) was significant for both taxonomic and ecological categories (p value = 0.0001999 and p value = 0.0145197, respectively). In particular, taxonomic differences were detected on PC2 (p value = 0.0005693) and PC3 (p value = 0.01274), and ecological ones were only significant in PC2 (p value = 0.0003418). The Tukey's test for the PC2 showed that among the ecological categories, runners and ambulatory mammals can be distinguished from climbers, and runners are also distinct from diggers.

In the hyperspace constructed with the first four PCs of PCAF, the rodents hypervolume (2.182×10^{-6}) was larger than the carnivorans one (5.765×10^{-7}). In addition, the proportion of partial disparities was almost the same as in PCAH: rodents have a greater contribution (54.12%; partial disparity = 0.001491) than carnivorans (45.88%; partial disparity = 0.001264) to the total disparity, although there is no statistically significant difference.
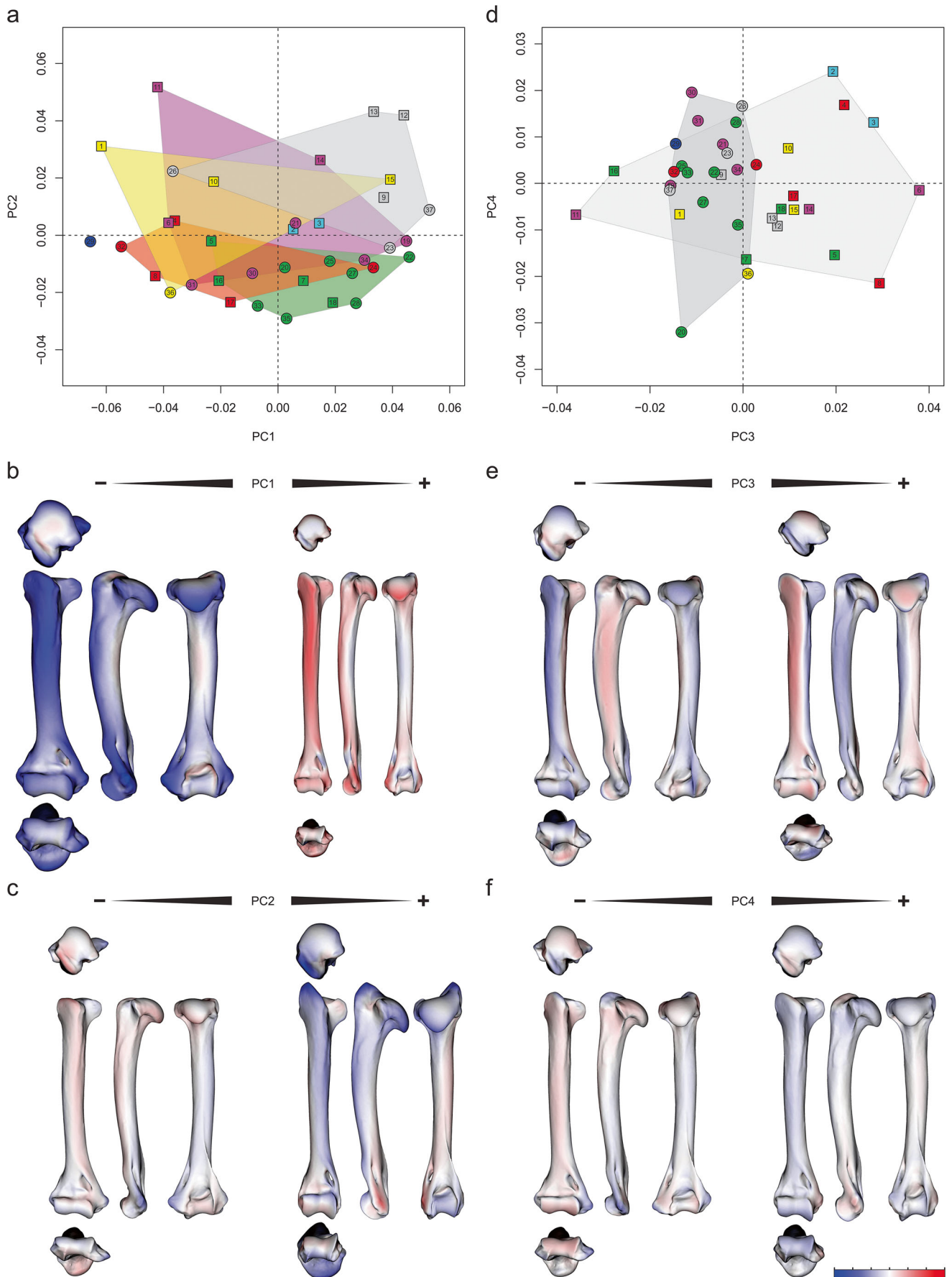
◀ **Fig. 2** PCAH. **a** Taxa distribution in the morphospace defined by PC1 and 2. **b** Shape changes in PC1. **c** Shape changes in PC2. **d** Taxa distribution in the morphospace defined by PC3 and 4. **e** Shape changes in PC3. **f** Shape changes in PC4. Taxa reference: squares, rodents; circles, carnivorans. Substrate use reference: green, climbers; yellow, occasional diggers; red, diggers; blue, swimmer; grey, runners; light blue, jumpers; pink, ambulatory. Shape changes (proximal, anterior, distal, medial, and posterior views) of extreme negative and positive values of each component. Color scale for shape distances = 0.01 mm

