



# Locomotion in some small to medium-sized mammals: a geometric morphometric analysis of the penultimate lumbar vertebra, pelvis and hindlimbs

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## ABSTRACT

We assessed the influence of a variety of aspects of locomotion and ecology including gait and locomotor types, maximal running speed, home range, and body size on postcranial shape variation in small to medium-sized mammals, employing geometric morphometric analysis and phylogenetic comparative methods. The four views analyzed, i.e., dorsal view of the penultimate lumbar vertebra, lateral view of the pelvis, posterior view of the proximal femur and proximal view of the tibia, showed clear phylogenetic signal and interesting patterns of association with movement. Variation in home range size was related to some tibia shape changes, while speed was associated with lumbar vertebra, pelvis and tibia shape changes. Femur shape was not related to any locomotor variables. In both locomotor type and high-speed gait analyses, locomotor groups were distinguished in both pelvis and tibia shape analyses. These results suggest that adaptations to both typical and high-speed gaits could explain a considerable portion of the shape of those elements. In addition, lumbar vertebra and tibia showed non-significant relationships with body mass, which suggests that they might be used in morpho-functional analyses and locomotor inferences on fossil taxa, with little or no bias for body size. Lastly, we observed morpho-functional convergences among several mammalian taxa and detected some taxa that achieve similar locomotor features following different morphological paths.

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## 1. Introduction

Locomotion imposes demands on the animal skeleton in terms of mechanical stress, which affect bone morphology as well as the architecture and organization of the attached musculature (Biewener, 1983a). The evolution of locomotion in mammals is characterized by the use of unique step sequences (i.e., asymmetrical gaits) that do not occur in other tetrapod lineages and the regionalization of the vertebral column into thoracic and lumbar regions, the latter being an actively dorsoventral flexor of the body axis (Gambaryan, 1974; Hildebrand, 1988; Schilling and Hackert, 2006). Exploiting this innovation, mammals have developed a diversity of locomotor strategies. Locomotor variants can be associated with size, and the necessity of high speed or long distance movement, which impose particular demands on the axial and appendicular skeleton and musculature.

The diversity of locomotor styles has traditionally been divided into two principal categories: symmetrical and asymmetrical gaits, distinguished by the sequence of successive support phases.

Symmetrical gaits include sequences in which the movement of a limb of one pair (e.g., forelimb) is followed by movement of a limb of the other pair (e.g., hindlimb) and, consequently, feet of the same pair land alternatively, evenly spaced in time. Symmetrical gaits include walk, pace and trot. Asymmetrical gaits are those in which footfalls of a pair of feet are unevenly spaced in time, such as bound, half-bound, pronk and gallop. In bipedal locomotion the hindlimbs entirely support the body (Slijper, 1946; Gambaryan, 1974; Hildebrand, 1988).

Several factors can be associated with locomotor variation in mammals. For example, animals with large body mass tend to have an upright posture and more robust limbs in relation to allometric changes (Biewener, 1983a), while animals with lower body mass tend to maintain a crouched posture (e.g., Biewener, 1983b; Hildebrand, 1988). On the other hand, large mammals tend to have a more rigid and straight vertebral column to more efficiently support their body mass, which in turn limits their locomotor repertoire (Slijper, 1946; Hildebrand, 1988; Biewener, 1983a,b; Schilling and Hackert, 2006). Home range and speed represent other dimensions of the diversity of locomotion, and are also related to the ecological requirements of each species. Many small mammals, which exploit resources that are little spread in space, have smaller home ranges (Gregory, 1912; Janis and Wilhelm, 1993;

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Johnson et al., 2000). Speed can be associated with the hunting strategy of predators or, conversely, with the predation avoiding strategies of prey, or simply with the style of locomotion inherent to each organism (Garland et al., 1988; Hildebrand, 1988; Garland and Janis, 1993; Janis and Wilhelm, 1993; Christiansen, 2002).

This information has been summarized in broad categories that allow grouping of taxa with similar features (see Carrano, 1999). For example, “cursorial” is widely used to describe animals that frequently travel far or fast on the ground and, in turn, these species are frequently associated with open environments (Gregory, 1912; Djawdan and Garland, 1988; Hildebrand, 1988; Andersson, 2004). Some researchers (e.g., Maynard Smith and Savage, 1956) had included to this classical definition a suite of qualitative and quantitative morphological parameters, such as the position of muscle attachments and limb proportions. On the other hand, other workers (e.g., Stein and Casinos, 1997 and references therein) prefer a biomechanical definition of cursoriality which defines cursorial mammals as those terrestrial quadrupeds that possess vertically oriented limbs which move in a parasagittal plane. The traditional definition of locomotor categories has neglected, to a great extent, the inclusion of gaits. A categorization based on gaits would allow constructing a universal classification system of mammals and potentially would be very informative and useful for explaining morphological changes (Gambaryan, 1974). Since one of the major milestones in the evolution of mammalian locomotion was the acquisition of asymmetrical gaits, the inclusion of gait sequences in these definitions could be quite helpful.

Keeping in mind the influence of locomotion on hindlimb morphology and the necessity of taking into account such an important locomotor aspect as the gait used by a mammal, we present here an analysis of the morphological diversity of several elements of the mammalian lumbar spine, pelvis and hindlimbs in relation to locomotion and other potential explanatory variables such as body size and phylogeny. Our working hypotheses are: (1) The morphology of the lumbar spine, pelvis and hindlimbs are associated with locomotor variables, phylogeny and/or body size. (2) Species with asymmetrical locomotor styles, especially in agile and smaller saltatorial animals and bounders, possess distinctive features of the lumbar vertebrae such as developed areas of attachment of flexor–extensor musculature and low mechanical interference between consecutive processes. (3) In bipedal bounders and cursorial species in which hindlimbs are the only or enhanced propulsors, the pelvis and hindlimb elements show larger attachment areas and mechanical advantage of principal propulsor musculature, and restrictions to the parasagittal plane. Additionally to hypotheses (2) and (3), we claim that slower runners, especially ambulatory trotters, show features linked to weak dorsoventral axial mobility, low restriction to parasagittal movements in hindlimbs and weak development of principal propulsor muscles.

Our first goal was to analyze the shape variation of some axial, pelvic and hindlimb elements and their relationship with locomotor variables, taking into account the phylogenetic structure of our datasets. In addition, a second goal was to formulate a locomotor classification system based on sequences of steps, an issue so far poorly explored, that can be used as a framework for the study of the postcranial shape variation and the evolution of mammalian locomotion.

## 2. Materials and methods

We analyzed 123 specimens representative of 58 species belonging to 25 families and 9 mammalian orders (Table 1; for a detailed list of specimens and collections whence they were obtained see Table S1 in the supplementary online Appendix A).

We included a wide sample of taxa ranging from small to moderate size (from 0.04 to 62 kg), including clades that span diverse locomotor habits. A body size around 50 kg is a ‘smaller mammal’ (Christiansen, 1999). Within this size range, the skeleton is not subject to strong allometric effects, which occur above 100 kg (Bertram and Biewener, 1990; Christiansen, 1999). Exclusion of larger mammals (i.e., ungulates) was motivated by the fact that these species display very different locomotor strategies and morphologies than those presented by small to medium-sized mammals (Slijper, 1946; Biewener, 1983a,b). Exclusion of groups and species that are highly specialized for using certain substrates (e.g., primates, xenarthrans) was motivated by the fact that their locomotory diversity is low and their morphology is strongly modified, which can make comparisons difficult. The sample design involved species of different lineages within each locomotor category in order to ensure the recovering of morphological convergences.

Shape variation was analyzed using geometric morphometric techniques. Two-dimensional coordinates were captured from digital images. We used both landmarks (types I and II, considered as homologous anatomical points; Bookstein, 1991) and semi-landmarks (or type III landmarks, delimiting homologous curves; Bookstein, 1991) (Fig. 1). We analyzed one view of the following postcranial elements: dorsal view of the penultimate lumbar vertebra (13 landmarks, 5 semi-landmarks; Fig. 1A); lateral view of the ischium–pubis plane (12 landmarks, 9 semi-landmarks; Fig. 1B); posterior view of the proximal femur (7 landmarks, 17 semi-landmarks; Fig. 1C); and proximal view of the tibia (9 landmarks, 16 semi-landmarks; Fig. 1D). The selection of views for analysis was focused on the inclusion of major muscular attachment areas (e.g., for epaxial, hypaxial, gluteal and hamstring muscular groups) and articular regions that are active during locomotion; we also attempted to avoid elements that are frequently missing from collections and the fossil record. We analyzed the penultimate element of the lumbar region instead of the last one because in the latter, the development of the transverse process is limited to the space left by the iliac wings.

The digitalization of landmarks and semi-landmarks was performed using the software tpsDig 2.16 (Rohlf, 2010). To remove differences in location, orientation, and scaling (i.e., non-shape variation) of the landmark and semi-landmark coordinates we performed a generalized Procrustes analysis (GPA) for each element (Rohlf and Slice, 1990). We calculated the consensus shape for each species for subsequent analyses. Principal component analyses (i.e., relative warp (RW) analyses) of Procrustes aligned coordinates (those obtained after a GPA) were carried out to obtain shape variables (i.e., RWs) that could be used in comparative phylogenetic analyses (described below). These morphometric analyses were carried out using MorphoJ 1.04a (Klingenberg, 2011).

To explore the shape variation among species while taking into account differences in locomotor features, we performed between-groups principal component analyses (bgPCAs; Mitteroecker and Bookstein, 2011). Shape data are projected onto eigenvectors calculated from a matrix containing the shape variance/covariance among groups (not overall variance/covariance as in a standard PCA). This analysis was performed using the software R 2.14.1 (R Development Core Team, 2011).

