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Form and function within a phylogenetic framework: locomotory habits of extant predators and some Miocene Sparassodonta (Metatheria)

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In this study, we analysed locomotory habits in extant predators and Sparassodonta species through geometric morphometric techniques and discriminant analyses of the distal humerus in anterior view, proximal ulna in lateral view, and tibia in proximal view. We included a wide sample of extant predators, and considered the phylogenetic and allometric structure in the data sets. We also included some Sparassodonta, a group of carnivorous metatherians that inhabited South America during the Cenozoic, and inferred their locomotory habits. Results suggest the presence of a close relationship between shape and locomotory habits, even after removing the shape component explained by phylogeny in the three postcranial elements. Terrestrial habits were inferred for *Arctodictis sinclairi*, *Borhyaena tuberata*, *'Lycopsis' longirostrus*, and *Thylacosmilus atrox*. Some degree of cursoriality was highlighted in *B. tuberata* and *T. atrox*, and climbing abilities in *'L.' longirostrus*, and to a lesser degree in *B. tuberata*. Scansorial habits were inferred for *Cladosictis patagonica*, *Sipalocyon gracilis*, *Prothylacynus patagonicus*, and *Pseudonotictis pusillus*, and in the case of *C. patagonica*, some digging ability was also tentatively inferred.

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ADDITIONAL KEYWORDS: allometry – comparative methods – geometric morphometrics – locomotion – phylogeny.

INTRODUCTION

In the last few decades, the relationships between form and locomotory habits of extant and fossil predators have been studied mainly through morphometric techniques (Van Valkenburgh, 1987; MacLeod & Rose, 1993; Andersson, 2003, 2004; Schutz & Guralnick, 2007, amongst others). These studies have validated morphofunctional relationships that had been previously established by means of descriptive and biomechanical approaches focused mainly on substrate use, hunting behaviour, or gaits (Ginsburg, 1961; Hildebrand, 1988; Taylor, 1989, amongst others), and sometimes dealing with constraining factors (e.g. phylogeny; Garland, Geiser & Baudinette, 1988). These studies have found partial or total morphological differentiation amongst predefined ecological groups, such as arboreal, scansorial, semifossorial, and terrestrial, identified through osteological indices measured on phalanges and metatarsals, olecranon process and long bone proportions, radial head and phalanx shape, amongst others (Van Valkenburgh, 1987; MacLeod & Rose, 1993). The information

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gathered in these studies has allowed subsequent inferences for fossil taxa, such as the reconstruction of locomotion behaviour in Oligocene carnivores (*Hyaenodon*, *Daphoenus*, and *Hoplophoneus*; Van Valkenburgh, 1987).

The Sparassodonta is a group of extinct carnivorous metatherians that inhabited South America from the Palaeocene to the Pliocene, between the Tiupampan and Chapalmalalan ages, from approximately 64 to 3 Mya (Simpson, 1950, 1980; Marshall, 1978a; Argot, 2004a; Forasiepi, 2009). They are found in deposits from Argentina, Bolivia, Brazil, Chile, Colombia, and Uruguay (Forasiepi, 2009). These mammals occupied the ecological niche of terrestrial carnivores before the arrival of placental carnivorans (order Carnivora) as part of the Great American Biotic Interchange (Late Pliocene–Pleistocene; Marshall, 1978a; Vieira & Astúa de Moraes, 2003; Forasiepi, Goin & Tauber, 2004; Argot, 2004a, b).

The greatest taxonomic and ecological diversification of the Sparassodonta is recorded in the early Miocene (Santacrucian age, ± 17 Myr), with arboreal to partially cursorial species (Muizon, 1998; Argot, 2003a, b, 2004a; Forasiepi, 2009), and a wide range of body masses, between 1 and 50 kg (Argot, 2003a; Wroe, Argot & Dickman, 2004; Ercoli, 2010; Vizcaíno *et al*., 2010; Ercoli & Prevosti, in press).

Most Sparassodonta species with preserved postcranial remains come from the Santa Cruz Formation (early Miocene, Santacrucian age), which bears the richest pre-Pleistocene mammalian assemblage on the continent (Hatcher, 1903; Vizcaíno *et al*., 2006, 2010; Kay *et al*., 2008). The Santa Cruz Formation belongs to the Austral Basin and crops out in the extreme south-east of Santa Cruz province, Argentina (Tauber, 1997a, b; Kay *et al*., 2008; Vizcaíno *et al*., 2010). Isotopic and magnetostratigraphical analyses suggest an age of 16.3 to 17.5 Myr (Flynn & Swisher, 1995; Vizcaíno *et al*., 2006, 2010).

Several studies have focused on the postcranial anatomy of Sparassodonta from a morphofunctional perspective (Sinclair, 1906; Riggs, 1934; Marshall, 1976, 1977a, 1978a; Muizon, 1998; Argot, 2001, 2002, 2003a, b, 2004a, b, c; Forasiepi, 2006, 2009; Argot & Babot, 2011). The Sparassodonta have been characterized as a group with mainly terrestrial habits, although some taxa have been described as showing some arboreal or cursorial specializations (Muizon, 1998; Argot, 2001, 2002, 2003a, b, 2004a, b, c; Forasiepi, 2006; Ercoli, 2010), and even fossorial capability (Argot & Babot, 2011). These studies have provided some insight on their locomotory habits on the basis of comparative descriptions, but without quantitative analyses of shape and with only few extant analogues included in the samples.

The goal of the present study was to identify relationships between shape and locomotory habits of living predators through shape analyses of some postcranial elements. We applied geometric morphometric methods to a wide sample of extant species and inferred locomotory habits for some Miocene Sparassodonta species, whilst also assessing possible allometric patterns and phylogenetic constraints.

BACKGROUND – THE LOCOMOTORY HABITS OF SPARASSODONTA

Previous morphofunctional analyses of *Arctodictis sinclairi* (Marshall, 1978a) assigned it to a category of terrestrial generalized habits (i.e. noncursorial), based on its limb morphology and proportions (Marshall, 1977a; Argot, 2004a; Forasiepi, 2006, 2009; Ercoli, 2010). The species was interpreted as having weak restriction of elbow and wrist movements, and a plantigrade posture (Forasiepi, 2006, 2009).

Since its first descriptions, *Borhyaena tuberata* (Ameghino, 1887) has been assigned to a terrestrial locomotory habit category on the basis of its appendicular morphology, particularly its ungual phalanges (Sinclair, 1906) and backward directed anticlinal vertebra (Muizon, 1998; Argot, 2003a; Forasiepi, 2006, 2009). These and other features led some authors to compare *B. tuberata* to extant canids and felids (Marshall, 1977a, 1978a), or explicitly suggest some degree of cursorial specialization (Muizon, 1998; Argot, 2003a).

Cladosictis patagonica (Ameghino, 1887) has been described as a scansorial or terrestrial form. An early description assigned this taxon to arboreal or scansorial locomotory modes (Sinclair, 1906), with some analogy to living didelphids and mustelids (Marshall, 1977a, 1978a). More recent studies have highlighted the peculiar combination of some typical terrestrial or cursorial features (e.g. deep humeral trochlea), combined with some scansorial traits (e.g. convex posterior margin of the ulna; Muizon, 1998; Argot, 2003b).

The known postcranial remains of *'Lycopsis' longirostrus* (Marshall, 1977b) are restricted to a single subadult specimen. This taxon was assigned to a terrestrial category based on the presence of a straight ulnar diaphysis, and an inferred semidigitigrade forelimb posture (Argot, 2004c). However, the well-developed hallux and relatively free tarsotibial articulation suggest the occasional use of arboreal substrates (Argot, 2004a, c).

Prothylacynus patagonicus (Ameghino, 1891) has been described as a primarily terrestrial taxon (Sinclair, 1906) capable of climbing, thus somewhat comparable to living ursids (Marshall, 1977a; Muizon, 1998), and able to perform powerful jumps (Muizon, 1998; Argot, 2004a). Argot (2003a) proposed ambush and climbing abilities for *Pr. patagonicus*, describing it as a tree-dwelling animal on the basis of its long and robust tail and inferred marked lumbar mobility, as well as its wide range of forelimb pronation-supination.

Only very few postcranial remains of a single specimen of *Pseudonotictis pusillus* (Ameghino, 1891) are known. The shape of the elbow articulation and the great development of muscular attachment areas have been considered as evidence of arboreal or, at least, scansorial habits (Argot, 2003b; Ercoli, 2010).

Sipalocyon gracilis (Ameghino, 1887) has been described as an arboreal or scansorial mammal (Sinclair, 1906; Marshall, 1977a, 1978a; Muizon, 1998; Argot, 2003b; Ercoli, 2010). The few postcranial elements found in the fossil record did not allow a more accurate description (Argot, 2003b).

Notwithstanding the numerous studies focused on the feeding and hunting strategies of *Thylacosmilus atrox* (Riggs, 1934; Churcher, 1985; Goin & Pascual, 1987), its postcranial morphology and locomotor mode remain little studied. *Thylacosmilus atrox* has been considered as an ambush hunter, similar to extant felids or sabre-tooth felids (Marshall, 1976, 1977a) and incapable of performing fast (Argot, 2004a, b; Ercoli, 2010) or sustained running (Argot, 2004a, b).

MATERIAL AND METHODS

Samples

Our analysis included the fossil species *B. tuberata*, *C. patagonica*, *Pr. patagonicus*, *Ps. pusillus*, and *S. gracilis* from the Santacrucian age; *A. sinclairi* and *'L.' longirostrus* from the Colhuehuapian and Laventan ages, respectively (although other species of these genera occur in Santacrucian deposits); and *T. atrox* and cf. *Thylacosmilus* from the Huayquerian, Montehermosan, and Chapadmalalan ages (see Supporting Information Appendix S1). The use of quotation marks for *'L.' longirostrus* suggests that the species currently included in the genus would not represent a natural group (Forasiepi, 2009).

We analysed over 250 specimens representing more than 100 extant carnivorous species (see Supporting Information Appendix S2), including marsupials of the orders Didelphimorphia (family Didelphidae), Dasyuromorphia (families Dasyuridae, Myrmecobiidae, and Thylacinidae), and Paucituberculata (family Caenolestidae), and placentals of the order Carnivora (families Ailuridae, Canidae, Felidae, Herpestidae, Hyaenidae, Nandinidae, Mephitidae, Mustelidae, Procyonidae, Ursidae, and Viverridae; Wilson & Reeder, 2005). Only adult specimens of both sexes were included (see Supporting Information Appendix S3).

Studied elements and locomotory habits

We selected postcranial elements that have been highlighted as informative with respect to locomotory habits (Hildebrand, 1952, 1954; Ginsburg, 1961; Van Valkenburgh, 1985, 1987; Taylor, 1989; Iwaniuk, Pellis & Whishaw, 1999, 2000; Lemelin, 1999; Argot, 2001, 2002; Andersson, 2004; Polly, 2007; Schutz & Guralnick, 2007). We also took into account the representation of postcranial elements within the Sparassodonta fossil record. Finally, we selected and studied the morphology of: (1) the distal humerus in anterior view (i.e. the axis of the distal diaphysis and of the articular surface parallel to the plane of the photograph; Fig. 1A); (2) proximal ulna in lateral view (i.e. diaphysis plane parallel to the plane of the photograph; Fig. 1B); (3) tibia in proximal view (i.e. both condylar surfaces parallel to the plane of the photograph; Fig. 1C). We included all well-preserved (i.e. not deformed or broken in relevant sectors) elements that allowed us to estimate unequivocally the shape of anatomical structures.