The first four PCs of the PCAF (Fig. 3) account for ~75% of cumulative variance, with the first two PCs accounting for ~60% of the total variance. The changes in PC1 (~45%) are mostly due to changes in the robustness. Towards the negative values the shapes are more robust, with a proximodistally higher greater trochanter with respect to the head, a more posteriorly protruded lesser trochanter, and a slight internal rotation of the distal epiphysis on the anteroposterior plane. Towards the positive values the shapes are slenderer, with a proximodistally lower greater trochanter, a more medially protruded lesser trochanter, and a slight external rotation of the distal epiphysis on the anteroposterior plane. Most rodents lie towards the negative side of this PC, whereas most carnivorans lie towards the positive side.

Towards the negative values of PC2 (~16%), the femora show a relatively smaller head, a proximodistally high greater trochanter with respect to the head, a posteriorly protruded lesser trochanter, and a slightly narrower patellar groove. Towards the positive values, the femora show a relatively larger head, a proximodistally low greater trochanter, a lesser trochanter not posteriorly protruded, and a slightly wider patellar groove. As on PC1, most of the rodents lie towards the negative values and the majority of the carnivorans lie towards the positive ones. The morphospace defined by the first two PC's show a clear segregation of the two mammalian orders in this study.

Towards the negative values of PC3 (~9%), the femur shows a proximodistally extended head, a more medially projected lesser trochanter, an anteriorly projected greater trochanter, and a head directed slightly posteromedially, creating

an obtuse anterior angle between the neck/head and the patellar groove on the proximodistal plane (i.e., distal epiphysis externally rotated), an anteroposteriorly compressed and mediolaterally elongated distal epiphysis, and a lateral condyle proximodistally shortened. Towards the positive values, the femur shows a proximodistally compressed head, a more posteriorly projected lesser trochanter, a posteriorly projected greater trochanter, and a head directed anteromedially, creating an acute (close to 90 degrees) anterior angle between the neck/head and the patellar groove on the proximodistal plane (i.e., distal epiphysis internally rotated), an anteroposteriorly elongated and mediolaterally compressed distal epiphysis, and lateral and medial condyles proximodistally equally developed. On this PC, most climbers, the swimmer, and both jumpers lie towards negative values and all runners and ambulatory mammals lie towards the positive ones.

Approaching negative values of the PC4 (~5%), the femur has a more medially protruded head, a proximodistally lower greater trochanter with respect to the head, a more posteriorly oriented lesser trochanter, and a distal epiphysis externally rotated on the proximodistal plane and posteriorly tilted on the sagittal plane (proximodistally longer patellar groove). Towards the positive values the bone has a less protruded head, a proximodistally higher greater trochanter with respect to the head, a more medially oriented lesser trochanter, and a distal epiphysis internally rotated on the proximodistal plane and anteriorly tilted on the sagittal plane (proximodistally shorter patellar groove). There is no clear ecomorphological or taxonomic patterns on this PC.