To evaluate the presence of phylogenetic structure in the shape datasets, we calculated the *K* statistic proposed by Blomberg et al. (2003) for the first three relative warps (approximately 65% of total variation explained), using the Picante package for R (Kembel et al., 2010). The *K* statistic provides a measure of the strength of phylogenetic signal data; values near 0 indicate a lack of signal, values near 1 are expected if the character evolved under a Brownian motion model and values above 1 show that phylogenetically closer taxa are more similar than expected (Blomberg et al., 2003). Additionally, the aligned Procrustes coordinates of each postcranial element

**Table 1**

Data set compiled for each species, indicating numerical code used in shape analyses (n°), taxonomic group (order, family), shape analyses in which each species was included (dorsal view of penultimate lumbar vertebrae (L), lateral view of ischio-pubic plate of pelvis (P), posterior view of proximal femur (F), and proximal view of tibia (T)), body mass (BM), maximal running speed (MRS), home range (HR), locomotor type (type), and gait at fast speed (gait). For bibliographic sources see Table S2 in the supplementary online Appendix.

n°	Species		Family	Shape analyses				BM (kg)	MRS (km h <sup>-1</sup> )	HR (km <sup>2</sup> )	Type	Gait
	Scientific name	Common name		L	P	F	T					
<b>Order Rodentia</b>												
1	<i>Abrocoma cinerea</i>	Ashy chinchilla rat	Abrocomidae	x	x			0.25	?	?	?	?
2	<i>Cavia aperea</i>	Brazilian guinea pig	Caviidae	x	x	x	x	0.8	8	0.0008	Ambulatory	Bound
3	<i>Dolichotis patagonum</i>	Patagonian mara	Caviidae	x	x	x	x	12	80	1	Cursorial	Bound
4	<i>Dolichotis salinicola</i>	Chacoan mara	Caviidae		x	x		2.05	?	9.79	Cursorial	?
5	<i>Galea musteloides</i>	Yellow-toothed cavy	Caviidae	x	x	x	x	0.235	4.68	?	?	Bound
6	<i>Hydrochoerus hydrochaeris</i>	Capybara	Caviidae	x	x	x	x	48.9	12.74	0.19	Cursorial	Bound
7	<i>Microcavia australis</i>	Southern mountain cavy	Caviidae	x	x	x	x	0.38	?	0.0045	?	?
8	<i>Chinchilla brevicaudata</i>	Chinchilla	Chinchillidae	x	x	x	x	0.75	?	?	Bounder	Bound
9	<i>Lagidium viscacia</i>	Southern viscacha	Chinchillidae	x	x	x	x	2.5	?	?	Bounder	Bound
10	<i>Lagostomus maximus</i>	Plain viscacha	Chinchillidae	x	x	x	x	5.01	?	0.032	Bounder	Bound
11	<i>Cuniculus paca</i>	Lowland paca	Cuniculidae	x	x	x	x	9	?	0.034	?	Bound
12	<i>Dasyprocta azarae</i>	Azara' agouti	Dasyproctidae		x	x	x	2.5	60	0.034	Cursorial	Bound
13	<i>Dipodomys</i> sp.	Kangaroo rat	Heteromyidae	x	x	x	x	0.046	26.5	0.005	Ricochetal	Bip.hop
14	<i>Octodon degus</i>	Degu	Octodontidae			x	x	0.18	20.52	0.0071	Bounder	Bound
15	<i>Pedetes capensis</i>	Spring hare	Pedetidae	x	x	x	x	3	10.1	0.5	Bounder	Bip.hop
16	<i>Callosciurus erythraeus</i>	Palla' squirrel	Sciuridae	x	x	x	x	0.385	?	0.0097	Bounder	Bound
17	<i>Sciurus vulgaris</i>	Eurasian red squirrel	Sciuridae	x	x	x	x	0.4	20	0.075	Bounder	Bound
<b>Order Lagomorpha</b>												
18	<i>Lepus callotis</i>	White-sided jackrabbit	Leporidae	x	x	x	x	5	50	0.25	Cursorial	Gallop
19	<i>Oryctolagus cuniculus</i>	European rabbit	Leporidae	x	x	x	x	2	56	0.0136	Bounder	Bound
20	<i>Sylvilagus brasiliensis</i>	Tapeti	Leporidae	x	x	x	x	1.5	40	0.04	Bounder	Bound
<b>Order Carnivora</b>												
21	<i>Canis lupus</i>	Gray wolf	Canidae				x	35.3	67	394	Cursorial	Gallop
22	<i>Canis lupus familiaris</i>	Dog	Canidae	x	x	x	x	25	54.95	394	Cursorial	Gallop
23	<i>Chrysocyon brachyurus</i>	Maned wolf	Canidae	x	x	x	x	25	?	57	Cursorial	?
24	<i>Lycalopex culpaeus</i>	Culpeo	Canidae	x	x	x	x	15.9	?	4	Cursorial	?
25	<i>Lycalopex gymnocercus</i>	Pampas fox	Canidae	x	x	x	x	5	?	2.63	Cursorial	?
26	<i>Nyctereutes procyonoides</i>	Raccoon dog	Canidae		x	x	x	6	?	1.5	Ambulatory	Gallop
27	<i>Acinonyx jubatus</i>	Cheetah	Felidae	x	x	x	x	37.5	110	62.1	Cursorial	Gallop
28	<i>Felis catus</i>	Cat	Felidae		x	x	x	3	?	0.32	Ambulatory	Bound
29	<i>Leopardus geoffroyi</i>	Geoffroy' cat	Felidae	x	x	x	x	4.3	?	5	Ambulatory	Bound
30	<i>Leopardus pajeros</i>	Pampas cat	Felidae		x	x	x	5	?	19.47	Ambulatory	Bound
31	<i>Leopardus pardalis</i>	Ocelot	Felidae	x	x	x	x	13.55	?	26	Ambulatory	Bound
32	<i>Puma concolor</i>	Cougar	Felidae				x	59.4	?	129	Ambulatory	Bound
33	<i>Crocuta crocuta</i>	Spotted hyena	Hyaenidae	x		x	x	61.75	65	25	Cursorial	Gallop
34	<i>Hyaena hyaena</i>	Striped hyena	Hyaenidae		x		x	45	50	152.8	Cursorial	Gallop
35	<i>Proteles cristata</i>	Aardwolf	Hyaenidae				x	8.5	?	1.5	?	?
36	<i>Conepatus chinga</i>	Molina' hog-nosed skunk	Mephitidae	x	x	x	x	1.9	?	0.194	Ambulatory	Gallop
37	<i>Spilogale gracilis</i>	Western spotted skunk	Mephitidae	x	x	x	x	4.45	?	0.45	Ambulatory	Bound
38	<i>Eira barbara</i>	Tayra	Mustelidae	x	x	x	x	4.62	19.44	12.5	Ambulatory	Bound
39	<i>Galictis cuja</i>	Lesser grison	Mustelidae	x	x	x	x	1.9	?	?	Ambulatory	Bound
40	<i>Gulo gulo</i>	Wolverine	Mustelidae		x	x	x	12.7	45	405	Ambulatory	Gallop
41	<i>Lyncodon patagonicus</i>	Patagonian weasel	Mustelidae	x	x	x	x	0.225	?	?	?	?
42	<i>Meles anakuma</i>	Japanese badger	Mustelidae		x	x	x	5.1	?	1	Ambulatory	Gallop
43	<i>Meles meles</i>	Eurasian badger	Mustelidae	x	x	x	x	11.6	30	0.87	Ambulatory	Gallop
44	<i>Mellivora capensis</i>	Honey badger	Mustelidae			x	x	9	?	333	Ambulatory	Gallop
45	<i>Mustela</i> sp.	Weasel	Mustelidae	x	x	x	x	0.94	?	0.1425	Bounder	Bound
46	<i>Procyon cancrivorus</i>	Crab-eating raccoon	Procyonidae	x	x	x	x	10.1	10.91	2.87	Ambulatory	Gallop
47	<i>Civettictis civetta</i>	African civet	Viverridae	x	x	x	x	10.65	?	?	Ambulatory	Gallop

<b>Order Erinaceomorpha</b>																				
48	<i>Atelerix frontalis</i>	Southern African hedgehog	Erinaceidae	x	x	x	x	0.468	7	0.283	Ambulatory	Trot								
49	<i>Erinaceus europaeus</i>	Western European hedgehog	Erinaceidae	x	x	x	x	1.191	?	0.158	Ambulatory	Trot								
<b>Order Hyracoidea</b>																				
50	<i>Procavia capensis</i>	Rock hyrax	Procaviidae	x	x	x	x	3.1	?	0.0042	Bounder	Bound								
<b>Order Macroscelidea</b>																				
51	<i>Macroscelides proboscideus</i>	Short-eared elephant-shrew	Macroscelididae	x	x	x	x	0.04	20	0.01	Cursorial	Bound								
52	<i>Petrodromus tetradactylus</i>	Four-toed elephant-shrew	Macroscelididae	x	x	x	x	0.22	?	0.012	Cursorial	Bound								
<b>Order Peramelemorpha</b>																				
53	<i>Isodon macrourus</i>	Northern brown bandicoot	Peramelidae	x	x	x	x	1.8	14.1	0.025	Bounder	Bound								
<b>Order Dasyuromorpha</b>																				
54	<i>Dasyurus hallucatus</i>	Northern quoll	Dasyuridae	x	x	x	x	0.25	?	0.035	Ambulatory	Bound								
55	<i>Sarcophilus harrisi</i>	Tasmanian devil	Dasyuridae	x	x	x	x	6.85	10	13.3	Ambulatory	Gallop								
56	<i>Thylacinus cynocephalus</i>	Tasmanian wolf	Thylacinidae	x	x	x	x	22.5	?	60	Cursorial	Gallop								
<b>Order Diprotodontia</b>																				
57	<i>Macropus</i> sp.	Kangaroo	Macropodidae	x	x	x	x	33.5	65	2,145	Ricochetal	Bip.hop								
58	<i>Vombatus ursinus</i>	Coarse-haired wombat	Vombatidae	x	x	x	x	26	?	0.177	Ambulatory	Trot								

**Table 2**

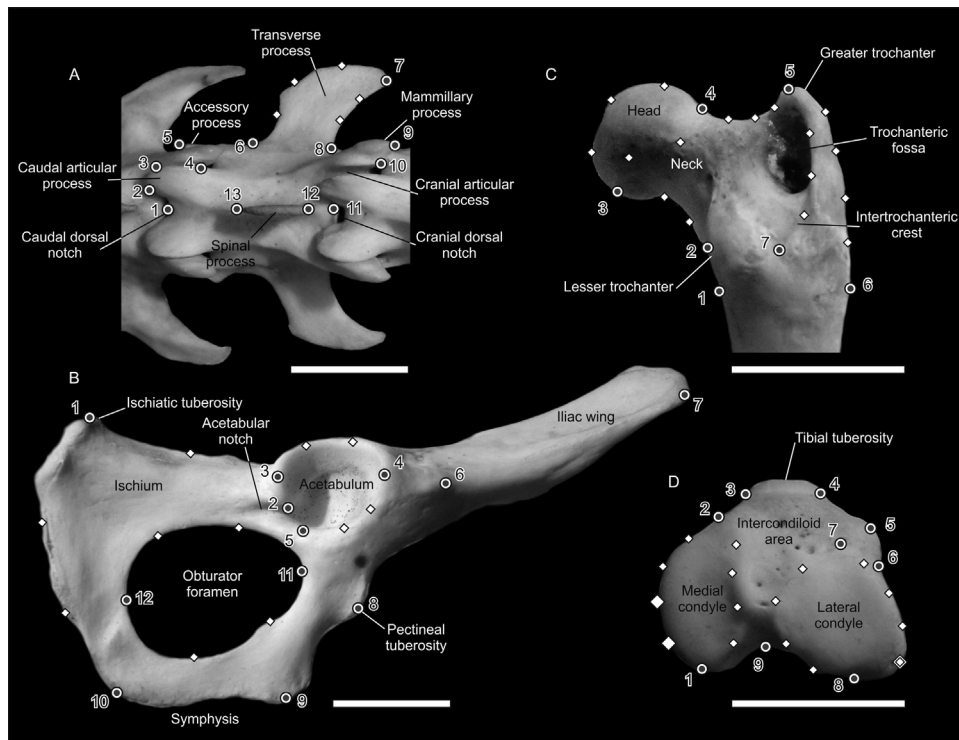
Definition of locomotor types and high-speed gait categories, based on Dagg (1973), Gambaryan (1974), Hildebrand (1988), Schutz and Guralnick (2007), Croft and Anderson (2007).