We followed the anatomical terminology used by Evans (1993) and Evans & deLahunta (1997). The assignment of species to locomotory categories primarily followed Van Valkenburgh (1987), but other data sources included: Taylor (1970, 1972), Long (1973), Marshall (1978b), Hildebrand (1988), Neuwall-Poglayen & Toweill (1988), Gompper (1995), Ray (1995), Strahan (1995), Gompper & Decker (1998), Larivière (1999), Nowak (1999), Presley (2000), Larivière & Calzada (2001), Kleiman, Geist & McDade (2003), Macrini (2004), Myers *et al*. (2006), Polly (2007), and Wilson & Mittermeier (2009). Assignment to these categories was based on behavioural data. The categories considered (Table 1) are broad and applicable to a wide diversity of mammals (Van Valkenburgh, 1987; Carrano, 1999). These categories are a simplification of both the continuum of real complexity and the non-exclusive nature of this variable (Hildebrand, 1977; Carrano, 1999).

Geometric morphometric analyses

We represented the morphology of postcranial elements through sets of selected landmarks and semilandmarks, which are shown and described in Figure 1. We used MakeFan6 software (Sheets, 2003) to build guidelines used to place the semilandmarks. The image files (TPS) were created using tpsUTIL 1.40 (Rohlf, 2008). Landmark digitization and scaling were carried out using tpsDIG 2.10 (Rohlf, 2006a).

The landmark + semilandmark configurations were superimposed by generalized Procrustes analysis (Goodall, 1991; Rohlf, 1999). Semilandmarks were slid using the minimum bending energy criterion (Bookstein, 1997) with ten iterations. Relative warp

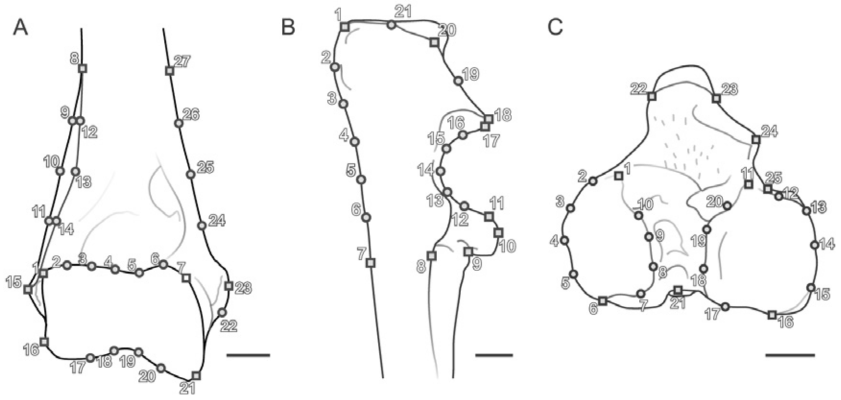

Figure 1. Analysed elements showing the position of landmarks (squares) and semilandmarks (circles). A, anterior view of distal humerus: 1, proximolateral extreme of articular surface, 2 to 6, proximal margin of articular surface, 7, proximomedial extreme of articular surface, 8, proximal end of lateral epicondylar crest, 9 to 11, lateral margin of lateral epicondylar crest, 12 to 14, medial margin of lateral epicondylar crest, 15, lateral extreme of lateral epicondyle, 16, distolateral corner of articular surface, 17 to 20, distal margin of articular surface, 21, distomedial corner of articular surface, 22, distomedial extreme of medial epicondyle, 23, medial extreme of medial epicondyle, 24 to 26, medial margin of supraepicondylar bridge, 27, medial projection of proximal end of lateral epicondylar crest. B, lateral view of proximal ulna: 1, posteroproximal extreme of olecranon, 2 to 6, posterior margin of proximal ulnar shaft, 7, posterior projection of distal tip of coronoid process, 8, posterior margin of radial notch at level of distal tip of coronoid process, 9, distal tip of coronoid process, 10, anterior end of coronoid process, 11, distal end of trochlear notch, 12 to 16, trochlear notch margin, 17, proximal end of trochlear notch, 18, anterior projection of anconeus process, 19, anterior margin of olecranon, 20, anteroproximal olecranon extreme (on olecranon lateral surface), 21, proximal olecranon margin. C, proximal view of tibia: 1, anterior end of medial condyle, 2 to 6, medial margin of medial condyle, 7, posterior end of medial condyle, 8 to 10, lateral margin of medial condyle, 11, anterior end of lateral condyle, 12 to 15, lateral margin of lateral condyle, 16, posterior end of lateral condyle, 17 to 20, medial margin of lateral condyle, 21, posterior end of intercondyloid area, 22, medial extreme of tibial tuberosity base, 23, lateral extreme of tibial tuberosity base, 24, maximum projection in anterior–lateral margin of non-articular surface, 25, lateral end of cranial intercondylar area. Modified from Ercoli (2010) and Ercoli & Prevosti (in press).

analyses (RWs) were performed in tpsRELW 1.45 (Rohlf, 2007a). The RWs scores of each species were averaged and the consensus forms were used for subsequent analyses.

COMPARATIVE METHODS

To assess the influence of phylogenetic structure on each dataset, we employed two comparative methods that partition data variance (in our case: RWs) into a 'phylogenetic' component (i.e. inherited or explained by phylogeny) and an 'adaptive' component (i.e. specific for each species). For this purpose, we obtained residuals (components not explained by phylogeny) from the regression of RWs variables against a phylogenetic vector (Cheverud, Dow & Leutenegger, 1985; Martins & Hansen, 1997; Diniz-Filho, 2000). These residuals of RWs variables were denominated RRWs.

Despite the considerable theoretical debate regarding the mode of implementation and choice of comparative methods to analyse morphological data (Martins & Hansen, 1997; Diniz-Filho & Torres, 2002; Rohlf, 2001, 2006b), several authors have highlighted the importance of applying them when comparing data from different species. This allows controlling for the lack of independence owing to phylogenetic structure in interspecific data sets and thus avoids misleading results and incorrect interpretations (Martins & Hansen, 1997; Diniz-Filho, 2000; Yves *et al.*, 2003).

We used a variance partitioning method instead of the regressive methods typically used to modify relationships between variables (e.g. phylogenetic generalized least squares; Martins & Hansen, 1997) because our goal was to perform discriminant analyses on nonphylogenetically biased shape components (see below). Variance partitioning comparative methods do not require the assumption of explicit evolutionary models (Diniz-Filho, 2000; Martins, Diniz-Filho & Housworth, 2002). Simulation studies have suggested good performance of these methods in a wide range of situations (Diniz-Filho, 2000; Diniz-Filho & Torres, 2002; Martins *et al.*, 2002). We used phylogenetic autoregression (PA; Cheverud *et al.*, 1985) and phylogenetic eigenvector regression (PVR; Diniz-Filho, Sant'Ana & Bini, 1998). We applied both methods because the efficiency of each varies depend-

Table 1. Description of locomotory habit categories used in this analysis, mainly based on definitions provided by Van Valkenburgh (1987) and Polly (2007)

Locomotory habit	Definition
Arboreal	Live mostly in trees, rarely travel on land
Scansorial	Travel on land and are able to climb, clinging with forelimbs and in some case with hindlimbs
Terrestrial	Travel on land and rarely or never climb, or use other substrates
Semifossorial	Use their limbs to dig frequently whilst foraging or building burrows. This is not a proper locomotory category but rather a typical specialization in terrestrial mammals
Cursorial	Able to run in open habitats, travel long distances, and develop high speeds. Rarely or never climb or use other substrates
Semiaquatic	Frequently swim. This habit category comprises many degrees of specialization.

ing on each data set, and we did not find any a priori reason to choose one method over the other (Diniz-Filho & Torres, 2002; Martins *et al*., 2002):

PA is an autoregressive method that incorporates phylogenetic information through a connectivity matrix. A parameter ρ or autoregressive coefficient (see Rohlf, 2001) describes the relationship between the original variables multiplied by the connectivity matrix, and the estimator of this original variable. The error term or residuals of this equation represents the portion of the original variable that is unexplained by phylogenetic relationships. These residuals can be used in standard statistical procedures (Martins & Hansen, 1997) because they are independent of the hierarchical structure imposed by phylogenetic relationships.

PVR converts the connectivity matrix into vectors through principal coordinates (PCo) analysis (Gower, 1966). These axes (PCo axes) summarize phylogenetic relationships amongst species. PCo axes are selected by a broken stick analysis (Jackson, 1993; Diniz-Filho, 2000) and used as independent variables versus each of the shape variables (RWs) in multivariate regressions. These regressions allow us to estimate the amount of RWs variation that can be explained by phylogenetic effects. The residual portions of these regressions are independent of the phylogenetic structure (Diniz-Filho, 2000; Garland & Ives, 2000; Martins *et al*., 2002).

The connectivity matrix used in both methods was obtained from a combined phylogenetic tree (see Supporting Information Fig. S1) built from recently published phylogenies (Krajewski & Westerman, 2003; Flynn *et al*., 2005; Gaubert *et al*., 2005; Johnson *et al*., 2006; Koepfli *et al*., 2006, 2007, 2008; Beck, 2008; Krause *et al*., 2008; Flores, 2009; Patou *et al*., 2009; Sato *et al*., 2009; Wolsan & Sato, 2009; Prevosti, 2010, for living taxa; and Forasiepi, 2009 for Sparassodonta). We assigned discrete values to nodes, starting at value '1' for the node furthest from the root, in the most diverse clade. Then we proceeded to number the intermediate nodes between this and the root, assigning increasing values to each node. The remaining node values were assigned in decreasing order from those already enumerated. To quantify phylogenetic distances, the distance between two species was coded as the value assigned to the nearest common ancestral node. Thus, all taxa belonging to a single clade are assigned shorter distances to other taxa of the same clade than to taxa that do not belong to that clade. Similar procedures have been used in previous studies (e.g. Grafen, 1989; Gittleman & Kot, 1990; Miles & Dunham, 1992), and are numerically similar to constructing an ultrametric distances matrix considering a length of '1' for all branches (Rohlf, 2001).

Finally, we built residual morphospaces using residual components, to evaluate changes to the location of species in phylogenetically free morphospaces.

Comparative analyses were performed using R 2.12.0 (R Development Core Team, 2010), with the MASS (Venables & Ripley, 2002) and APE libraries (Paradis, Claude & Strimmer, 2004). Multivariate regressions between each RRW and the PCo axes were performed using TPsREGR 1.35 (Rohlf, 2007b), in order to reconstruct the deformation grids for residual morphospaces.

Allometric component analyses

We analysed the relationship between shape and size for each postcranial element through multivariate regressions. We considered RWs as dependent variables, and the natural log-transformed centroid size as the explanatory variable (ordinary least squares, OLS). In order to take into account the phylogenetic structure of the data sets, we constructed a phylogenetic covariance matrix from the combined phylogenetic tree, and performed the same regressions but incorporating this matrix into the error term of the regression equations (phylogenetic generalized least squares, PGLS; Martins & Hansen, 1997). These analyses were carried out using APE library (Paradis *et al*., 2004) for R 2.12.0 (R Development Core Team, 2010).