The MANOVA executed for the PCAF (Table 4) was significant for both taxonomic and ecological categories (p value = 1.043e-08 and p value = 0.01237, respectively), as was the case for the PCAH. The first two PCs showed only taxonomic differences (p value = 1.214e-06 and p value = 0.00182, respectively), and PC3 had significant differences among ecological categories (p value = 0.0001316). The Tukey's test for the PC3 showed that runners and ambulatory mammals are distinct from climbers (as in the PCAH), and runners can be distinguished from occasional diggers.

Table 3 Explained variances of PCAH and MANOVA, with significance of the taxonomic component and the ecological component

	Var %	Taxonomic component		Ecological component		
		$F_{(1, 28)}$	p value	$F_{(4, 28)}$	p value	Tukey
PCs 1–4	73,47,307	8.3627	0.0001999 ***	2.0680	0.0145197 *	
PC1	43,4,174,815	2.1009	0.15832	2.4622	0.06828	
PC2	15,4,067,352	15.1050	0.0005693 ***	7.3850	0.0003418 ***	R = A > C; R > D
PC3	933,930,602	7.0835	0.01274 *	0.6548	0.62840	
PC4	53,095,456	2.6541	0.1145	0.6992	0.5990	

PC = Principal Component; Var % = percent of variance explained by each PC; R = runners; A = ambulatory mammals; C = climbers; D = diggers. Significance codes: *** < 0.001; ** < 0.01; * < 0.05
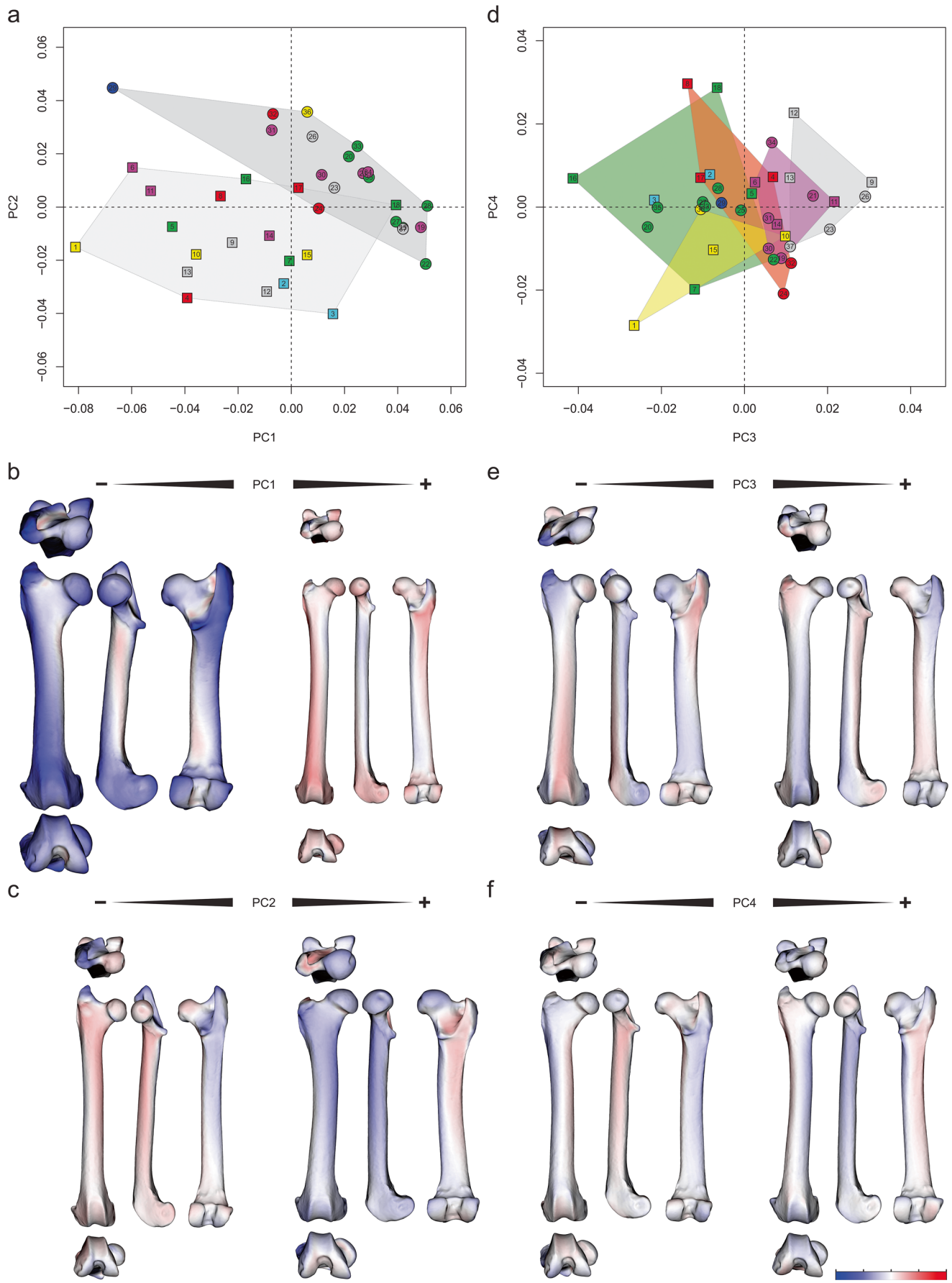
◄ Fig. 3 PCAF. **a** Taxa distribution in the morphospace defined PC1 and 2. **b** Shape changes in PC1. **c** Shape changes in PC2. **d** Taxa distribution in the morphospace defined by PC3 and 4. **e** Shape changes in PC3. **f** Shape changes in PC4. Taxa reference: squares, rodents; circles, carnivorans. Substrate use reference: green, climbers; yellow, occasional diggers; red, diggers; blue, swimmer; grey, runners; light blue, jumpers; pink, ambulatory. Shape changes (proximal, anterior, distal, medial and posterior views) of extreme negative and positive values of each component. Color scale for shape distances = 0.02 mm