Locomotor types	
Ambulatory	Frequently uses symmetrical, economical gaits; usually moves at slow speed
Bipedal bounder	Most of the time uses exclusively hindlimbs for moving
Cursorial	Frequently travels fast and/or over long distances
Saltatorial	Frequently uses asymmetrical, energetic gaits; can reach high speeds
High-speed gaits	
Bounder	Asymmetrical gait; hindlimbs move together or nearly together, and forelimbs (together or not) participate in the locomotion
Bipedal bounder	Hindlimbs move together or nearly together, and forelimbs do not participate in locomotion
Galloper	Asymmetrical gait; right and left limbs of each pair perform different movements in a stride
Trotter	Symmetrical gait of intermediate speed; two diagonal limbs usually support the body

were optimized onto a phylogeny (see below; cf. Fig. S1 in the supplementary online Appendix A) to obtain ancestral state reconstructions with the goal of exploring the morphological evolution of the postcranium. This analysis was made using the software TNT (Goloboff et al., 2008).

The relationship between shape variation, body mass and each locomotor variable was analyzed through multivariate regressions (ordinary least squares regression model, OLS). We regarded RWs as the response variables. As explanatory variables, we used body mass, maximal running speed, home range, locomotor type, and gait at fast speed. We defined each locomotor type as a summary of the principal locomotor strategies of each species, considering speed (e.g., swifter quadrupeds were categorized as cursorial, see Section 1) and the most frequently used gaits (not necessarily the gait used at top speed; see Table 2 for a description of each locomotor type). In particular for the “cursorial” category, we preferred to use the classical definition, avoiding any biomechanical or structural implications. Thus, the variable “gait at fast speed” involves only the footfall pattern recorded for each species at high running speed (see Table 2 for a description of each gait), while the “locomotor type” variable summarizes many aspects of locomotion. The categories and values of variables for each species were obtained from the literature (Table 1; for details of the variables and bibliographic references see Table S2 in the supplementary online Appendix). In cases in which species-specific data were not available, we used data from congeneric species. In order to take into account the phylogenetic structure of the datasets, we performed phylogenetic regressions (ordinary least squares (OLS) regression of phylogenetically independent contrasts (OLS-PIC)) among the independent contrasts of each variable (i.e., shape and explanatory variables) (Felsenstein, 1985). Significant shape variation related to changes in the explanatory variables was shown as deformation grids. Before performing the regressions, we transformed the variables “locomotor type” and “gait at fast speed” into dummy variables, and the continuous variables were natural-log transformed. In those phylogenetic analyses where global shape changes were non-significantly related to any explanatory variable, but one or more local changes of shape were noted, we reanalyzed the relationship including only the subset of landmarks that represented the local changes. The threshold for *p*-values was set to 0.05 in the regressions with total shape datasets, and to 0.01 in subset analyses. These analyses were performed with the software MorphoJ (Klingenberg, 2011).

The sample size varied among different analyses according to the availability of bibliographic data and collection specimens. Each analysis required a different phylogenetic tree due to the



**Fig. 1.** Landmarks (circles) and semi-landmarks (diamonds) used to capture the shape of (A) the penultimate lumbar vertebra in dorsal view, (B) the ischio-pubic plate in lateral view, (C) the proximal femur in posterior view, and (D) the tibia in proximal view, shown on a specimen of *Galictis cuja*. Scale bars = 10 mm. Definition of landmarks: (A) penultimate lumbar vertebra: 1, maximum curvature of the caudal dorsal notch; 2–4, caudomedial, caudolateral and cranio-lateral ends of the caudal articular process; 5, tip of the accessory process; 6, 8, caudal and cranial ends of the base of the transverse process; 7, cranial extreme of the transverse process; 9, maximum projection of the mammillary process; 10, cranio-lateral end of the cranial articular process; 11, maximum curvature of the cranial dorsal notch; 12, 13, cranial and caudal ends of the dorsal margin of the spinous process. (B) Femur: 1, 6, medial and lateral projections of the diaphysis at the level of the lesser trochanter; 2, maximum medial projection of the lesser trochanter; 3, 4, ventral and dorsal limits between femoral head and neck; 5, proximal projection of the greater trochanter; 7, maximum distal projection of the intertrochanteric crest. (C) Pelvis: 1, dorsal projection of the ischial tuberosity; 2, 5, dorsal and ventral margin of the acetabular notch; 3, 4, caudal and cranial ends of the acetabulum; 6, maximum cranial projection of the tuberosity of the rectus femoris muscle; 7, maximum cranial projection of the iliac wing; 8, maximum projection of the pectineal line; 9, 10, cranial and caudal ends of the pelvic symphysis; 11, 12, cranial and caudal ends of the obturator foramen. (D) Tibia: 1, 2, caudal and cranial projections of the medial condyle; 3, 4, medial and lateral ends of the base of the tibial tuberosity; 5, maximum projection of the cranio-lateral margin of the tibia in proximal view; 6, intersection between the lateral margin of the lateral condyle and the lateral margin of the non-articular surface of the tibia in proximal view; 7, 8, cranial and caudal projections of the lateral condyle. All the landmarks used are type II landmarks (*sensu* Bookstein, 1991), except landmarks 3 and 4 of the femur, 9 and 10 of the pelvis, and 3, 4 and 6 of the tibia (type I landmarks *sensu* Bookstein, 1991).

differences in taxonomic samples among analyses. We used combined phylogenetic trees built from recently published phylogenies (Huchon and Douzery, 2001; Huchon et al., 2002; Rowe and Honeycutt, 2002; Spotorno et al., 2004; Flynn et al., 2005; Robinson and Matthee, 2005; Johnson et al., 2006; Koepfli et al., 2006, 2008; Seiffert, 2007; Beck, 2008; Bininda-Emonds et al., 2007; Sato et al., 2009; Prevosti, 2010) (Fig. 2). Because comparable branch-length data were not available for all the taxa studied, arbitrary branch lengths of 1 were set in the combined phylogenetic trees.

### 3. Results

#### 3.1. Phylogenetic signal and shape optimization

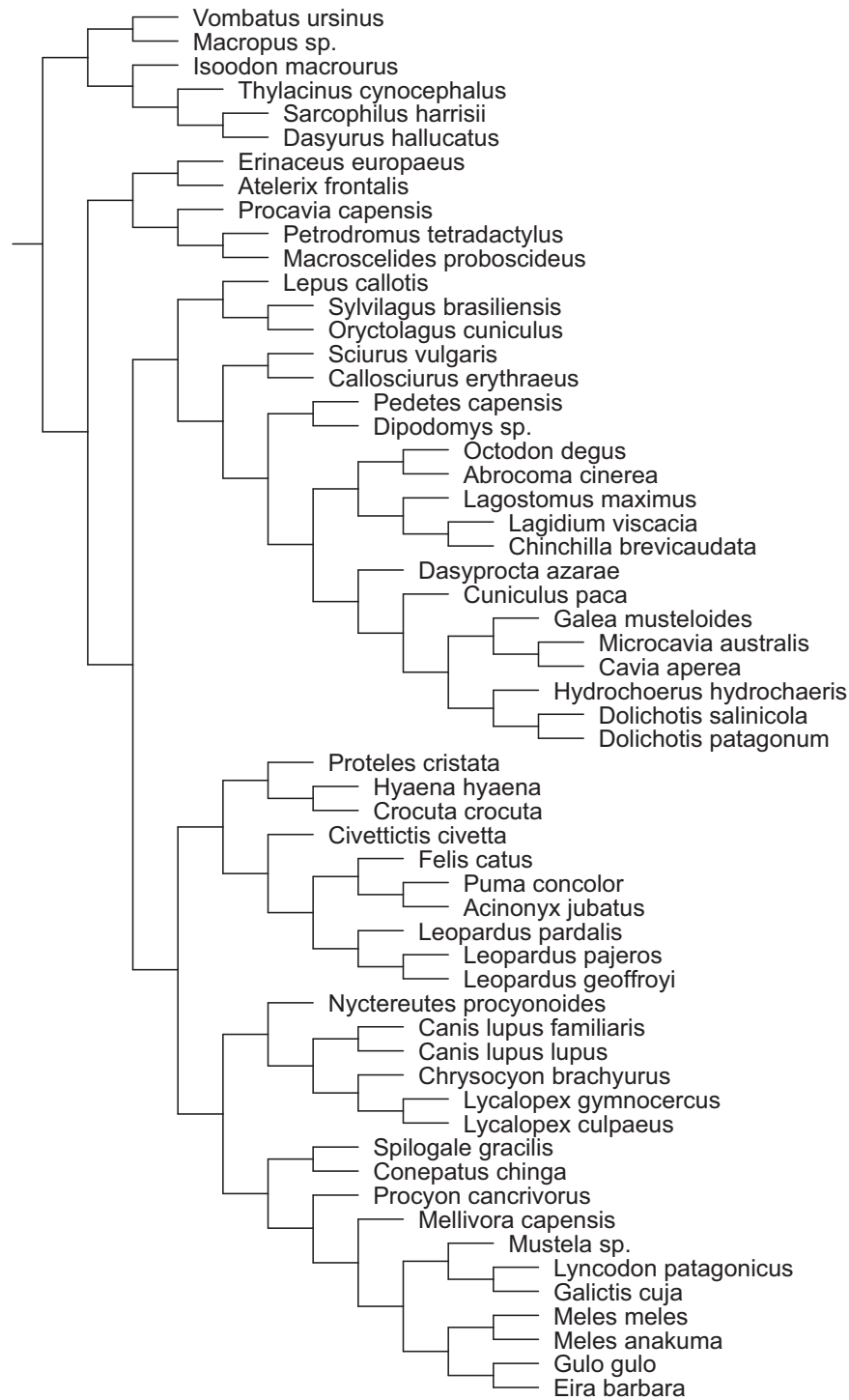
The  $K$  statistic suggested significant phylogenetic signal ( $p$ -value  $\leq 0.01$ ) for all shape axes, except the third shape axis of the pelvis.  $K$  values ranged from 0.29 to 1.5. All shape axes of the four analyzed elements showed values below 1, except the first shape axis of the proximal tibia, which showed a value near 1.5. These results were supported, to some extent, by shape optimization. For the penultimate lumbar vertebra, pelvis and femur, we observed marked shape changes among terminal nodes of the phylogeny. For the tibia, shape changes observed among the terminal nodes were similar compared with those observed in internal nodes and in the other optimizations (see supplementary online Fig. S1).