DISCRIMINANT ANALYSES AND LOCOMOTORY HABIT PREDICTIONS

We performed discriminant analyses with the purpose of maximizing separation amongst locomotory classes and obtaining functions that would allow us to classify unknown cases (i.e. Sparassodonta) (Legendre & Legendre, 1998). We used the first RWs or RRWs as explanatory variables and locomotory habit (i.e. cursorial, terrestrial, scansorial, arboreal, and semifossorial) as the categorical variable. The number of selected explanatory variables was equal to the number of species in the lowest represented class minus one (Neff & Marcus, 1980). We excluded the semiaquatic class from the discriminant analyses to maximize the discrimination abilities of the discriminant vectors. It should be noted that 'semiaquatic' is not an expected locomotory habit for the Sparassodonta (Muizon, 1998; Argot, 2004a; Ercoli, 2010) and that the inclusion of this category in the analysis does not significantly alter class assignment (see Ercoli, 2010).

Three discriminant analyses were performed for each postcranial element, one for each type of explanatory variable: (1) RWs; (2) RRWs from PA analyses (PA-RRWs); and (3) RRWs from PVR analyses (PVR-RRWs). For each analysis, we calculated the percentage of correct reclassification per locomotory group and for the total sample, recalculating the latter by cross-validation procedures, to evaluate the performance of the functions. In the case of analyses 2 and 3, we considered as more reliable those functions with the highest total percentage of correct reclassification after cross-validation (a posteriori evaluation). Discriminant analyses were performed in R 2.12.0 (R Development Core Team, 2010) with the MASS library (Venables & Ripley, 2002).

RESULTS

SHAPE ANALYSES OF THE DISTAL HUMERUS

The RWs analysis showed clear separation of taxonomic and ecological groups in the morphospace defined by RW1 and RW2 (Fig. 2A, B). The variance explained by these axes was 69.57% (RW1: 50.42%, RW2: 19.15%). As a general trend, positive values of RW1 and RW2 were associated with an increase in the articular area at the expense of major muscle attachment areas (e.g. epicondyles, lateral epicondylar crest; Fig. 2A, B).

Closely related species, especially at the order level, tended to be clustered in the morphospace (Fig. 2A). Didelphimorphia and Paucituberculata (the latter represented only by *Caenolestes* sp.) showed lower RW2 scores than Eutheria and Dasyuromorphia. Sparassodonta occupied an intermediate position with mostly negative values of RW2, showing a greater width–height ratio of the humeral articular area (including the trochlea), medial epicondyle, and lateral epicondylar crest. The families Canidae and Hyaenidae had positive values of RW1, whereas most species of the superfamilies Arctoidea and Feliformia plotted together in a restricted space with negative values for RW1 and generally positive values for RW2. The Felidae occupied intermediate positions between these values. The Didelphidae were mainly restricted to negative values of both RW1 and RW2. Most Lutrinae (Mustelidae) species presented positive values of RW1 and negative values of RW2.

With respect to locomotory habits, this analysis showed a distribution gradient from arboreal forms (negative values for RW1 and RW2) to cursorial ones (positive values on both axes), with clear separation of the cursorial taxa. Other RWs did not contribute to the separation amongst locomotory modes.

In this analysis, cursorial species were characterized by a deep distal humeral articular zone, especially at the trochlea. Additionally, positive values of RW1 were associated with a decrease in height of the lateral epicondylar crest, whereas the width of this feature decreased toward positive values of RW2. Consequently, the articular zone becomes similar in depth to the width of distal humeral shaft (Fig. 2B). These features explain the separation of cursorial forms in the morphospace (except for *Thylacinus cynocephalus* and *Acinonyx jubatus*, which are located near scansorial and terrestrial forms).

The arboreal taxa had negative values of RW1; along RW2, they were split into two groups formed by marsupials (didelphids) and placentals. This group was morphologically opposed to the cursorial forms, with a wide but low articular zone (especially at the trochlea), and well-developed medial epicondyle, medial supraepicondylar zone, and lateral epicondylar crest (Fig. 2B). Some non-arboreal taxa (e.g. the scansorial *Nasua* sp. and *Myrmecobius fasciatus*, and the semifossorial *Conepatus* sp.) shared this sector of the morphospace.

Most scansorial, terrestrial, semifossorial, and semiaquatic species were distributed between the arboreal and cursorial taxa, filling the middle zone of the morphospace with a high degree of superposition. However, the values for most terrestrial species were higher on RW1 and RW2 than those of the scansorial ones, in accordance with the deeper trochlea and capitulum, as well as the narrower and secondarily shorter lateral epicondylar crest of the former. Semifossorial species tended to have negative values of RW1 and positive values of RW2. These taxa were characterized by a moderately developed articular zone, higher lateral epicondylar crest, and medially and mediodistally projected medial epicondyle

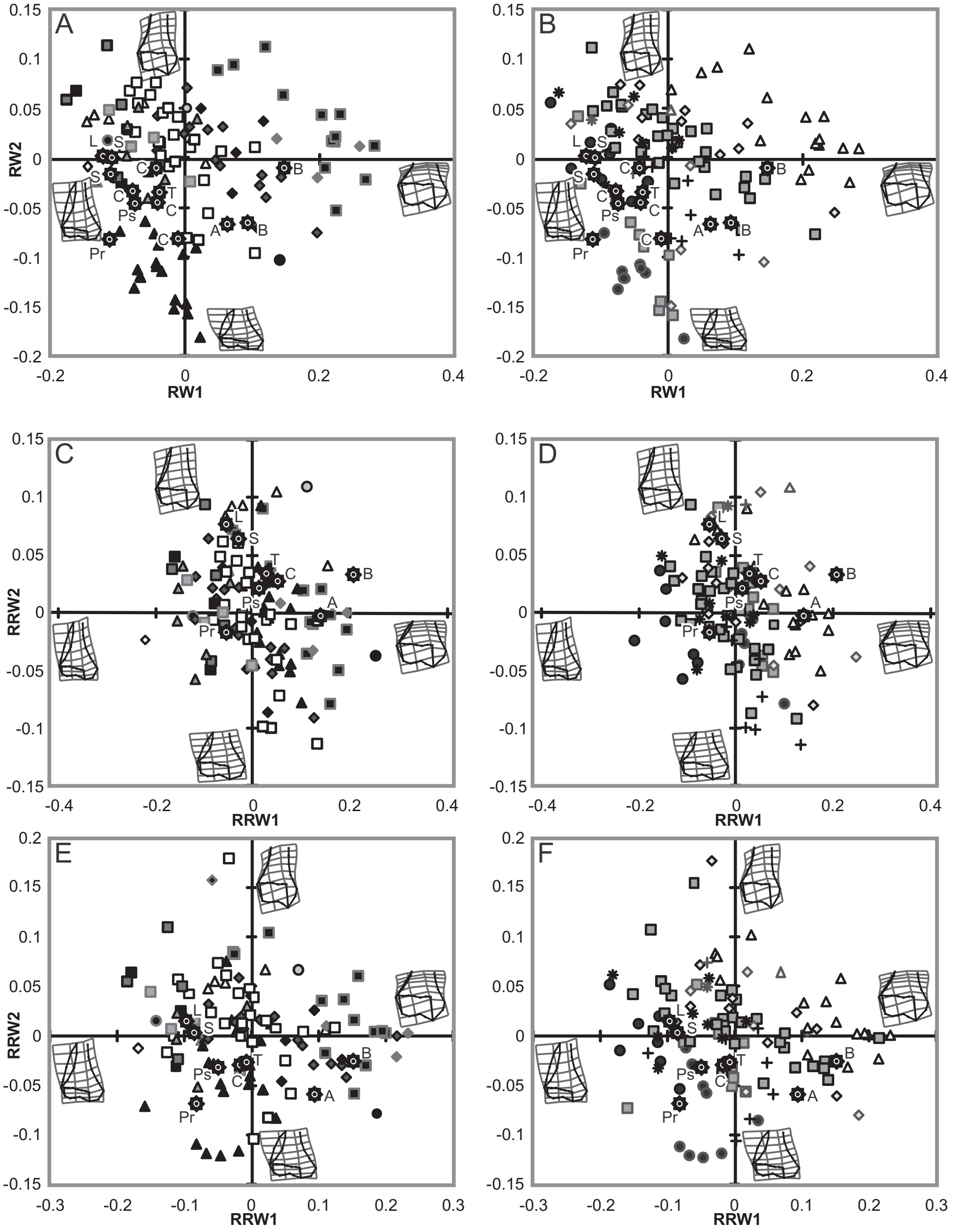

Figure 2. Morphospaces defined by the first two shape axes for the humerus. A, B, relative warps (RWs); C, D, relative warps residuals (RRWs) after phylogenetic autocorrelation analysis; E, F, RRWs after phylogenetic eigenvector regression analysis. In A, C, and E, taxonomic groups are indicated by the symbols. In B, D, and F, locomotory groups are indicated by the symbols. Taxonomic group symbols: ● Ailuridae, ● Caenolestidae, ■ Canidae, △ Dasyuridae, ▲ Didelphidae, ◆ Felidae, ◆ Herpestidae, ◆ Hyaenidae, ◇ Nandiniidae, ■ Mephitidae, □ Mustelidae, ▲ Myrmecobiidae, ■ Procyonidae, ○ Thylacinidae, ■ Ursidae, △ Viverridae, ✪ Sparassodonta species. Locomotory groups symbols: △ cursorial eutherians, △ cursorial metatherians, ◇ terrestrial eutherians, ◇ terrestrial metatherians, ■ scansorial eutherians, ■ scansorial metatherians, ● arboreal eutherians, ● arboreal metatherians, ✳ semifossorial eutherians, ✳ semifossorial metatherians, + semiaquatic eutherians, + semiaquatic metatherians. Abbreviations for Sparassodonta species: A, *Arctodictis sinclairi*; B, *Borhyaena tuberata*; C, *Cladosictis patagonica*; L, *'Lycopsis' longirostrus*; Pr, *Prothylacynus patagonicus*; Ps, *Pseudonotictis pusillus*; S, *Sipalocyon gracilis*; T, *Thylacosmilus atrox*.

(Fig. 2B). Both scansorial and arboreal species, as well as most of the semifossorial species, showed great mediolateral development of the condyle compared to the humeral shaft. Semiaquatic species showed positive values of RW1 and negative values of RW2, and were located in the centre of the morphospace (Fig. 2B). This group was characterized by a well-developed lateral epicondylar crest, with a greater width–height ratio compared to most arboreal forms, and moderate to deep articular zone.

Comparative methods applied to the humerus data set

As a general trend, the application of PA and PVR methods notably modified the distribution of species in the RRW morphospaces. Both resulted in a continuous distribution within each locomotory group, rather than separated (phylogenetic) subsets (Fig. 2C–F). In the case of PA residual analysis (RRW1 vs. RRW2), the arboreal group remained divided into marsupials and placentals, with only the arboreal placental species differentiating more clearly than in the RW analysis. The cursorial group completely lost its exclusive morphospace, which was in this case invaded by many terrestrial marsupial and placental species. In the PVR residual analysis (RRW1 vs. RRW2), the arboreal group occupied a better-defined sector (compared to the RW analysis) whereas cursorials were less differentiated, although some areas still remained exclusively occupied by cursorials.