Discussion

The lack of allometry among the femora and humeri could be explained by the chosen sample to analyze, showing the success of the sample selection method explained in Materials and Methods. Although there are body size differences (e.g., a few hundred grams in *Ctenomys* or 1–3 kg in *Galictis* vs. 27–79 kg in *Hydrochoerus* or 40–86 kg in *Crocuta*; Nowak and Paradiso 1983), all species are small- to medium-sized. Here, the connection between robustness and size of the studied bones that could be expected is not supported and it appears to be another factor influencing the former. In both analyses, most of the variation (PC1 in both PCA) is concentrated in changes in robustness but the probable explanation is different in each one.

In both the PCAH and the PCAF, the rodents tended to occupy a more extended area of the morphospace and had more morphological variability than the carnivorans (see hypervolume and disparity results). Therefore, the Rodentia seem to have more extreme modifications of the common body plan for each ecological context than the Carnivora.

The principal differences among the humeri are due to changes in robustness (PC1 of PCAH; Fig. 2). In the analysis of this element, most diggers and the swimmer display a robust configuration, while most runners and jumpers show a slender one, although no significant differences were detected in the MANOVA (Table 3). It could be expected to find a robust configuration among the climbers; however, they present a wide range of shape in this feature. This is probably due to the presence of different climbing styles among the

specimens of the sample. As it has been noted before, a mammal can move slowly through the branches as well as jump or run through this substrate (Cartmill 1985). Among the climbing rodents, *Capromys* and *Coendou* have the most robust configurations and *Sciurus*, which runs through the branches (Youlatos 1999; Schmidt 2011), has the slenderest one. Among the climbing carnivorans, *Nasua* has the most robust humerus, while *Genetta*, which also runs and jumps (Taylor 1974), has the slenderest one. The presence of robust architectures in diggers and the swimmer is in agreement with their habits, as they do not depend as much on speed as they do on force, needing great muscle mass to apply forces into the substrate (Maynard Smith and Savage 1956). The opposite occurs in the case of runners and jumpers, in which velocity is preferred over force (Maynard Smith and Savage 1956).

Morgan and Álvarez (2013) found similar results on a 2-D geometric morphometrics analysis of the humerus in caviomorph rodents. These authors showed that there was a segregation along the axis accounting for most of the variation: diggers and climbers on one side and jumpers and most runners on the other. Most of the variation was due to changes in robustness and the elongation of the deltoid process. The former is in agreement with the results showed in this work, but the latter is a feature not included here. Other inconsistencies among the two works can be explained by different categorization (e.g., *Hydrochoerus* as a runner/ambulatory mammal) and the mammal sample.