#### 3.2. Shape analyses

##### 3.2.1. Gait groups

**3.2.1.1. Penultimate lumbar vertebra.** The first two principal components of the bgPCA of gait groups explained 95.3% of the total variation among groups (Fig. 3A). Toward positive values of RW1, both transverse and spinous processes do not surpass the anterior margin of the vertebra and the cranial articular surfaces, the spinous process becomes antero-posteriorly reduced, and the accessory process also becomes reduced. Toward positive values of RW2, the cranial notch becomes wide and deeper. In the same direction, the lateral development of the transverse process decreases, the cranial articular processes are located more anteriorly, and the antero-posterior development of the dorsal margin of the spinous process increases.

**3.2.1.2. Pelvis.** The first two principal components of the bgPCA of gait groups explained 93.3% of total variation among groups (Fig. 3B). Toward positive values of RW1, the acetabulum becomes reduced, the obturator foramen and symphysis extend antero-posteriorly, the rectus femoris and pectineal tuberosities have a more anterior position, and the ischial tuberosity is located posteriorly. Toward positive values of RW2 the acetabulum is relatively larger, the symphysis is longer, the ischial tuberosity and the



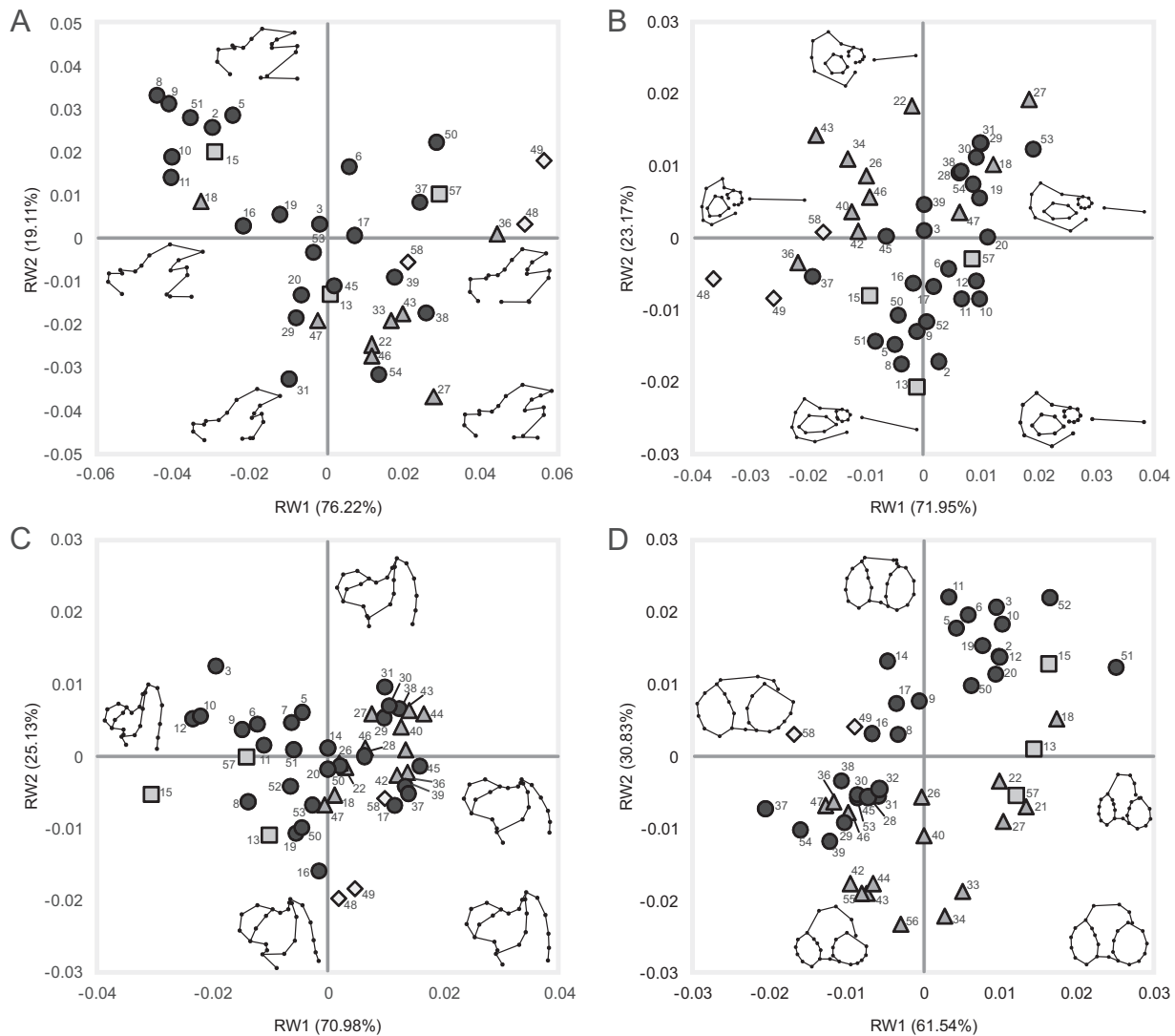
**Fig. 2.** Combined phylogenetic tree showing the relationships among the taxa included in the analyses of the present study.

posterior ramus of the ischium are expanded, and the distal end of the ilium is located dorsally.

**3.2.1.3. Femur.** The first two principal components of the bgPCA of gait groups explained 96.1% of the total variation among groups (Fig. 3C). Toward positive values of RW1, the extension of the greater trochanter is markedly reduced from a very high position to reach the same level or even lower than the femoral head and becomes narrower, the diaphysis and the neck widen, and the lesser trochanter and trochanteric fossa are oriented posteriorly. In addition, the femoral head tends to be tilted cranially. Toward positive

values of RW2, the medial projection of the lesser trochanter is reduced, the femoral neck becomes longer and more slender, the greater trochanter becomes long and its base is reduced.

**3.2.1.4. Tibia.** The first two principal components of the bgPCA of gait groups explained 92.4% of the total variation among groups (Fig. 3D). Toward positive values of RW1, the cranial intercondyloid area becomes elongated antero-posteriorly, while the caudal intercondyloid area becomes shorter. The base of the tibial tuberosity tends to reach a far anterior position and becomes narrower.



**Fig. 3.** The first two relative warps of a between-groups principal component analysis of “high-speed gait” groups regarding the (A) dorsal view of the penultimate lumbar vertebra, (B) lateral view of the ischio-pubic plate, (C) posterior view of the proximal femur, and (D) proximal view of the tibia. The percent value is the proportion of shape variation between groups explained by each axis. Wireframes represent shape changes at the extremes of each axis. The consensus shape is represented in the lower right corner. Symbols: black circles are bounders, gray squares are bipedal bounders, gray triangles are gallopers, and light gray diamonds are troppers. Numbers indicate the species as labeled in Table 1.

Just anterior to the lateral condyle, the lateral margin of the tibia is deeper, forming a well developed sulcus muscularis. Both articular condyles become reduced, narrower and positioned posteriorly. Finally, the lateral condyle widens. Toward positive values of RW2 the cranial intercondyloid area is strongly reduced, and the base of the tibial tuberosity is wide. Furthermore, the lateral margin of the tibia is deeper, forming a well developed sulcus muscularis, both articular condyles expand and become elongated antero-posteriorly, and the lateral condyle becomes narrow.

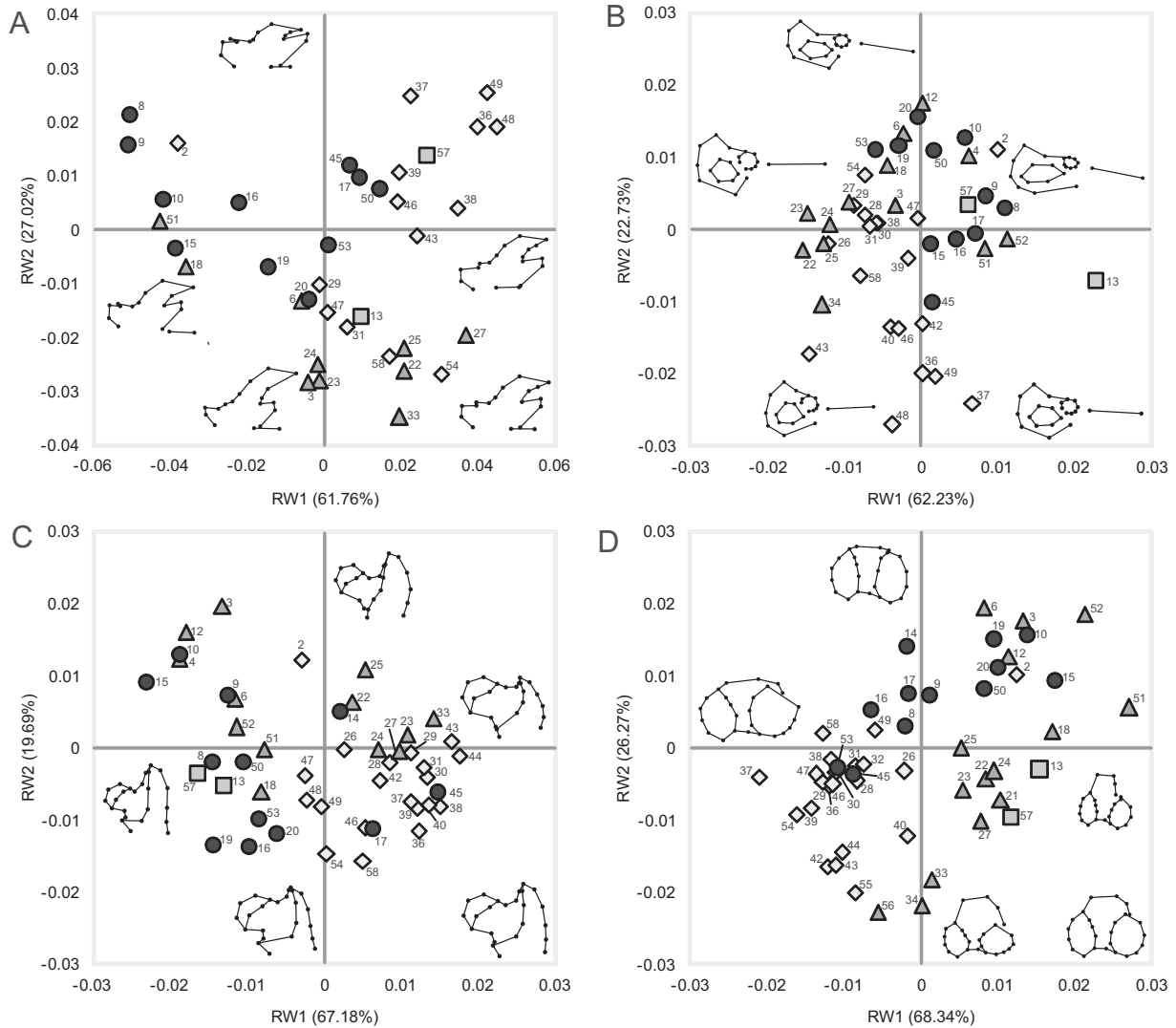
### 3.2.2. Locomotor type groups

**3.2.2.1. Penultimate lumbar vertebra.** The first two principal components of the bgPCA of locomotor type groups explained 88.76% of the total variation among groups (Fig. 4A). Toward positive values of RW1 the spinous process has a more central position with respect to the vertebral body, the accessory process is more lateralized and shorter, and the anterior projection of the transverse process is slightly reduced. Regarding RW2, from negative to positive values the shape changes involve an extreme reduction of the transverse process associated with a more posterior position of its

anterior end (without surpassing the cranial end of the vertebral body in extreme values), the accessory process is present and it is well developed (it is absent in the taxa located on negative values), and, finally, both anterior and posterior articular processes have a lateral position, and the caudal articular area widens.