Comparing the deformation grids obtained before and after the application of comparative methods (Fig. 3A), it was apparent that an important portion of shape variation could be explained by phylogeny (i.e. there were substantial differences between shape grids of RWs and RRWs axes), especially for the RW2 axis. In both comparative methods, part of the proximodistal variation in the distal humerus could be explained by phylogeny. However, for the negative values on this axis, the PA method suggested that widening of the distal humerus could be explained by phylogeny, whereas PVR suggested the contrary: that the narrowing can be explained by phylogeny. For the negative values of RRW2, both methods agreed in explaining part of the narrowing of the humeral shaft, and part of the flattening of the whole structure (especially at the lateral epicondylar crest and

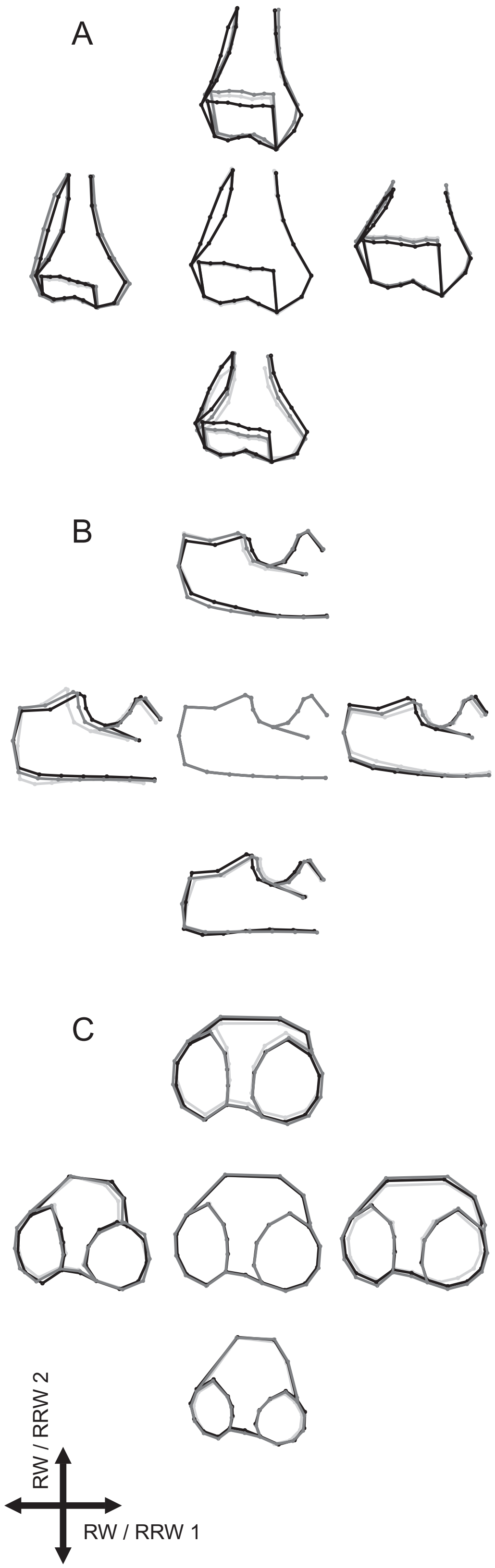

Figure 3. Deformation grids of the first two shape axes. Relative warp grids (pale grey), phylogenetic autocorrelation residual grids (dark grey), and phylogenetic eigenvector regression residual grids (black). A, humerus analyses. B, ulna analyses. C, tibia analyses.

articular region) as being a result of phylogenetic structure. However, for positive values of this axis, PA analysis suggested an increase in depth of the articular surface owing to phylogeny, whereas PVR analysis suggested the opposite trend.

LOCATION OF FOSSIL TAXA IN THE HUMERUS MORPHOSPACE

Most of the fossil specimens failed to occupy a defined position with respect to the locomotory classes in the humerus shape analysis (Fig. 2B). *Borhyaena tuberata* and *A. sinclairi* fell within the zone occupied by scansorial, semiaquatic, and terrestrial placentals, and terrestrial marsupials. These species have a well-developed articular surface and weak lateral epicondylar crest. It should be noted that *B. tuberata* shows weaker medial projection of the medial epicondyle and has a shorter trochlea than other Sparassodonta. One of the specimens of *B. tuberata* (MACN-A 2074–2078) presents strong development of the articular surface, especially at the capitulum, differing from the other specimen (MACN-A 6203–6265). *Arctodictis sinclairi* shows a wide (lateromedially projected) articular surface and medial epicondyle (Fig. 2B) and a shallow trochlea. As a result of these features, *A. sinclairi* was placed at a lower position on the RW2 axis than the other sparassodonts except *Pr. patagonicus* and a specimen of *C. patagonica*. The main shape difference between *C. patagonica*, *Ps. pusillus*, and *T. atrox* with respect to *'L.' longirostrus* and *S. gracilis* is the shorter lateral epicondylar crest of the former species. *Thylacosmilus atrox* has a medial epicondyle that is medially projected, but located proximally with respect to the articular zone, similar to the condition in *A. sinclairi*, *B. tuberata*, and to a lesser extent, *'L.' longirostrus*. *Thylacosmilus atrox* also has a robust capitulum, especially at its lateral end, similar to that of *B. tuberata* and *A. sinclairi*. *Prothylacynus patagonicus* was clearly situated within the exclusive morphospace of arboreal marsupials (Fig. 2B). This taxon has a strongly developed lateral epicondylar crest and a wide medial epicondyle, whereas its trochlea is poorly developed.

Both RRW morphospaces (Fig. 2D, F) showed a change in the position of *B. tuberata* with respect to the locomotory groups. This taxon was included within an area dominated by cursorial placentals (canids and hyenids), and secondarily by some scansorial felids and terrestrial marsupials. Both analyses agreed in locating *A. sinclairi* closer to the terrestrial forms, and *Pr. patagonicus* nearer to scansorial (mainly felids and procyonids, in the PA analysis) or arboreal forms (PVR). The remaining Sparassodonta species (*C. patagonica*, *'L.' longirostrus*, *Ps. pusillus*, *S. gracilis*, and *T. atrox*) were assigned to different categories, but always close to the scansorial species.

SHAPE ANALYSES OF PROXIMAL ULNA

The RWs analysis showed clear separation of some taxonomic and ecological groups in the morphospace defined by RW1 and RW2 (Fig. 4A, B). The variance explained by these axes was 46.68% (RW1: 27.04%, RW2: 19.64%). As a general trend, negative values of RW1 were associated with progressive proximal shortening of the olecranon process, accompanied by a widening of its proximal margin, and an enlargement of the trochlear notch area. From negative to positive values of RW2, the two main trends were: change from concave to convex posterior margin, and expansion of the trochlear notch. Along both axes, from negative to positive values, the anconeal process was reduced and the coronoid process became larger, altering the orientation of the trochlear and radial notches (Fig. 4A, B).

Along RW1, the placental forms showed lower values than the marsupials; however, there was still a wide range of overlap between these groups. The Didelphimorphia, Sparassodonta, and to a lesser extent Dasyuromorpha, had mostly extreme positive values of this variable. Thus, marsupials tended to have a projected olecranon and a proximally tilted trochlear notch (Fig. 4A). The families Canidae and Hyaenidae presented negative values on both axes, whereas the Felidae and most Feliformia species were located in the centre of the morphospace. Members of the Mustelidae mainly had moderate values of RW1 and positive values of RW2, whereas the Mephitidae tended to occupy a central position on the RW2 axis and positives values for RW1, and the Ursidae had extreme negative values of RW1 (Fig. 4A).

The arboreal and cursorial locomotory groups were the best differentiated, located at positive positions for both axes and negative positions for both axes, respectively. Transitional locomotory habits (scansorial and terrestrial groups) occupied an intermediate position between the aforementioned groups, whereas the semifossorial and semiaquatic groups were not differentiated in the morphospace (Fig. 4B).

The cursorial species occupied negative positions for both axes, and were distributed in a mostly exclusive morphospace sector, shared only by some scansorial forms (ursids). All were characterized by a concave posterior margin of the ulna, an olecranon that is moderate or short but wide anteroposteriorly (except for *Thylacinus cynocephalus*, which shows a long and narrow olecranon), and a radial notch anteriorly orientated in comparison to other locomotory forms. The anconeal process tends to be more anteriorly projected than the coronoid process, so that the