The changes on PC2 of the PCAH (Fig. 2) are useful to distinguish climbers and diggers on one side and runners on the other (Table 3). The humeri of the former two display a narrow proximal epiphysis, a low greater tuberosity, a protruded entepicondyle, and a mediolaterally elongated distal articular surface. The low greater tuberosity allows a wide range of motion for the shoulder, the protruded entepicondyle supports a great area of insertion for the flexor muscles of the autopodium, and the elongated distal articular surface can be related with the increase of rotational movements in the radius for pronation/supination movements (Taylor 1974; Candela and Picasso 2008; Muñoz et al. 2019). All of these

Table 4 Explained variances of PCAF and MANOVA, with significance of the taxonomic component and the ecological component

	Var %	Taxonomic component		Ecological component		
		$F_{(1,\ 28)}$	p value	$F_{(4,\ 28)}$	p value	Tukey
PCs 1–4	74,5565	26.7204	1.043e-08 ***	21,097	0.01237 *	
PC1	44.5013	37.8580	1.214e-06 ***	1.8820	0.1415	
PC2	15.6698	11.8652	0.00182 **	0.7838	0.54533	
PC3	8.93208793	0.8778	0.3568182	8.4618	0.0001316 ***	R = A > C; R > O
PC4	5.4533	3.0426	0.09207	1.5032	0.22812	

PC = Principal Component; Var % = percent of variance explained by each PC; R = runners; A = ambulatory mammals; C = climbers; O = occasional diggers. Significance codes: *** < 0.001; ** < 0.01; * < 0.05

characteristics are found in the forelimb of climbers and diggers according to several authors (Taylor 1974; Candela and Picasso 2008; Toledo et al. 2013; Muñoz et al. 2019). On the other hand, the morphology displayed by the runners (a high greater tuberosity, short entepicondyle, and mediolaterally compressed distal surface) is in agreement with the restriction of movement to the parasagittal plane, favoring the stability of the limb over the range of motion outside this plane (Candela and Picasso 2008; Muñoz et al. 2019).

On PC3 of the PCAH (Fig. 2), although no relationship with the proposed categories is found, taxonomic differences are observed (Table 3). The humeri of most rodents tend to be anteroposteriorly compressed, have an internal rotation of the distal epiphysis, and a less developed entepicondyle. On the other hand, the carnivorans tend to have the opposite morphology, being closer to the consensus of the variation. However, some rodents also show the other extreme of the variation differentiating apart from the rest of them (e.g., *Hydrochaerus* and *Coendou*). Therefore, an alternative functional hypothesis to the one addressed in this work could be formulated for this morphological gradient.

In the case of the femur, most of the variation can be associated with taxonomic differences (Table 4). On PC1 of the PCAF (Fig. 3), the femora of the rodents are basically more robust than those of the carnivorans, with the principal exceptions *Lontra* and *Sciurus*. These exceptions could be partially explained by the same parameters discussed previously for the robustness of the humerus. *Lontra* has a more robust femur than that expected for a carnivoran and is the only swimmer in the carnivoran sample, a mode of locomotion related with great development of the limb musculature. Furthermore, *Sciurus* has a slenderer femur than that expected for a rodent, being the more agile climber of the sample, with light bones that allow it to run through the branches (Youlatos 1999; Schmidt 2011).

PC2 of the PCAF (Fig. 3) shows the same trend of taxonomic differences as PC1, although with much superposition. The femora of most rodents tend to have a relatively smaller head, a higher greater trochanter, and a posteriorly oriented lesser trochanter. It should be further analyzed if there are functional explanations related to these anatomical configurations in each order, or if it could be only the result of structural constraints. Alternative hypotheses such as constraints, allometry, and heterochrony among others have to be considered along with the functional interpretations to avoid teleologic explanations.