**3.2.2.2. Pelvis.** The first two principal components of the bgPCA of locomotor type groups explained 84.96% of the total variation among groups (Fig. 4B). Toward positive values of RW1, the ischio-pubic complex becomes less developed dorso-ventrally and elongated backwards, the symphysis is shorter and posteriorly placed, the acetabulum is more closed, the obturator foramen becomes wider, the symphysis shorter, and the pectineal tuberosity is positioned forward. Toward positive values of RW2, the shape changes are similar to those observed on positive values of RW1 but the pelvic symphysis becomes elongated, and the pectineal tuberosity reduced.

**3.2.2.3. Femur.** The first two principal components of the bgPCA of locomotor type groups explained 86.87% of total variation among



**Fig. 4.** The first two relative warps of a between-groups principal component analysis of “locomotor type” groups regarding the (A) dorsal view of the penultimate lumbar vertebra, (B) lateral view of the ischio-pubic plate, (C) posterior view of the proximal femur, and (D) proximal view of the tibia. The percent value is the proportion of shape variation between groups explained by each axis. Wireframes represent shape changes at the extremes of each axis. The consensus shape is represented in the lower right corner. Symbols: black circles are saltatorials, gray squares are bipedal bounders, gray triangles are cursorials, and light gray diamonds are ambulatory taxa. Numbers indicate the species as labeled in Table 1.

groups (Fig. 4C). Toward positive values of RW1, the greater trochanter is shorter and does not surpass the level of the femoral head, its base becomes wider, the femoral head and its neck are massive. The trochanteric fossa becomes dorso-ventrally shorter and its lateral margin becomes laterally positioned. Toward positive values of RW2, the great trochanter becomes higher, the femoral head smaller and its neck relatively longer, and the trochanteric fossa is covered due to the medial location of its lateral margin.

**3.2.2.4. Tibia.** The first two principal components of the bgPCA of locomotor type groups explained 94.61% of the total variation among groups (Fig. 4D). The shape changes observed in this morphospace were almost identical to those observed in the gait group morphospace. From negative to positive values of RW1, the base of the tibial tuberosity reaches a forward position and becomes narrower, both articular condyles become reduced, and the sulcus muscularis more developed. The lateral condyle changes from being wider than the medial one to having similar size. On RW2, from negative to positive values, the cranial intercondyloid area is

reduced, the base of the tibial tuberosity is closer to the articular condyles, and the latter become narrower and elongated.

### 3.3. Patterns of association among postcranial shape and ecological variables

#### 3.3.1. Shape vs. body mass regressions

For all the postcranial elements analyzed, body mass explained less than 11% and 9% of the shape variation before and after taking the phylogeny into account, respectively (OLS and OLS-PIC analyses; Table 3). The relationship between pelvis and femur shape and body mass remained significant after taking the phylogeny into account (Fig. 5A and B). On the other hand, the analyses of penultimate lumbar vertebra and tibia shape showed a non-significant relationship with body mass after taking the phylogeny into account. The global shape changes of the pelvis and femur explained by body mass were minor, and similar results were obtained when local changes were analyzed after taking into account the phylogenetic structure (8%,  $p = 0.007$  and 13%,  $p = 0.002$ , respectively). In the case of the pelvis, when body mass increased, the local changes were related to a dorsally projected ischial



**Table 3**  
Percentage of shape variation explained by each explanatory variable (body mass, home range, maximal running speed, gait preferred at top speed, and locomotor type) for dorsal view of penultimate lumbar vertebra (L), lateral view of ischio-pubic plate of pelvis (P), posterior view of proximal femur (F), and proximal view of tibia (T). Bold font indicates statistically significant regressions ( $p < 0.05$ ).

Regressions	L		P		F		T	
	%	<i>p</i>	%	<i>p</i>	%	<i>p</i>	%	<i>p</i>
<b>Body mass</b>								
OLS	<b>6.91</b>	<b>0.024</b>	<b>10.86</b>	<b>0.000</b>	<b>5.78</b>	<b>0.007</b>	<b>7.92</b>	<b>0.004</b>
OLS-PIC	3.36	0.213	<b>5.50</b>	<b>0.014</b>	<b>7.23</b>	<b>0.001</b>	3.12	0.097
<b>Home range</b>								
OLS	<b>16.18</b>	<b>0.000</b>	<b>15.10</b>	<b>&lt;0.001</b>	<b>7.57</b>	<b>0.003</b>	<b>19.54</b>	<b>&lt;0.001</b>
OLS-PIC	2.21	0.598	3.85	0.114	2.89	0.250	<b>7.11</b>	<b>0.002</b>
<b>Maximal running speed</b>								
OLS	11.53	0.059	<b>14.63</b>	<b>0.004</b>	3.95	0.495	5.24	0.233
OLS-PIC	6.23	0.287	<b>10.19</b>	<b>0.044</b>	5.08	0.325	7.89	0.074
<b>High-speed gait</b>								
OLS	<b>17.04</b>	<b>0.019</b>	<b>21.92</b>	<b>&lt;0.001</b>	<b>11.16</b>	<b>0.029</b>	<b>22.22</b>	<b>&lt;0.001</b>
OLS-PIC	10.18	0.290	<b>18.55</b>	<b>0.001</b>	8.37	0.230	<b>22.02</b>	<b>&lt;0.001</b>
<b>Locomotor type</b>								
OLS	<b>20.38</b>	<b>0.002</b>	<b>13.70</b>	<b>0.009</b>	<b>14.32</b>	<b>0.001</b>	<b>28.48</b>	<b>&lt;0.001</b>
OLS-PIC	11.66	0.152	<b>19.81</b>	<b>0.000</b>	6.19	0.538	<b>18.99</b>	<b>&lt;0.001</b>

OLS, ordinary least squares regression; OLS-PIC, ordinary least squares regression of phylogenetically independent contrasts.

tuberosity and a more elongated symphysis (Fig. 5A). Regarding the femur, when mass increased, the femoral diaphysis and neck became more robust, the lesser trochanter became less medially projected, and the head dorsally oriented (Fig. 5B).

### 3.3.2. Shape vs. home range regressions

Home range explained a moderate but significant proportion of the shape variation of all elements analyzed (i.e., 7–20%) before considering the phylogenetic relationships (OLS analyses; Table 3). However, after taking into account the phylogenetic structure, the penultimate lumbar vertebra, pelvis, and femur regressions became non-significant, and the shape variation explained by home range variation decreased to 4% or less. On the other hand, the shape variation of the tibia explained by home range variation remained significant, but decreased from 19.54% to 7.11% (Table 3). Although the global shape changes of the tibia explained by home range variation were minor after considering the phylogeny, some locally marked changes were noted: when home range increased, the anterior intercondyloid area became larger with respect to the articular condyles, the base of the tibial tuberosity became narrow and forward located, and the lateral condyle reduced (Fig. 5C). When we reconstructed the phylogenetic regression including only the subset of landmarks corresponding to the local changes described above, the variation of this subset explained by the home range was 12% ( $p = 0.001$ ).

### 3.3.3. Shape vs. maximal running speed regressions

In the analyses of the penultimate lumbar vertebra, femur and tibia, the maximal running speed explained a minor amount of the shape variation (i.e., 4–11%) and the relationships were non-significant both before and after taking into account the phylogenetic structure of the datasets (Table 3). Maximal running speed explained a relatively more substantial proportion (14.63%) of shape variation in the pelvis, which decreased to 10.19%, although remaining significant, after taking the phylogeny into account (Table 3). Many changes were observed in the pelvis: the ischial tuberosity and the posterior margin of the ramus of the ischium extended posteriorly, the length of the symphysis increased, the ilium projection diminished, and the acetabular dorsal margin became flattened (Fig. 6B). Although the global shape changes of the penultimate lumbar vertebra and tibia explained by maximal running speed were few and were marginally significant or