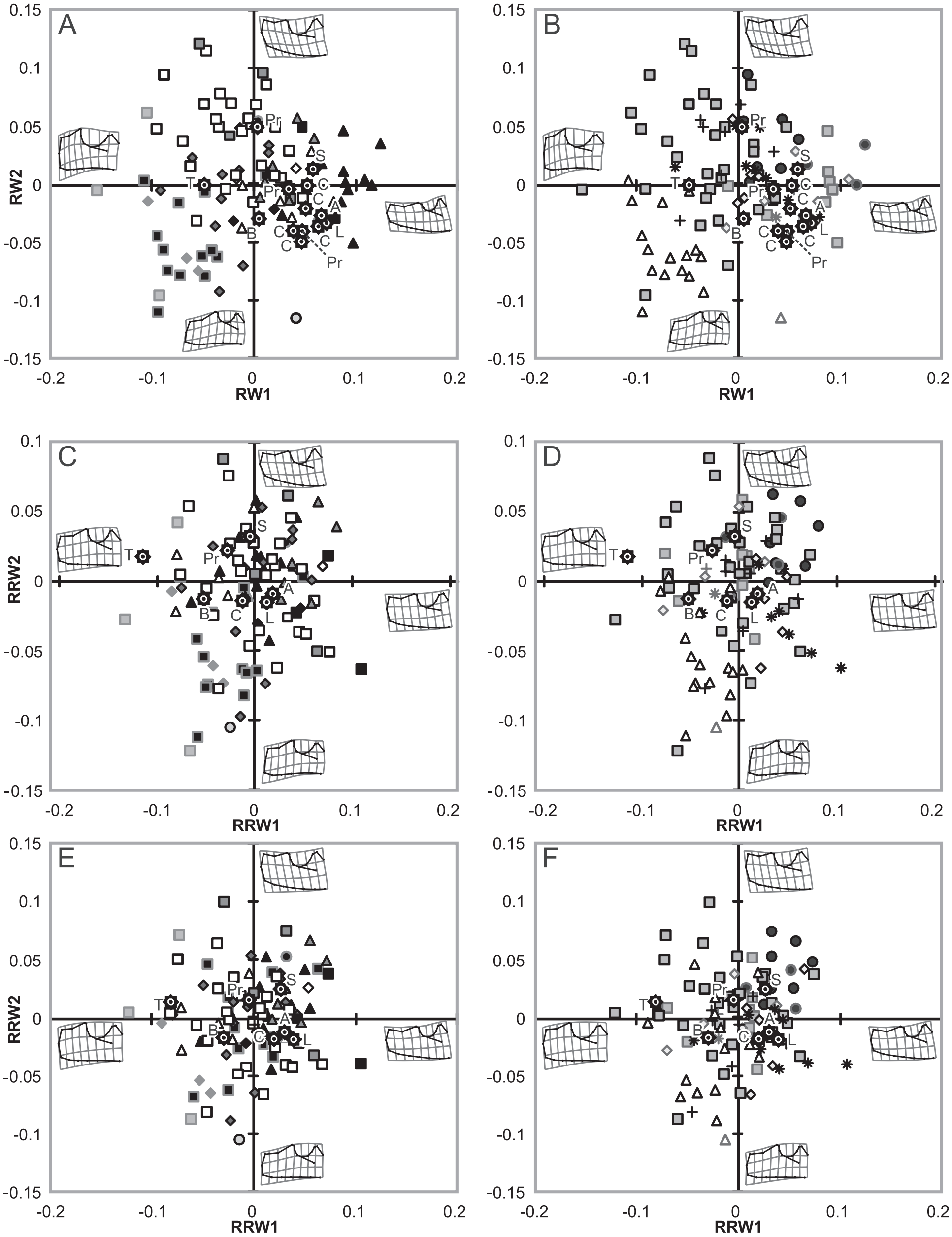

Figure 4. Morphospaces defined by the first two shape axes for the ulna. A, B, relative warps (RWs); C, D, relative warps residuals (RRWs) after phylogenetic autocorrelation analysis; E, F, RRWs after phylogenetic eigenvector regression analysis. In A, C, and E, taxonomic groups are indicated by the symbols. In B, D, and F, locomotory groups are indicated by the symbols. Taxonomic group symbols: ● Ailuridae, ■ Canidae, △ Dasyuridae, ▲ Didelphidae, ◆ Felidae, ◆ Herpestidae, ◆ Hyaenidae, ◇ Nandiniidae, ■ Mephitidae, □ Mustelidae, ▲ Myrmecobiidae, ■ Procyonidae, ○ Thylacinidae, ■ Ursidae, △ Viverridae, ⚙ Sparassodonta species. Locomotory groups symbols: △ cursorial eutherians, △ cursorial metatherians, ◇ terrestrial eutherians, ◇ terrestrial metatherians, ■ scansorial eutherians, ■ scansorial metatherians, ● arboreal eutherians, ● arboreal metatherians, ✳ semifossorial eutherians, ✳ semifossorial metatherians, + semiaquatic eutherians, + semiaquatic metatherians. Abbreviations for Sparassodonta species: A, *Arctodictis sinclairi*; B, *Borhyaena tuberata*; C, *Cladosictis patagonica*; L, *'Lycopsis' longirostrus*; Pr, *Prothylacynus patagonicus*; S, *Sipalocyon gracilis*; T, cf. *Thylacosmilus*.

trochlear notch becomes inclined distally (i.e. the articular surface faces anteroventrally instead of anterodorsally; Fig. 4B). Along their range from positive to negative values of RW2, the cursorials showed marked shape variation from species with a short and robust olecranon (e.g. *Chrysocyon brachyurus* and *Hyaena hyaena*), to species in which this structure is long and slender (e.g. *Acinonyx jubatus* and *Thylacinus cynocephalus*).

The arboreal species were distributed exclusively at a positive position for RW1 and RW2 axes, and in the central sector of the morphospace, which was also shared by scansorial and some terrestrial (especially didelphids) and semifossorial (mustelids and mephitids) forms. Typical arboreal forms were characterized by a convex posterior margin and a proximally tilted trochlear notch, owing to a large and anteriorly projected coronoid process. The olecranon is more slender than the remaining proximal shaft and the radial notch reaches a more posterior position in comparison to other forms. All these characteristics contrast with those of cursorial forms (Fig. 4B). Scansorial, terrestrial, semifossorial, and semiaquatic taxa were widely distributed along RW1 and RW2, with generalized ulnar morphologies. One of the few detectable tendencies for these groups along these axes is the location of terrestrial and semifossorial forms at positive and central positions for RW1 and central positions for RW2, which implies the possession of an elongated olecranon in comparison with other locomotory groups.

Other shape axes did not provide information regarding locomotory group separation, except RW3 which showed a trend of separation between semiaquatic and terrestrial classes, with positive and negative values, respectively (15.64% of explained variance; result not shown).

COMPARATIVE METHODS APPLIED TO ULNA DATA SET

As a general trend, the application of PA and PVR methods notably modified the species distribution in the RRW morphospaces (Fig. 4C–F). As in the analysis of the humerus, both resulted in a continuous distribution within each locomotory group, rather than separated phylogenetic subsets. For PA residual analysis (RRW1 vs. RRW2), the differentiation of all groups was similar (e.g. cursorial) or even better (e.g. arboreal and semifossorial) than for RW results. Semifossorials tended to have positive RRW1 and negative RRW2 values, and were better differentiated than in the RW analysis. In the case of PVR residual analysis (RRW1 vs. RRW2), the separation of locomotory groups did not improve compared with RWs (for the arboreal group) or was even poorer (e.g. cursorial, terrestrial, and scansorial groups). Only the semifossorial taxa were more clearly differentiated, similar to the results described for PA analysis.

Again, application of PA and PVR analyses showed that an important portion of shape variation could be explained by phylogeny (Fig. 3B), with PA assigning a comparatively greater portion to phylogeny. Both methods agreed in explaining by phylogeny most of the olecranon robustness and variation in trochlear notch width, as well as an important fraction of the curvature of the posterior margin observed in RRW1. On RRW2, both methods agreed in explaining by phylogeny an important portion of the relative size of the trochlear notch and position of the anconeal process. However, RRW2 of the PA analysis suggested, contrasting with PVR, that some changes observed in the anterior margin of the olecranon and anconeal process could be explained by phylogeny. By contrast, PVR suggested that part of the shape change of the posterior margin of the shaft could be explained by phylogeny (Fig. 3B).

LOCATION OF FOSSIL TAXA IN THE ULNA MORPHOSPACE

Most Sparassodonta species were clustered in a restricted area within the marsupial-dominated morphospace, but cf. *Thylacosmilus* departed toward negative values of RW1 (Fig. 4A, B), occupying a sector dominated by scansorial placentals (e.g. large felids) and some cursorial mammals. This was because of the robust, short, and straight olecranon, anteriorly projected coronoid and anconeal process, and a trochlear notch opening perpendicular to the shaft. *Borhyaena tuberata*, with an intermediate position and morphology between cf. *Thylacosmilus* and the remaining Sparassodonta species, was located in a sector dominated by scansorial and terrestrial taxa, having a slightly convex proximal posterior margin of the shaft and being very similar to the consensus shape in most features (Fig. 4B).

The other sparassodont taxa (*A. sinclairi*, *C. patagonica*, *'L.' longirostrus*, *Pr. patagonicus*, and *S. gracilis*) were located in a morphospace sector dominated by scansorial, and, to a lesser degree, terrestrial and semifossorial taxa, and, in some cases (some specimens of *Pr. patagonicus* and *S. gracilis*), close to arboreal species. *Arctodictis sinclairi*, *'L.' longirostrus*, *C. patagonica*, *Pr. patagonicus*, and *S. gracilis* have a slender olecranon with convex posterior margin (Fig. 4B), characteristics shared with scansorial and terrestrial forms. *Arctodictis sinclairi*, *'L.' longirostrus*, and *C. patagonica* have a straighter and longer olecranon than *S. gracilis*. *Prothylacynus patagonicus* shows considerable intraspecific morphological variance, especially in the curvature of the posterior margin, and spans the range occupied by arboreal, scansorial, and terrestrial species (Fig. 4B).

After applying the PA method (RRW1 vs. RRW2; Fig. 4C, D), *B. tuberata* and *T. atrox* were located in a sector of the morphospace mainly occupied by cursorial and scansorial species. In both PA and PVR analyses (Fig. 2D, E), *S. gracilis* showed close association with arboreal and scansorial forms. The remaining Sparassodonta taxa (*A. sinclairi*, *C. patagonica*, *'L.' longirostrus*, and *Pr. patagonicus*) were relocated near scansorial species but did not show clear association with any locomotory group.

Shape analyses of proximal tibia

The RW analysis showed clear separation of some taxonomic and ecological groups in the morphospace defined by RW1 and RW2 (Fig. 5A, B). The variance explained by these axes was 43% (RW1: 26.04%, RW2: 17.20%). Positive values of both RWs were associated with widening of the cranial intercondyloid area and the base of the tibial tuberosity. Toward positive values of RW1, the articular condylar anteroposterior axes diverge anteriorly, and the sulcus muscularis becomes shallower. Toward positive values of RW2, the cranial intercondyloid area decreases and the tibial tuberosity base has a more posterior position (i.e. closer to the articular condyles; Fig. 5A, B).

High-level taxonomic groups were separated along RW1. Metatherian mammals occurred from central to extreme positive positions, whereas placentals were widely distributed. Marsupials present marked anterior divergence of the anteroposterior condylar axis and very wide cranial intercondyloid area (Fig. 5A). The Hyaenidae, placed at the negative extreme of RW2, have a particular morphology with well-developed cranial intercondyloid area. The Canidae were located mainly at extreme negative positions of RW1 and RW2, whereas the Ursidae and Felidae had negative, but not extreme, values for RW1. RW3 (10.62% of explained variance) also showed differentiation between taxonomic groups, with metatherians distributed from positive to central positions, and placentals occurring from positive to negative extremes (results not shown).

With respect to locomotory groups, the analysis showed a distributional gradient from arboreal (positive values of RW2) to cursorial forms (negative values of RW1 and RW2), with good differentiation of the cursorials. The remaining locomotory groups were largely overlapping.

Cursorial species were widely distributed along negative values for the first two axes, having a very anteriorly placed tibial tuberosity, associated with anterior elongation of the cranial intercondyloid area. Another remarkable feature is the great lateral expansion of the insertion for m. biceps femoris forming the anterior edge of the sulcus muscularis, which becomes deeper. The articular condylar surfaces are reduced in comparison to the whole proximal surface of the tibia, and are asymmetric: the medial condyle shows a reniform shape, whereas the lateral one is circular. The medial condyle is more anteroposteriorly developed than the lateral one; the position of the latter is shifted slightly backwards (Fig. 5B). The hyaenids and *Thylacinus cynocephalus* displayed a particular morphology, with a vestigial or even absent sulcus muscularis; both condylar anteroposterior axes are anteriorly divergent (different from the condition observed in felids and canids), and there is an extremely well-developed cranial intercondyloid area (Fig. 5A, B).

Some arboreal taxa were located at positive positions for RW1 and RW2. They showed wide overlap with other locomotory categories, especially semiaquatic and scansorial taxa. One extremely specialized arboreal taxon (the procyonid *Potos flavus*) stood alone at an extreme positive position for RW1, with semicircular condyles that are mirror images of each other, and with a reduced cranial intercondyloid area. The most remarkable feature of the arboreal taxa was the atrophy of anterior structures, including the cranial intercondyloid area, sulcus muscularis, and tibial tuberosity (Fig. 5B). However, viverrids occupied a central position in the morphospace, with more generalized morphologies.

Terrestrial and semifossorial species overlapped widely, especially amongst placentals, and they were partially superimposed with scansorial ones in the central portion of the space, with positive values on RW1. They were characterized by moderate to important forward extension of the tibial tuberosity, although lesser than in cursorials (Fig. 5B). Within the terrestrial locomotory morphospace, marsupials and placentals occupied clearly differentiated positions, the first having positive values of RW1 and with little overlap with other locomotory groups, and showing a wide cranial intercondyloid area. Scansorial species were widely distributed in the centre of the morphospace, spanning a wide range of shapes (Fig. 5B). Semiaquatic species generally had positive values on the first axes (except *Chironectes minimus*), sharing morphological features and morphospace positions with arboreal and scansorial species, although they showed greater development of the anterolateral margin of the tibia.