On PC3 of the PCAF (Fig. 3), there is an ecomorphological segregation (Table 4). The femora of climbers, the swimmer, and the jumpers tend to have a medially projected lesser trochanter, an externally rotated and anteroposteriorly compressed distal epiphysis, and a proximodistally reduced lateral condyle. On the other extreme are the runners and the ambulatory mammals. A medially projected lesser trochanter

benefits the rotation of the femur and a posterior one, the flexion of this bone (Taylor 1976). An externally rotated distal epiphysis allows the foot to have outward orientation and the tibia-fibula complex to move from a posteromedial position to an anterolateral direction in the extension/flexion movement. An anteroposteriorly compressed distal epiphysis is associated with a flexed limb posture while an anteroposteriorly extended one facilitates the extension of the knee (Sargis 2002). A proximodistally reduced lateral condyle can cause an outward orientation of the tibia-fibula complex, or maintain its verticality if the femur is rotated inwards on the anteroposterior plane. The configuration of the features found in the climbers/swimmer/jumpers group are mostly in agreement with the movements made during climbing, such as the position of the lesser trochanter and the rotation of the anteroposteriorly compressed distal epiphysis (Argot 2002; Candela and Picasso 2008). Notwithstanding, the reduction of the lateral condyle and its probable functional implications need to be further studied, as well as the relation of the above mentioned features and the swimming/jumping habit.

Each of these features taken separately do not suffice to characterize a particular substrate use, but their combination in each configuration allows to separate different ecomorphological categories. This should be considered for each one of the morphological gradients exposed above.

The influence of ecomorphological and taxonomic aspects in the shape of the elements analyzed in this work seems to be radically different. Based on the MANOVA (Tables 3 and 4), most of the morphological variation observed in the humerus cannot be related to the proposed taxonomic and ecological categories (PC1; ~43% of the total variance in PCAH). The proportion of the morphological change that can be associated with differences between rodents and carnivorans (PC2 and 3; ~24% of the total variance in PCAH) and with differences in the substrate use (PC2; ~15% of the total variance in PCAH) is similar. In addition, although the MANOVA was not significant for PC1, some minor ecological trends could be recognized (see Results and Fig. 1). On the other hand, most of the variation in the femur can be related to differences between rodents and carnivorans (PC1 and 2; ~60% of the total variance in PCAF) and only a small part appears to be due to substrate use (PC3 ~ 9% of the total variance in PCAF). A differential selective pressure may be inferred from the contrast between the main element of the forelimb and the hind limb, with a stronger ecomorphological correlation on the former. This could suggest that the forelimb is more involved than the hind limb in several activities performed with the limbs, other than walking. Even though the specializations for climbing or digging involve changes in both limbs, most of the modifications are on the forelimb. Another aspect that can influence the morphological trends of the forelimb is the ability to grasp and manipulate (Fabre et al. 2013), and could be systematically analyzed comparing rodents and

carnivorans in further studies. In addition to being useful for climbing, these skills are utilized to grab and hold food in both orders and to catch prey in the case of the Carnivora (although some rodents can hunt small insects; Ivanco et al. 1996).

From an ecological point of view, it could be argued that the two mammalian orders analyzed in this work should be studied separately: while most rodents are herbivorous, the carnivorans are mostly carnivorous. This drastic ecological dichotomy may lead to the avoidance of searching morphological similarities in their postcranium. However, for a profound understanding of the evolution of the locomotor apparatus, it is necessary to study the differences and similarities underlying the ecological and taxonomic variability. This approach permits to recognize similar patterns hidden under taxonomic differences.

In sum, the differences in postcranial morphology between rodents and small carnivorans is undeniable, but there are also several points in common. Different phylogenetic histories from a common ancestor several million years ago led to dissimilar combinations of traits in their limb bones. Nevertheless, there are common structural modifications that are useful in certain circumstances and have been acquired independently (e.g., changes in the relative mediolateral width between both epiphyses and the greater tuberosity height in the humerus; changes in the relative rotation between both epiphyses and their anteroposterior elongation in the femur). These convergences, which respond mainly to interactions with the multiple dimensions of the environment, allow the identification of morphological features that could be related to ecological and ethological aspects.

Radinsky (1985: 2) stated that "the discovery of patterns in morphological diversity can play an important role in uncovering the processes and constraining factors responsible for producing these patterns." Therefore, for understanding the evolutionary processes that led to the increasing diversity in the morphological configuration of the limbs, we could analyze its variability and the interaction with each ecological niche. In this comparative work, the common features as well as the differences in the general shape of the humerus and femur of rodents and carnivorans were scrutinized in an ecomorphological framework. And what is comparative biology for if not to find the subjacent morphological and behavioral patterns of variation and try to understand the complex processes of biological evolution.

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