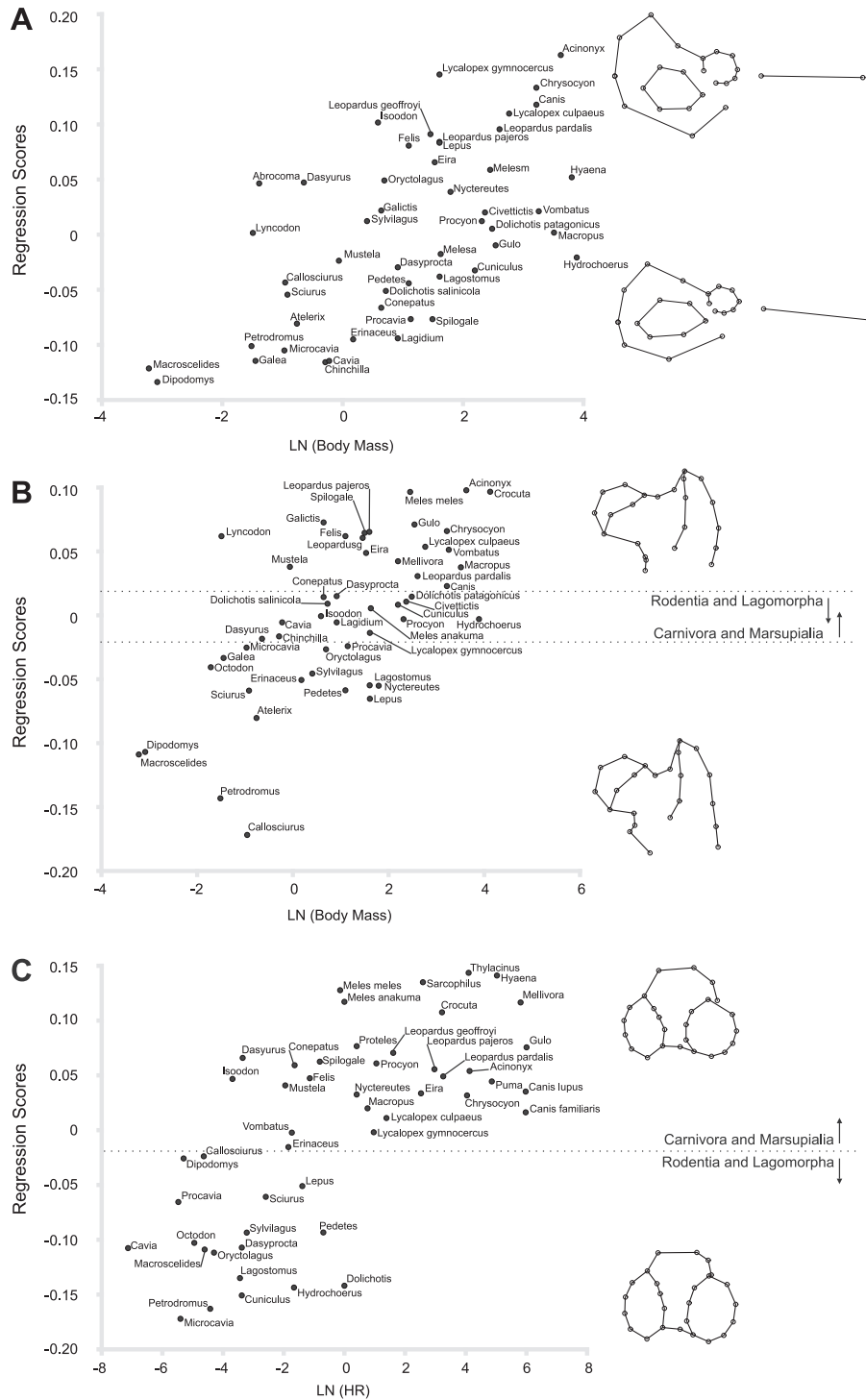
non-significant after considering the phylogeny, some marked local changes were noted. In the case of the penultimate lumbar vertebra, when speed increases, the transverse processes become more antero-laterally extended (surpassing the articular process), the anterior and posterior articular processes become more medially located and narrower, and the cranial and caudal vertebral notches become deeper (Fig. 6A). When we reconstructed the phylogenetic regression including only the subset of landmarks corresponding to the local changes described above, the variation of this subset explained by the maximal speed was about 17% and non-significant, although marginally ( $p = 0.011$ ). In the case of the shape of the tibia, when speed increases, the cranial intercondyloid area expands, the base of the tibial tuberosity achieves a forward position, the sulcus muscularis becomes deeper, and the lateral condyle becomes less antero-posteriorly elongated and more rounded (Fig. 6C). When we reconstructed the phylogenetic regression including only the subset of landmarks corresponding to the local changes described above, the variation of this subset that was explained by the top speed became marginally significant and amounted to about 14% ( $p = 0.010$ ).

### 3.3.4. Shape vs. high speed gait regressions

In all analyses, the variable high speed gait explained a significant amount of shape variation before considering the phylogenetic structure of the four datasets (Table 3). The shape variation explained by this variable was 17.04% and 11.16% in the penultimate lumbar vertebra and femur analyses, respectively, and decreased and became non-significant after taking into account the phylogenetic structure. On the other hand, in the analyses of pelvis and tibia, the amount of shape variation explained by the high speed gait variable was relatively important (approximately 20%) and remained significant before and after taking the phylogeny into account (Table 3).

### 3.3.5. Shape vs. locomotor type regressions

As in the case of the fast speed gait variable, the locomotor type variable explained a relatively important (i.e., 13–29%) and significant amount of shape variation in all analyses before considering the phylogenetic structure (Table 3). As in the fast speed gait regressions, locomotor type variation explained a relatively important (19.81% and 18.99%, respectively) and significant amount of the total shape variation after accounting for the phylogenetic



**Fig. 5.** Regression scores are the output of a multivariate regression between shape (aligned Procrustes coordinates) and log-transformed variables: (A) pelvis vs. body mass, (B) femur vs. body mass, and (C) tibia vs. home range (HR). Wireframes represent shape changes at axis extremes. Limits of distribution of some major clades discussed in the text are indicated by dashed lines.

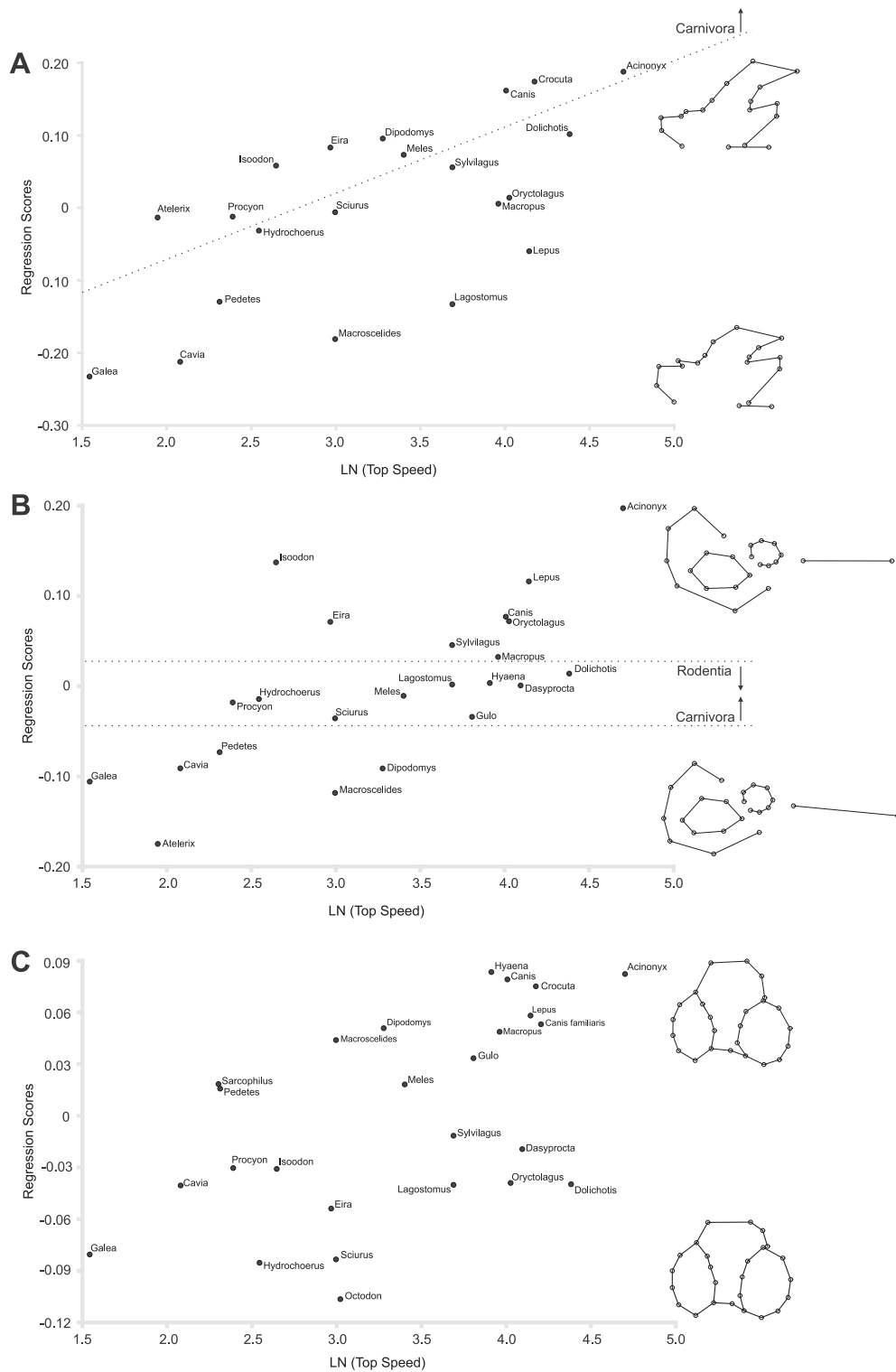
structure of the datasets (Table 3) only for the pelvis and tibia analyses. In both analyses, some locally marked changes were noted, and were similar to those described for the gait group analyses.

#### 4. Discussion

##### 4.1. Phylogenetic signal

The shape of the four postcranial elements analyzed showed significant phylogenetic signal. In most cases, the value of the

calculated *K* statistic was below 1; the first shape axis of the proximal tibia showed a value near 1.5. These results suggest that mammalian postcranial elements have evolved under some evolutionary processes that cause characters to depart from a Brownian motion model of evolution (Blomberg et al., 2003; Losos, 2008). Values for the *K* statistic higher than 1, as shown by the first axis of the tibia morphospace, would suggest stasis in character change (Losos, 2008). In the analysis of the tibia, the first axis summarizes changes related mainly to the articular condyles and the sulcus muscularis (see Fig. 6C). In contrast to other elements, the shape



**Fig. 6.** Regression scores are the output of a multivariate regression between shape (aligned Procrustes coordinates) and log-transformed maximal running speed) for the (A) penultimate lumbar vertebra, (B) pelvis, and (C) tibia. Wireframes represent shape changes at axis extremes. Limits of distribution of some major clades discussed in the text are indicated by dashed lines.

optimization of the tibia (see supplementary online Fig. S1D) shows changes among both terminal and internal nodes that are relatively subtle and similar in intensity. Many of the changes optimized among the more basal nodes occur at the articular condyles and the *sulcus muscularis*, coinciding with the high  $K$  value of the first shape axis of this bone (e.g., nodes: Caniformia, Feliformia, Marsupialia, Glires, Cavoidea). On the other hand, terminals tend to

show more changes of the tibial tuberosity (the principal muscular attachment area of the view). The optimization of other elements suggests that changes among terminals are typically more marked than those observed among internal nodes. These results suggest that muscular attachment areas are less conserved than articular. The influence of phylogenetic structure on the morphological variation of postcranial elements was evident in the ordination of species

**Table 4**

Principal traits and related functions discussed for each postcranial element analyzed. Bibliographic sources for the penultimate lumbar vertebra: Slijper, 1946; Gambaryan, 1974; Alexander and Jayes, 1981; Sargis, 2002; Salesa et al., 2008; for the femur: Maynard Smith and Savage, 1956; Gambaryan, 1974; Hildebrand, 1977, 1988; Jenkins and Camazine, 1977; García-Esponda and Candela, 2010; for the pelvis: Taylor, 1976; Evans, 1993; Argot, 2002; Heinrich and Houde, 2006; Fisher et al., 2008; for the tibia: Haines, 1942; Spoor and Badoux, 1989; Wang, 1993; Sargis, 2002; Williams et al., 2008; Hunt, 2009.