Comparative methods applied to the tibia data set

As a general trend, the application of both methods notably modified the distribution of species in the

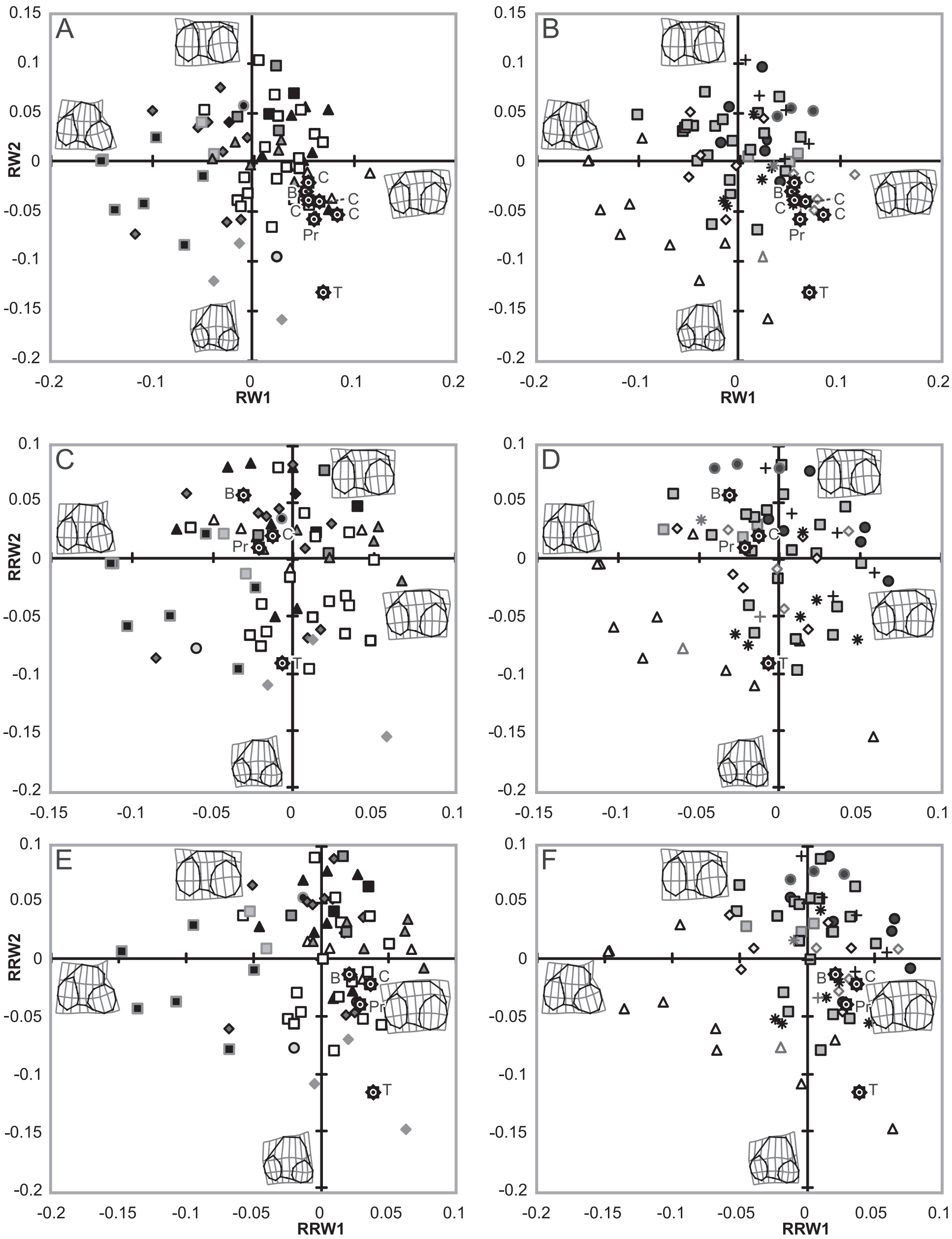

Figure 5. Morphospaces defined by the first two shape axes for the tibia. A, B, relative warps (RWs); C, D, relative warps residuals (RRWs) after phylogenetic autocorrelation analysis; E, F, RRWs after phylogenetic eigenvector regression analysis. In A, C, and E, taxonomic groups are indicated by the symbols. In B, D, and F, locomotory groups are indicated by the symbols. Taxonomic group symbols: ● Ailuridae, ■ Canidae, △ Dasyuridae, ▲ Didelphidae, ◆ Felidae, ◆ Herpestidae, ◆ Hyaenidae, ■ Mephitidae, □ Mustelidae, ■ Procyonidae, ○ Thylacinidae, ■ Ursidae, △ Viverridae, ✪Sparassodonta species. Locomotory groups symbols: △ cursorial eutherians, △ cursorial metatherians, ◇ terrestrial eutherians, ◇ terrestrial metatherians, ■ scansorial eutherians, ■ scansorial metatherians, ● arboreal eutherians, ● arboreal metatherians, ✳ semifossorial eutherians, ✳ semifossorial metatherians, + semiaquatic eutherians, + semiaquatic metatherians. Abbreviations for Sparassodonta species: B, *Borhyaena tuberata*; C, *Cladosictis patagonica*; Pr, *Prothylacynus patagonicus*; T, *Thylacosmilus atrox*.

RRW morphospaces (Fig. 5C–F). Both resulted in a continuous distribution within each locomotory group, similar to the cases of the humerus and ulna. In both analyses, the separation of cursorial, arboreal, and semifossorial groups was similar or better than that observed in the RWs analysis, but strong overlap persisted amongst the scansorial, terrestrial, and semiaquatic forms.

Comparison of the deformation grids obtained before and after application of the comparative methods (Fig. 3C) shows that only a minor portion of shape variation can be explained by phylogeny. Both PVR and PA agree in explaining through phylogeny a minor portion of the cranial intercondyloid anteroposterior compression and lateral condyle rotation observed at positive values of RW1, and a portion of the narrowing of the cranial intercondyloid area and tibial tuberosity associated with negative values of this axis. Both methods also agree in explaining by phylogeny a minor portion of the cranial intercondyloid anteroposterior compression observed at positive values of RW2.

LOCATION OF FOSSIL TAXA IN THE TIBIA MORPHOSPACE

In the morphospace defined by the first two RWs, *T. atrox* fell near cursorial taxa (*H. hyaena* and *Thylacinus cynocephalus*). These taxa share an extremely forward-extended and moderately wide tibial tuberosity, without a well-developed sulcus muscularis, and symmetrical condyles, with the lateral condyle located posteriorly (Fig. 5B). *Borhyaena tuberata*, *C. patagonica*, and *Pr. patagonicus* share similar morphologies, with a poorly developed cranial intercondyloid area, and consequently, posteriorly located tibial tuberosity, compared to *T. atrox*. The former taxa were located in a zone of the morphospace occupied by relatively few taxa, mainly terrestrial species (Fig. 5B). The values of *Pr. patagonicus* for RW2 were lower than those of *B. tuberata* and *C. patagonica*, with a more anteriorly located tibial tuberosity.

In the analyses of the RRW1 vs. RRW2 morphospaces (Fig. 5D, F, C), *T. atrox* maintained strong affinity to cursorial forms, and secondarily to some scansorial felids. The remaining Sparassodonta species (*B. tuberata*, *C. patagonica*, and *Pr. patagonicus*) were closer to each other and mainly associated with scansorial and arboreal forms (in PA analysis; Fig. 4D), or terrestrial and scansorial taxa (in PVR analysis; Fig. 4F).

DISCRIMINANT ANALYSES

As shape was not significantly influenced by size when phylogeny was considered (see below), allometric factors were not considered in subsequent discriminant analyses. Discriminant analyses of shape components that were not explained by phylogeny (i.e. RRWs) showed correct reclassification percentages, similar to or greater than those obtained when we considered the original variables (i.e. RWs; Table 2, Supporting Information Appendix S4). In the analyses of the humerus, the use of RRWs of PVR yielded the best results: 68.32% of total correct reclassification (54.45% after cross-validation). For the ulna, we got the best result using RRWs of PA, resulting in 70.11% of total correct reclassification (62.07% after cross-validation). Finally, in the discriminant analyses of the tibia, both PA and PVR residuals obtained 68.85% of total correct reclassification (40.98% after cross-validation).

Arctodictis sinclairi was classified in different ways by different discriminant functions of the humerus and ulna, but the most probable assignments, when posterior probabilities of assignment and correct reclassification values of functions were taken into account, corresponded to the terrestrial and scansorial categories.

Using humerus discriminant functions, specimens of *B. tuberata* were assigned primarily as cursorial and terrestrial, and only secondarily to the scansorial class. By contrast, ulna functions assigned this taxon to the scansorial group with high probabilities. Tibia functions did not clarify the situation, as they assigned similar low probabilities to the terrestrial, scansorial, and arboreal classes with both PA and PVR residuals.

All discriminant analyses agreed on the assignment of *C. patagonica* to scansorial habits. However, the functions constructed with PVR residuals assigned this taxon to the semifossorial group in the first or second instances.

'Lycopsis' longirostrus was classified as scansorial in the best humerus function, and as terrestrial in the best ulna function.

Prothylacynus patagonicus was assigned to scansorial or arboreal habit categories with high probabilities by both humerus and ulna functions, and secondarily to the semifossorial group in the PA residuals ulna function. The tibia functions did not clarify this situation, and instead added some support for terrestrial habits.

Pseudonotictis pusillus, only included in the humerus analyses, was classified as arboreal with high probability.

Sipalocyon gracilis was classified as terrestrial, semifossorial, and scansorial with moderate to low probability according to the humerus and ulna functions, without preference for any category.

Thylacosmilus atrox was assigned to the terrestrial group by most functions. However, using the PVR

Table 2. Locomotory habit classifications of Sparassodonta species obtained from discriminant analyses of humerus, ulna, and tibia, using: relative warps (RWs), residual component after phylogenetic autoregression analyses (RRWs PA), and residual component after phylogenetic eigenvector analyses (RRWs PVR) as explanatory variables

	Discriminant analyses of the humerus		
Species	RWs (59.41%; 52.47%)	RRWs PA (56.44%; 41.58%)	RRWs PVR (68.32%; 54.45%)
Arctodictis sinclairi	T-S (64-27%)	T-C (67-21%)	**S-T (46-33%)**
Borhyaena tuberata	T-S (65-29%)	C-T (65-32%)	**C-T-S (35-33-28%)**
Cladosictis patagonica	S-A (44%-42%)	T-S-F (30-29-28%)	**S-F (57-20%)**
'Lycopsis' longirostrus	A-S (55-35%)	S-C-F (30-29-28%)	**S (68%)**
Prothylacynus patagonicus	A (89%)	F-A-S (49-31-20%)	**A (80%)**
Pseudonotictis pusillus	A (78%)	T-F-A (46-26-17%)	**A (81%)**
Sipalocyon gracilis	A-S (60-20%)	F-T (46-26%)	**F-A-S (42-28-26%)**
Thylacosmilus atrox	T-S (38-35%)	C (73%)	**S-T-F (39-23-17%)**
	Discriminant analyses of the ulna		
	RWs (67.82%; 57.47%)	RRWs PA (70.11%; 62.07%)	RRWs PVR (65.52%; 49.43%)
Arctodictis sinclairi	A-T (65-26%)	**T-A (64-28%)**	A-C-F-S (55-13-11-11%)
Borhyaena tuberata	S (93%)	**S (99%)**	S (94%)
Cladosictis patagonica	S-A (73-17%)	**S (87%)**	S-F (61-27%)
'Lycopsis' longirostrus	T-A (35-34%)	**T (75%)**	F-T-S-A (34-22-21-15%)
Prothylacynus patagonicus	S-F (60-36%)	**S-F (61-36%)**	F-S (56-42%)
Sipalocyon gracilis	F-T-A-S (39-22-20-19%)	**T-F-S (63-19-14%)**	F-S-T (54-21-15%)
cf. *Thylacosmilus*	C (99%)	**C (100%)**	C (93%)
	Discriminant analyses of the tibia		
	RWs (59.02%; 40.98%)	RRWs PA (68.85%; 40.98%)	RRWs PVR (68.85%; 40.98%)
Borhyaena tuberata	T-A (43-37%)	**A-T-S (55-22-19%)**	**T-A-S (38-22-22%)**
Cladosictis patagonica	T-F (42-39%)	**S (66%)**	**F-S (41-34%)**
Prothylacynus patagonicus	F-T-A (39-26-22%)	**A-T-S (34-30-28%)**	**T-F-S (39-29-23%)**
Thylacosmilus atrox	T-F (52-43%)	**F-T (69-25%)**	**F-T (84-12%)**

For each analysis, total correct reclassification percentage before and after cross-validation is indicated in parentheses (in each column header, respectively). For each class assignment, posterior probabilities are also indicated in parentheses (in decreasing order, next to assignments).

A, arboreal; C, cursorial; F, semifossorial; S, scansorial; T, terrestrial.

Bold type indicates the most reliable assignment based on correct reclassification values.

Underlined abbreviations denote habit categories consistently assigned by different methods.

residuals function of the humerus, this taxon was assigned as scansorial in the first instance but with low probability (39%). This result disagrees with the cursorial assignment given by the function built using RRWs of PA. The analyses of the ulna and the tibia agreed in assigning this taxon (cf. *Thylacosmilus* in the cases of the ulna analysis) to the terrestrial group, with maximum probability for the cursorial category in the case of the ulna analysis. The tibia analysis classified this taxon as semifossorial or terrestrial with high probability.

Allometric analyses

OLS regressions between shape axes (RWs) and size (natural logarithm of centroid size; means by species) suggested a significant relationship of the humerus (Wilks's lambda = 0.206, $F_s = 5.089$, $P < 0.001$) and ulna data sets (Wilks's lambda = 0.192, $F_s = 6.984$, $P < 0.001$) with size. There was no significant relationship for the tibia data set (Wilks's lambda = 0.192, $F_s = 1.168$, $P = 0.344$). However, when the phylogenetic effect was considered using PGLS regressions, these relationships became nonsignificant for the humerus (Wilks's lambda = 0.413, $F_s = 0.733$, $P = 0.949$) and ulna (Wilks's lambda = 0. 340, $F_s = 1.187$, $P = 0.197$), and remained nonsignificant for the tibia (Wilks's lambda = 0.206, $F_s = 0.654$, $P = 0.961$).

DISCUSSION

DISCRIMINANT ANALYSES AND PHYLOGENETIC CORRECTIONS

Discriminant analyses showed lower correct reclassification values than those typically shown by previously published analyses (e.g. Croft & Anderson, 2007; Schutz & Guralnick, 2007). However, we emphasize that there are important differences regarding the treatment of data sets in the various analyses, which could affect the reliability of the functions. The inclusion of more explanatory variables than recommended (Neff & Marcus, 1980; Legendre & Legendre, 1998), working at specimen level without weighting (Mendoza & Palmqvist, 2008), or the use of ecological groups represented by one or few clades, or without phylogenetic treatment (i.e. enhancing discrimination of functional groups by common inherited characteristics), may overestimate the confidence of functions, improperly increasing correct reclassification values.

Regarding the humerus data set, when discriminant functions were built from specimens instead of species whilst maintaining the number of explanatory variables constant (i.e. eight RWs), reclassification values increased by 5% (7% after cross-validation). When the number of explanatory variables was recalculated as a function of specimen sample size (i.e. 21 RWs), reclassification values increased by 15% (10% after cross-validation). Thus, correct reclassification values for the humerus, ulna, and tibia reach as high as 71 to 80%, similar to previously published values (e.g. Schutz & Guralnick, 2007). The number of discriminant groups must also be taken into account when comparing with previous discriminant analyses: 50% of total correct reclassification is equal to what we would expect by chance if only two classes were defined, but is informative if more groups are defined. We hope that the consideration of these factors can lead us to obtain more conservative and 'realistic' functions. However, given that reclassification values obtained were not very high and that we were dealing with groups that have no living representatives, these classifications must be taken with caution and in combination with exploratory analyses (i.e. RWs analyses).

In all the RW analyses, we observed a subdivision or locomotor 'sectorization' into taxonomic subgroups. This phenomenon decreased or disappeared in residual analyses after application of phylogenetic methods, which is expected because 'specific' shape components are retained and functional convergence of locomotor style between phylogenetically distant species (e.g. methaterian arboreal and eutherian arboreal; Figs 2, 4, 5) is highlighted.

Regarding morphofunctional differentiation, if high correlation between locomotion and phylogeny occurs, then removal of the phylogenetic component may lead to a loss of useful information rather than just 'phylogenetic interference'. Different responses in the differentiation of locomotory habits were observed depending on the elements analysed and methods applied (Fig. 3, Table 2). In any case, discrimination capacity was similar or better when phylogenetic comparative methods were applied (PVR method in humerus, PA in ulna, and PA and PVR in tibia), which is desirable given the goal of this study. The results of these discriminant analyses suggest that the application of comparative methods allows the building of more precise and less biased functions in classificatory instances, modifying in many cases the assignment of fossil specimens (Table 2).

Differences between the performance of PA and PVR methods can be evaluated through comparison of grid deformations before and after their application (Fig. 3). In analyses of both the humerus and ulna, both methods explained a large amount of shape variation as being a result of the phylogenetic structure of the data sets, in agreement with statistical parameters (e.g. Moran's *I*; result not shown). For the humerus, the shape changes explained by phylogeny in the PA residual analysis are very different from those suggested by PVR methods. In the analyses of the ulna, both methods explained the same shape changes, although PA suggested a greater amount of variation owing to the inherited component. These variations in performance can be linked to differences between PA and PVR residual discriminant analyses. In the tibia analysis, PA and PVR deformation grids suggested that only a minor fraction of shape variation could be explained by phylogeny, both methods showing similar performances in classificatory instances. These results suggest that different comparative methods can show different performances with different data sets, agreeing with the simulation studies of Martins *et al*. (2002), who postulated that the performance of comparative methods can vary as a function of the data sets and phylogenetic hypotheses.

MORPHOFUNCTIONAL ANALYSIS OF HUMERAL SHAPE VARIATION

In the shape analysis of the humerus (Fig. 2), the metatherians tended to show a more restricted distribution in the morphospace than the eutherians.

This is related to the absence of metatherian forms with an extremely reduced lateral epicondylar crest. In other words, all metatherian taxa present some degree of development of a lateral epicondylar crest. This feature may be linked to the constraint imposed on forelimb morphology by the mode of metatherian reproduction, in which the immature neonates crawl to their mother's pouch immediately after birth (Sears, 2004); in turn, this requires the development of strong flexor and extensor forelimb muscles to climb.

With regard to the locomotory groups, the cursorial group was the most clearly differentiated one. The trochlea of cursorials is distally expanded and narrower with respect to the capitulum than in other groups. These features have been linked to the fact that in cursorial mammals, body mass is supported mainly by the radius instead of the ulna (Andersson, 2003, 2004). A wide and anteriorly located proximal articular surface of the radius (Hildebrand, 1954) has been linked to a marked restriction of the rotational movement in the parasagittal plane (Andersson, 2004). The reduction of muscular attachment areas observed in cursorial species has been related to reduction of distal muscular masses in their limbs, which decreases inertial forces and favours good running performance (Andersson, 2004). This results in loss of pronation, supination, and manipulation abilities (Taylor, 1974; Munthe, 1989; Wang, 1993; Andersson, 2004).

Scansorial placental mammals have a wide distribution in the morphospace, overlapping with other locomotory groups. Similar observations were made in previous studies (Sargis, 2002; Schutz & Guralnick, 2007). This overlap (observed also in the ulna and tibia analyses; Figs 4B, 5B) is expected because of the continuous and non-exclusive nature of locomotory styles (Carrano, 1999), and the influence of other factors that were not contemplated in these analyses (e.g. behaviour, gait pattern).

A strong lateral development of the lateral epicondyle and its corresponding crest is observed in arboreal, scansorial, and some semiaquatic mammals. These structures provide muscular attachment for flexors, extensor, and the supinator of the elbow, and digital extensors (brachioradialis, extensor carpi radialis, supinator, lateral head of triceps, amongst others; Evans, 1993; Argot, 2001; Szalay & Sargis, 2001). The development of these structures improves antebrachial supination abilities and allows considerable extension of the forelimb during swimming (Schutz & Guralnick, 2007) and the same functions plus manipulation during climbing (Lemelin, 1999; Argot, 2004b). The lateral epicondylar crest is shorter in semiaquatic species than in arboreal and scansorial placental species, which may be related to differential development of some muscular groups. Arboreal, scansorial, and semiaquatic forms share a medially developed medial epicondyle and supraepicondylar area. These features might be related to pronation–supination abilities in both locomotory activities (climbing and swimming), because those areas represent the site of origin of carpal flexors (digital flexors, flexor carpi ulnaris and radialis) and the pronator teres, which are the main muscles controlling wrist movements (Evans, 1993; Flores & Díaz, 2009). The moderate to strong development of the trochlea and capitulum in semiaquatic taxa suggests some degree of restriction of movements during elbow flexion and extension in comparison to arboreal and scansorial mammals. The less developed articular zones of arboreals and most scansorials have been related to a greater freedom of movement at this articulation (Argot, 2001, 2003a; Candela & Picasso, 2008) and thus, enhanced muscular control.

The distal humeral morphology of semifossorial mammals shares some features with that of the consensus shape and the scansorial taxa (Fig. 2B). This was noted by Schutz & Guralnick (2007) in a similar analysis involving mustelids. However, semifossorials show greater mediodistal and medioproximal projection of the medial epicondyle (Fig. 2B), to which digital and carpal flexors are attached (e.g. flexor carpi radialis and flexor carpi ulnaris; Taylor, 1974; Evans, 1993). This morphology has been linked to greater forces applied by digits on the substrate during digging and climbing activities (Taylor, 1974; Argot, 2001; Candela & Picasso, 2008), which can partially explain the overlap between these groups.

The discriminant analyses of the humerus agreed with this pattern, suggesting that the greatest morphological differentiation occurs in cursorial and arboreal groups, given that most taxa are correctly reclassified and few others are misclassified into these groups. By contrast, members of the semifossorial, scansorial, and terrestrial groups were frequently misclassified for each other. The same trend was observed in the analyses of the ulna and tibia described below (Supporting Information Appendix S4).

MORPHOFUNCTIONAL ANALYSIS OF ULNAR SHAPE VARIATION

In the ulnar shape analysis (Fig. 4), as in the case of the humerus, metatherian mammals tended to show a more restricted distribution in the morphospace compared to eutherians. This is related to the absence of metatherian forms with extremely reduced olecranon process and coronoid process. As in the humerus, this may be linked to the requirement for strong flexor and extensor forelimb musculature used to climb up into the pouch (Sears, 2004).