Feature	Function
<b>Penultimate lumbar vertebra</b>	
1L Lateral development of the transverse processes	Increase of the areas of origin and insertion of the bundles of lumbar flexors and extensors (e.g., m. quadratus lumborum and m. sacrospinalis)
2L Anteriorly directed tips of the transverse processes	Greater muscular mass and increase of the mechanical advantage for ventral flexion of the spine
3L Deeper cranial and caudal notches	Greater flexion and extension movements between vertebral joints
4L Sharp transverse processes	Avoid mechanical interferences and promote lateral flexion
5L Posteriorly located spinous processes	Avoid mechanical interferences and allow flexion and rotation
6L Wide and flat transverse processes, especially at their lateral margins	Increase surface area for ligament attachment, and reduce lateral and rotational movements
7L Spinous processes robust and forward-directed	Increase surface area for ligament attachment, and reduce flexion–extension and rotational movements
<b>Pelvis</b>	
1P Elongated ischium	Increase of the mass and the mechanical advantage of the hamstring group (strong hip extensors) and some other extensor muscles
2P Elongated pubic symphysis	Increase of the mass and the mechanical advantage of adductors and stabilizers of the hip
3P Well-developed pectineal line	Increase of the mass and the mechanical advantage of short adductors
4P Elongated ilium	Increase of the mass and the mechanical advantage of knee extensor and gluteal group (weak hip extensor musculature, secondarily abductor)
5P Closed acetabulum	Mechanical stabilization of the hip joint
<b>Femur</b>	
1F Strong development of the greater trochanter and the trochanteric fossa	Increase of the insertion area and mechanical advantage of the gluteal muscle group and other extensors and abductors of the hip
2F Reduced or caudally oriented lesser trochanter	Lesser importance of the iliopsoas muscle group
<b>Tibia</b>	
1T Anteriorly located base of the tibial tuberosity	Strong mechanical advantage for m. quadriceps femoris at extended position of the knee
2T Wide cranial intercondyloid area	Stabilization and prevention of over-extension of the knee
3T Deeper sulcus muscularis	Strongly developed m. extensor digitorum longus
4T Antero-posteriorly elongated condyles	Wide range of flexion and extension of the knee
5T Wide lateral condyle	Higher mass support in the lateral condyle than in the medial one
6T Narrow tibial tuberosity	Some degree of restriction of movement to the parasagittal plane

in all analyses: rodents and macroscelideans were always grouped together in the morphospaces of all elements and in both gait and locomotor type analyses. Lagomorphs and sciurids were situated at times close to the above-mentioned groups and in other analyses they occupied intermediate positions between the former groups and carnivores and marsupials. All these taxa were always separated from carnivores, marsupials and hedgehogs (Figs. 3 and 4). Similar ordination patterns for these clades have already been described in previous works (e.g., Gambaryan, 1974; Seckel and Janis, 2008).

## 4.2. Shape and function

### 4.2.1. Penultimate lumbar vertebra

Only some features of the penultimate lumbar vertebra were associated with maximal running speed (as expected – see hypothesis 2). Many swift mammals employ marked flexion and extension movements of the spine during fast asymmetrical gaits (Slijper, 1946; Hildebrand, 1961, 1988; Gambaryan, 1974; Spoor and Badoux, 1988) using the vertebral column as an active propeller during the supporting phase, and to increase stride length and the distance that the body moves forward while it is unsupported during the swing phase (Hildebrand, 1988). In swifter taxa (*Dolichotis*, *Lepus*, *Crocota* and *Acinonyx*; Fig. 6A) the lumbar vertebrae have laterally developed transverse processes with anteriorly directed tips and deeper cranial and caudal notches (Table 4: 1L, 2L, 3L). These features allow an increase of the areas of attachment and of the mechanical advantage of lumbar flexors and extensors (e.g., quadratus lumborum and sacrospinalis muscles; Slijper, 1946; Gambaryan, 1974; Alexander and Jayes, 1981) which, in turn, enable greater flexion and extension movements of the spine. An interesting fact is the presence of marked differences between swift

carnivores and the remaining swift mammals (i.e., caviomorphs and lagomorphs). In carnivores, the shape of both the transverse and spinous processes (Table 4: 4L, 5L) avoids mechanical interferences and promotes lateral flexion and rotation (Gambaryan, 1974; Salesa et al., 2008). On the other hand, the lumbar vertebrae of caviomorphs and lagomorphs bear wide and flat transverse processes, especially at their lateral margins (Table 4: 6L), and spinous processes that are robust and forward-directed (Table 4: 7L). These features reduce the range of movements and could be related to an increased elastic storage of energy in ligaments (especially in caviomorphs; see Gambaryan, 1974; Biewener and Blickhan, 1988). In contrast, slow runners have relatively reduced spinous and transverse processes and wide articular processes, which suggest little lumbar mobility. Again, different phylogenetic groups showed different morphological features: carnivores and hedgehogs on the one hand, and rodents (some caviids and *Pedetes*) on the other hand (Fig. 6A).

### 4.2.2. Pelvis

In the body mass analysis, larger taxa showed an elongated ischium and pubic symphysis compared to the ilium and acetabulum (Fig. 4A). The presence of allometric trends is a common pattern within mammals that span a wide range of sizes (Gasc, 2001). When body mass increases, the musculo-skeletal system that supports the body has to increase in greater proportion to sustain the same strength (Hildebrand, 1988). The pelvic shape changes observed in larger taxa would suggest non-isometric shifts of some muscular groups (Table 4: 1P, 2P) which in turn provide the necessary powerful stabilization of the pelvis and propulsion of the body.

Focusing on maximal running speed, the slower taxa (all of them ambulatory and saltatorial species), which include many rodents, some mustelids, *Atelerix*, *Isoodon*, *Macroscelides* and

*Procyon*, showed a wide range of shapes (Figs. 4B and 6B), from extremely short ischium and symphysis, and elongated ilium (e.g., *Aterix*) to extremely well developed ischium and symphysis, and reduced ilium (e.g., *Isoodon*). This great variation could be related to other variables, such as phylogeny and gaits, or simply to a lack of selection. The pelvic shapes exhibited by species able to reach higher maximal running speeds converge to a more restricted range of shapes (Figs. 4B and 6B). Although they belong to different clades and locomotor groups, they share an elongated ischium and symphysis (Table 4: 1P, 2P) that can be related to the capability of reaching higher running speeds and to the necessary high power output to accelerate and to control direction (Table 4: 1P; Williams et al., 2007). *Acinonyx* takes this form–function relationship to the extreme (Fig. 6B). This pattern, in which the relationship between shape and speed was strong only at higher speeds, highlights how informative the pelvic shape is, even beyond the non-significant relationship considering the whole range.

In the gait type analysis, the bipedal bounder and bounder species, such as *Procyon*, macroscelideans and rodents, share an elongated ilium and ischium and a well-developed pectineal line (Fig. 3B and Table 4: 1P, 3P, 4P) that can be related to the great amount of energy needed at the hip and knee joint for supporting and moving the body upward with the hindlimbs pushing together during the propulsive phase of bounding gaits (Maynard Smith and Savage, 1956; Gambaryan, 1974; Hildebrand, 1977, 1988; García-Esponda and Candela, 2010). Another trait is the presence of a moderated or elongated symphysis which, along with a well developed pectineal tuberosity (Table 4: 2P, 3P), can be related to a marked extension and stabilization of the hip during bounds and rapid changes of direction in running (Williams et al., 2007). Furthermore, an elongated symphysis could assist in the resistance against the strain on the pelvis induced by the impact after each footfall. Lastly, a closed acetabulum (Table 4: 5P) suggests mechanical stabilization of the hip during hopping (Jenkins and Camazine, 1977; Polly, 2007). Carnivoran, marsupial and lagomorph bounders, together with bipedal bounders, showed less marked adaptations to jumping than rodents of the same gait group (Fig. 3B). Gallopers (*Lepus* and some carnivores) share a relatively open acetabulum and weak pectineal tuberosity (similar to trotters; Fig. 3B, Table 4: opposed to 3P, 5P) that may be related to the wide range and independent excursion of the limbs relative to the hip required in gallop (compared with bound). Furthermore, muscular or mechanical stabilization is less necessary because the gallop is a more stable gait than the bound, due to the higher number of independent footfalls at each strike (Van de Graaff et al., 1982; Hildebrand, 1988), resulting in reduced strain on bones (Gambaryan, 1974; Jenkins and Camazine, 1977). However, the more agile galloper species (e.g., *Lepus*, *Acinonyx*) shared features (Table 4: 1P, 2P, opposed to 4P) similar to those of the bounders. This convergence is due to the fact that these mammals run with marked changes of direction and acceleration and frequently use bounding gaits (Hildebrand, 1961; Williams et al., 2007), in the same way as bounders. Trotters such as hedgehogs and *Vombatus* showed an extremely reduced symphysis and ischium body, high ischio–pubic complex, open acetabulum, elongated ilium, and forward-directed ischial tuberosity (Fig. 3B and Table 4: 4P, opposed to 1P, 2P, 5P). These traits are associated with the presence of rapid but weak hip extensor and abductor muscles and an increase of the speed of movement generated by the latter muscular groups, since slow running diminishes the need for strong hip stabilization (Jenkins and Camazine, 1977).

In the locomotor type analysis, the saltatorial taxa and bipedal bounders were grouped together and their space was shared by some cursorial and ambulatory taxa that bound at speed (e.g., *Dasyurus*, *Eira*, *Galictis*, feliforms, some caviomorphs and macroscelideans). Similarly to the shape changes observed for

bounders in the gait analysis, the shape that characterizes saltatorial taxa (e.g., elongated ilium and ischio–pubic complex; Fig. 3B and Table 4: 1P, 2P, 4P) is linked to strong propulsion of the body and stabilization of the hip (Maynard Smith and Savage, 1956; Jenkins and Camazine, 1977). Cursorials showed a disjunct distribution: those that use gallops at top speed (carnivorans) clustered with ambulatory species, while those cursorials that use bound or half-bound at top speed (many caviomorphs and macroscelideans) clustered with saltatorials or bipedal bounders (Fig. 4B), showing different kinds of cursorial adaptations and capabilities. However, all these species share some features (e.g., elongated ilium, wide vertical ramus of the ischium, and a reduced pectineal tuberosity; Table 4: 1P, 2P, 4P, opposed to 3P), many of them linked with both rapid and powerful hip extensor muscles that provide the possibility of reaching and sustaining fast running. Most ambulatory species were grouped together (Fig. 4B), showing an open acetabulum, moderate to short symphysis and ischio–pubic complex, and a moderate to elongated ilium (Table 4: 4P, opposed to 1P, 2P, 5P). These traits suggest a generalized condition with moderate or weak propulsion of the hindlimbs and a wide range of possible movements of the hip. As in the penultimate lumbar vertebra analysis, skunks and hedgehogs also converged in a pelvic shape that suggests weak and ample movements at the hip.

#### 4.2.3. Femur

The shape changes of the femur related to body mass were mostly subtle (Fig. 5B). Larger taxa showed a major development of the greater trochanter and the trochanteric fossa (Table 4: 1F) in association with an increase of muscular mass and mechanical advantage of hip extensor and abductor muscles (Evans, 1993; Argot, 2002; Fisher et al., 2008). These traits together with the more robust femoral neck, also observed in larger taxa, might be a response to the requirements imposed by the increase of body mass (Hildebrand, 1988), as was also inferred in the analysis of the pelvis. The reduction and/or caudal orientation of the lesser trochanter (Table 4: 2F) in larger forms suggest restricted rotation and movements out of the parasagittal plane (Taylor, 1976; Argot, 2002; Heinrich and Houde, 2006).

In contrast to many other studies and contrary to what we expected (hypothesis 3), locomotion variables were not significantly related to the shape variation of the femur (Table 3). Supporting this, the principal component analyses (Figs. 3 and 4) showed a wide superposition of locomotor groups. Some authors (e.g., Elissamburu and Vizcaino, 2004; Croft and Anderson, 2007; Osbahr et al., 2009; García-Esponda and Candela, 2010), through different methods, established a functional relationship between the shape of the proximal femur and speed. In our study, phylogeny seems to be a more important factor for understanding the shape variation of the proximal femur than other factors, even speed or cursoriality. This discrepancy might be due to differences in sample size. The pattern observed within a wide taxonomic range as shown here does not exclude the possibility that within some specific clades or functional groups the relation between these variables and femur shape variation may be significant.

#### 4.2.4. Tibia

In the home range analysis, all the taxa with wider home ranges were carnivores and dasyuromorphs of medium or large size, including most canids, felids, large mustelids, hyaenids, *Sarcophilus* and *Thylacinus*. Features observed in these taxa (e.g., wide cranial intercondyloid area and anteriorly located base of the tibial tuberosity; Fig. 5C and Table 4: 1T, 2T) allow strong extension of the knee when the hindlimb is extended. This feature seems to be emphasized in cursorial species that travel long distances and use economical gaits.

In maximal running speed analysis, swifter taxa, including many rodents, lagomorphs, canids, felids, hyaenids, *Macropus* and *Gulo*, shared a moderately to highly anterior location of the tibial tuberosity (Fig. 6C). As mentioned above (Table 4: 1T), this favors strong extension of the knee and promotes the propulsion and acceleration of the body. However, swifter taxa display a wide shape variation. Within the faster taxa, some caviomorphs and lagomorphs share a moderately anterior location of the tibial tuberosity (Fig. 6C). This feature may be related to the locomotion styles preferred by these lineages, including bound and half-bound gaits with more crouched postures in which sustaining an extended position of the knee plays a minor role during propulsion (Gambaryan, 1974). A typical but not exclusive feature of swifter taxa (e.g., caviomorphs, lagomorphs, felids, canids) is the presence of a deeper sulcus muscularis protecting the extensor digitorum longus muscle (Wang, 1993; Table 4: 3T), possibly in relation to the use of gaits with strong flexion and extension of the knee such as bound and swifter half-bound and gallop. Some traits that differentiate *Gulo* and hyaenids (Table 4: 2T, absence of the sulcus muscularis) may provide stabilization and prevent over-extension of the knee (Haines, 1942). Slower taxa showed features converse to those exhibited by swift taxa, but at the same time were differentiated by locomotor styles and phylogenetic affinities (Fig. 6C).

In the gait analysis, bounders showed a wide range of shapes. Many rodents, lagomorphs, and macroscelideans share many traits (Table 4: 4T, opposed to 1T, sub-equally sized articular condyles; Fig. 3D) related to a typically crouched posture. On the other hand, carnivorous bounders showed other traits (e.g., rounded condyles and a wide lateral one; Table 4: 1T, 5T) that suggest a more extended habitual posture (Sargis, 2002; Williams et al., 2008; Hunt, 2009). A wide lateral condyle might be related to the importance of the transmission of body mass to the lateral condyle and the degree of fusion between tibia and fibula. Conversely, in many rodents, lagomorphs and macroscelideans, the fibula and tibia are fused at the level of the medial shaft, as an adaptation to swift jumps, while this does not occur in carnivores (Barnett and Napier, 1953; Hildebrand, 1988). Many gallopers, including canids, hyaenids, some larger dasyuromorphs (*Sarcophilus* and *Thylacinus*), *Acinonyx*, *Lepus*, and larger mustelids (*Gulo*, *Meles* and *Mellivora*), shared traits (Table 4: 1T, 2T, 6T; Fig. 3D) that relate to parasagittal movements and attainment of an extended position of the knee. On the other hand, *Conepatus*, *Civettictis*, and *Procyon* showed a more generalized shape of the tibia, which may be related to the infrequent use of galloping in the first two taxa, and arboreal adaptations in the latter one (Azara, 1802; Cabrera and Yepes, 1940; Ewer and Wemmer, 1974; Taylor, 1976). Hyaenids, *Meles*, *Mellivora*, *Sarcophilus*, and *Thylacinus* shared features (Table 4: 2T, 5T, absence or reduction of the sulcus muscularis) related with the enhancement of the weight support function over speed and range of movements at the knee, resulting in moderate or slower running. These features might be magnified in species in which hindlimb support is enhanced by different factors: forelimb digging (*Meles* and *Mellivora*; Heptner and Naumov, 1967; Van de Graaff et al., 1982), transportation of large prey (hyaenids; Spoor and Belterman, 1986; Turner and Antón, 1996), or phylogeny (Ercoli et al., 2012).

Finally, trotters, represented by *Erinaceus* and *Vombatus*, had a morphology similar to that of the more generalized bounders and gallopers (e.g., sciurids; Fig. 3D). They present a posteriorly located tibial tuberosity, rounded condyles, a wide lateral one, and absence of the sulcus muscularis. These traits might be related to a crouched habitual posture with limited flexion and extension movements, and a wide range of movements outside of the parasagittal plane (Argot, 2002; Sargis, 2002). These features are compatible with trotting, but they do not represent a requirement since many other mammals can trot at intermediate speed without possessing these features.

In the locomotor type analysis, the distribution of species in the morphospace was very similar to the one observed in the gait analysis (Figs. 3D and 4D). The saltatorials showed a wide distribution in the morphospace and shared traits (e.g., Table 4: opposed to 1T) and related functions similar to those described for bounders in the gait analysis. In the same way, the distribution of cursorial species was very similar to the one described for gallopers, due to the fact that many cursorials are also gallopers (canids, felids, hyaenids, and *Thylacinus*). However, cursorials that use bounding gaits when running at top speed (cavioids and macroscelideans) together with bipedal bounders were located close to, or overlapping with, saltatorials (Fig. 4D). They shared features that suggest rapid and wide-range flexion and extension of the knee, and, as in other cursorial species, powerful extension of the limb at an extended posture (Sargis, 2002; Williams et al., 2008; Hunt, 2009). Most ambulatory mammals shared rounded and antero-posteriorly short condyles, with a more or less ample lateral condyle, and a reduced or absent sulcus muscularis (Fig. 4D), in association with a wide range of movements out of the parasagittal plane.

#### 4.3. Evolutionary trends in mammalian locomotion

We were able to distinguish, in part, the major taxonomic locomotor groups proposed by Gambaryan (1974): carnivores and sciurids, other rodents such as caviomorphs, and lagomorphs.

Morphological traits that characterize macroscelideans, caviomorphs, and some other rodents (see supplementary online Fig. S1) are related to relatively rigid backs, wide flexion–extension on the parasagittal plane of the knee, and a typically crouched posture of the hindlimb. Lagomorphs are similar but with a more mobile (semi-rigid) back and with strong lumbar flexion that is marked in *Lepus* (see also Williams et al., 2007). It has been proposed that this might be an adaptation to avoiding obstacles, asymmetrical gaits, and to jumping on rocks and other discontinuous substrates (Gambaryan, 1974; Hildebrand, 1977; Seckel and Janis, 2008), and, in particular for lagomorphs, for landing in small areas (Gambaryan, 1974).

Carnivores, hedgehogs and marsupials showed a very wide range of functional adaptations. Lumbar mobility and strength range from reduced to very high (from mephitids and hedgehogs to some canids and felids) and there exists a wide variation in the strength of the proximal hindlimb musculature. Carnivores, hedgehogs and marsupials have an adaptive history more linked to symmetrical gaits at low to moderate speeds, selecting gallops or secondarily bounding gaits (for carnivores and marsupials) at higher speeds (Dagg, 1973; Hildebrand, 1977, 1988). The relative high mobility of the hindlimbs outside of the parasagittal plane observed in hedgehogs, and in some marsupials and carnivores, was also observed in scansorial rodents such as sciurids, and is associated with a well developed fibula and considered an adaptation to discontinuous substrates, but may also represent the retention of a primitive condition in some cases (Barnett and Napier, 1953; Hildebrand, 1988; Argot, 2002).

Furthermore, some cases of convergence between species belonging to different lineages but with similar functional demands must be emphasized. Many cursorial species that are not close phylogenetically, such as some caviomorphs, *Lepus*, *Thylacinus*, canids, hyaenids, and felids, share many convergent features (see supplementary online Fig. S1) which have frequently been mentioned in the literature (e.g., restrictions to the parasagittal plane, an extended posture, and powerful proximal hindlimb musculature) (Maynard Smith and Savage, 1956; Gambaryan, 1974; Hildebrand, 1988; Garland and Janis, 1993). It is necessary to point out that the penultimate lumbar vertebra and femur retain many features linked with phylogeny, suggesting different evolutionary ways to reach sustained or swift locomotion. Skunks and hedgehogs, and

secondarily *Vombatus*, which present extremely slow running and trot as preferred or exclusive swifter gait, showed many convergent features in all analyzed elements (see supplementary online Fig. S1), including indicators of weak musculature and/or mobility of the penultimate lumbar vertebra (for a review see Slijper, 1946), weak development of the hamstring and adductor of the hip, and a wide range of hindlimb movements outside of the parasagittal plane. These traits are related to the fact that these species do not need to pursue their prey and present alternative defensive strategies instead of swift running (Azara, 1802; Nowak, 1991; Caro, 2009).

#### 4.4. Conclusions

In the present study we were able to identify both overall and local shape changes of several postcranial elements. In addition, the inclusion of several potentially explanatory variables allowed us to take a broader view of the interaction between shape and key ecological factors. The gait-based classification proposed in this study led to a locomotor group segregation as clear as that obtained with the traditional classification scheme. Studies that delve into the performance of both schemes are pending. Our results highlight the importance of phylogenetic control, given the marked differences in the results obtained before and after taking into account the phylogenetic structure of the data.

Body mass was, in some cases, a significant factor for explaining shape variation. When allometric relationships are significant, it is crucial to identify associated shape changes because they could mask purely morpho-functional relationships. Among the elements analyzed here, the penultimate lumbar vertebra and the tibia showed a non-significant relationship with body mass; thus it might be advisable to preferably use those two elements in morpho-functional analyses.

The significance and intensity of the relationship between shape and each locomotor variable was very variable among the different elements studied. Phylogenetic and allometric interference can make it difficult to establish a simple or direct morpho-functional relationship. Our results suggest that the studied postcranial elements might be relevant when studying these variables in fossil or extant taxa with poorly known ecological traits.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.zool.2013.08.007>.

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