As previously mentioned, cursorial species were well differentiated in the ulnar shape space (Fig. 4B). The olecranon process is posteriorly projected in cursorial and some terrestrial species. This has been interpreted as an indicator of erect limb posture because the triceps moment arm is maximized when the elbow is extended (Taylor, 1974, 1989; Van Valkenburgh, 1987; Williams *et al.*, 2008a; Fujiwara, 2009). In cursorials, the coronoid process is little projected anteriorly. This feature has been interpreted as a consequence of transferring body mass support from ulna to radius, increasing the radius–humerus contact that assumes the role of the coronoid process of the ulna (Hildebrand, 1954; Taylor, 1989; Sargis, 2002; Candela & Picasso, 2008). The exclusive cursorial morphospace shows a wide range of shapes, from the short, truncated, and robust olecranon of *Chrysocyon brachyurus* and *H. hyaena* to the slender and elongate one of *Acinonyx jubatus* and *Thylacinus cynocephalus*. This variation may be explained by differences in gait pattern (Spoor & Belterman, 1986; Spoor & Badoux, 1989; Taylor, 1989) or hunting behaviour (Iwaniuk *et al.*, 1999, 2000). As this pattern of variation holds after taking into account phylogenetic influence (Fig. 2D, F), it is probable that heredity is not a major factor (except for *Thylacinus cynocephalus*, see below). The distribution of taxa in the morphospace could be related to maximal running speeds. On the negative side of RW1, and close to zero for RW2, are *H. hyaena*, which is a slow (14 m s^{-1}; Janis & Wilhelm, 1993) but persistent (Spoor & Belterman, 1986; Taylor, 1989; Janis & Wilhelm, 1993) runner, and some poorly studied canids that are not characterized as frequent fast runners (*Chrysocyon brachyurus*, *Urocyon cinereoargenteus*, and *Cerdocyon thous*; Hildebrand, 1952, 1954; Savage, 1977; Nowak, 1999). The remaining canids and *Crocuta crocuta* were located in an intermediate position of the morphospace. These are fast runners (between 14 and 20 m s^{-1}; Janis & Wilhelm, 1993), generally able to travel long distances (Munthe, 1989; Taylor, 1989; Janis & Wilhelm, 1993; Andersson, 2004). Finally, *Acinonyx jubatus* had the lowest RW2 values and was near zero for RW1. This species is able to move very fast (30 m s^{-1}; Janis & Wilhelm, 1993) but only for short periods (Hildebrand, 1959, 1984; Taylor, 1989; Rusell & Bryant, 2001). Given the significant change in the position of *Thylacinus cynocephalus* after taking into account phylogenetic influence, its morphology could be at least partially explained by the phylogeny.

Arboreal and scansorial species have a robust humeral shaft at the trochlear notch level (Fig. 4B), where digital flexors (medially) and extensors (laterally) are attached (Argot, 2003a; Muizon & Argot, 2003). The robustness of the shaft has been linked to digit convergence and substrate grasping during climbing. These features are enhanced in terminal branch climbers (McClearn, 1992; Lemelin, 1999; Argot, 2002; Slice, 2005; Schmidt, 2008; Delciellos & Vieira, 2009). A different, and even complementary, factor to explain the robustness of the ulnar shaft is the presence of well-developed elbow flexors that insert on the anterior edge of the ulnar shaft below the coronoid process. These muscles (e.g. brachialis, anconeus; Argot, 2001, 2003a; Candela & Picasso, 2008) generate the strong elbow flexion and stabilization required for tree climbing. In arboreal species, the olecranon is anteriorly orientated, and the posterior ulnar margin is convex. These features have been directly related to climbing abilities in a crouched position, by keeping a low centre of gravity and allowing the maximum moment arm for the biceps and triceps brachii at the same time (Van Valkenburgh, 1987; Argot, 2001, 2003a). Arboreal and scansorial forms also show anteriorly developed coronoid processes that increase ulna–humerus contact. This configuration allows body weight to be borne by the ulna and not by the radius, as well as an increase of supination–pronation capabilities, because the radius is free to move with respect to the ulna (Sargis, 2002; Andersson, 2004; Candela & Picasso, 2008). The lateral position of the radial notch in arboreal mammals has been interpreted as an indicator of the wide range of movement in their elbow articulation, and supination–pronation movements (Hildebrand, 1988; Andersson, 2003, 2004; Peigné *et al.*, 2008; Fig. 4B).

Semifossorial species are characterized by a straight and elongate olecranon. This has been considered advantageous for digging because it maximizes the moment arm of the main elbow extensor, the triceps brachii (Iwaniuk *et al.*, 1999). However, marsupials without this functional requirement have similar shapes when phylogenetic influence is not considered (Fig. 4A, B).

MORPHOFUNCTIONAL ANALYSIS OF TIBIAL SHAPE VARIATION

In the tibial shape analysis (Fig. 5), as in previous analyses, metatherian mammals tended to show a more restricted distribution in the morphospace compared to the eutherians. All metatherians have a lateromedially extended tibial tuberosity and cranial intercondyloid area, at least to some degree.

Cursorial species are clearly differentiated in the morphospace, mainly because of the important development of the cranial intercondyloid area and the forward position of the tibial tuberosity (Fig. 5B).

This morphology has been interpreted as an indicator of powerful extension and an extended position of the knee, increasing the moment arms of the extensor muscles (e.g. quadriceps femoris) (Candela & Picasso, 2008; Williams *et al*., 2008b; Hunt, 2009).

Faster cursorials, such as canids and *Acinonyx jubatus*, are characterized by an expanded anterolateral margin and a deeper sulcus muscularis (see Hildebrand, 1954; Hunt, 2009). There are at least two possible explanations for these shape differences. Firstly, this morphology could be related to the wide knee flexion–extension range observed when these mammals run (Hildebrand, 1984, 1988), because it results in a wide insertion area for the biceps femoris (flexor and stabilizer of the knee; Spoor & Badoux, 1989; Evans, 1993; Williams *et al*., 2008b). Secondly, it could be related to the presence of strongly developed digital extensors that could be encased and protected by a deeper sulcus muscularis (Spoor & Badoux, 1989; Wang, 1993). Regarding articular areas, faster cursorials have asymmetric condyles, greater anteroposterior development of the medial condyle, and more posterior position of the lateral one (Fig. 5B). These features may also be related to ample flexion–extension of the knee (Hildebrand, 1984), by increasing the contact range between femur and tibia. In cursorial hyaenids, the sulcus muscularis is not present, perhaps because of the fact that their gait is restricted to a transverse gallop when they run (Spoor & Belterman, 1986) and to their poorly developed extensor digitorum longus (Spoor & Badoux, 1989). Regarding the articular area, *H. hyaena* and *Proteles cristatum*, which are slow runners, show weak asymmetry and little anteroposterior extension. These features could be linked to a small knee flexion–extension range. In *H. hyaena*, and secondarily in the remaining hyaenids, the tibial tuberosity has a particular very forward position, a feature frequently related to powerful extension and an extended position (see above; but see Spoor & Belterman, 1986). *Crocuta crocuta*, the fastest living hyaenid (Garland & Janis, 1993), shows an intermediate morphology between slow running hyaenids and the remaining cursorials.

Arboreal and semiaquatic species were located close together in the morphospace, with poorly developed cranial intercondyloid area and tibial tuberosity, features that have been related to a crouched posture of the knee (Sargis, 2002; Candela & Picasso, 2008; Williams *et al*., 2008b; Flores, 2009; Hunt, 2009). In most semiaquatic species analysed here (i.e. Lutrinae), propulsion in water is achieved by undulatory movements of the body and tail, which may be related to the possession of less-powerful extensors of the knee joint (Fish, 1994; Peigné *et al*., 2008). Both groups share a wide base of the tibial tuberosity. It is noteworthy that in both locomotory groups, the accessible substrate is a three-dimensional environment. The wide tibial tuberosity base (closely associated with a wider and shallower femoral trochlea) could provide greater freedom of movement beyond the parasagittal plane (e.g. crural abduction) or even rotation, and foot reversal (Wang, 1993; Szalay & Sargis, 2001; Argot, 2002; Candela & Picasso, 2008). Arboreal species have semicircular condyles, with similar area development or a wider lateral condyle. These morphologies are related to a wide range of movements outside the parasagittal plane (Argot, 2002), abduction of the hindlimbs (Szalay & Sargis, 2001; Argot, 2002; Flores, 2009), and homogeneous distribution of body mass support (Szalay & Sargis, 2001; Sargis, 2002; Flores, 2009).

Terrestrial, scansorial, and semifossorial species were widely distributed and overlapping in the morphospace. These wide shape ranges could be related to the wide variation in locomotory styles not analysed here (e.g. halfbound, transverse gallop, rotary gallop, trot) and the continuous nature of these classes (Hildebrand, 1977; Carrano, 1999). Semifossorial species show an anteriorly located but not necessarily narrow base of the tibial tuberosity. This may be related to body stabilization and body weight support on hindlimbs whilst digging, owing to an increase of the moment arms of knee extensors (van de Graaff, Harper & Goslow, 1982; Vizcaíno & Milne, 2002; Gorsuch & Larivière, 2005).

LOCOMOTORY HABITS OF SPARASSODONTA

These shape and discriminant analyses suggested that Sparassodonta species were relatively diverse regarding locomotory habits, but did not reach the degree of cursorial or arboreal specialization seen in extant Carnivora. All fossil taxa evidenced some degree of forelimb manipulation capabilities, and an extended hindlimb posture; such as was inferred in previous studies (Sinclair, 1906; Muizon, 1998; Argot, 2003a; amongst others).

Arctodictis sinclairi

In *A. sinclairi*, the humeral trochlear surface is wide and shallow (Fig. 2; see also Supporting Information Fig. S2). The ulnar trochlear notch is strongly enclosed by the coronoid and anconeus processes, and the radial notch is deep and slightly anteriorly positioned (Fig. 4). Regarding muscular attachment areas, the lateral epicondylar crest of the humerus is poorly developed, whereas the medial epicondyle projects strongly; the olecranon is long and the proximal half of the ulna is robust, with a slightly convex posterior margin.

All these features suggest some restriction of elbow joint movements, with little supination capability, and a slightly crouched position of the forelimbs. In addition, the carpal and digital flexors, and elbow, carpal, and digital extensors would have been well developed. All these observations agree with Forasiepi (2006, 2009), who suggested an important range of movements at the wrist and plantigrade posture, based on limb proportions and morphology of the bones of the autopodium, and also suggested constrained elbow movements, based on the presence of deep scars for the interosseous ligament, amongst other features.

The discriminant analyses assigned *A. sinclairi* to the terrestrial and scansorial categories. However, the restricted supination and muscular stabilization inferred for the elbow joint of this taxon, as well as the straight radius and restricted movements of the ankle joint (Forasiepi, 2006, 2009), are not expected for large scansorial mammals (e.g. *Panthera pardus*, *Ursus americanus*).

In brief, we support for this taxon terrestrial non-cursorial locomotory habits, as previously suggested (Marshall, 1977a; Argot, 2004a; Forasiepi, 2006, 2009).

Borhyaena tuberata

Borhyaena tuberata has a wide and deep elbow joint (especially at the trochlea) and a strong development of the medial epicondyle and lateral epicondylar crests. The posterior margin of the ulna is mostly straight instead of convex (similar to extant felids), whereas the proximal ulnar shaft is robust, and the coronoid process projects anteriorly. The proximal tibia has a moderately developed cranial intercondyloid area (Figs 2, 4, 5; see also Supporting Information Fig. S2).

The features observed in the humerus and ulna suggest a stabilized and extended posture of the elbow joint mostly restricted to the parasagittal plane, in relation to terrestrial habits (Sinclair, 1906; Marshall, 1977a) or even some degree of cursorial specialization (Muizon, 1998; Argot, 2003a). Other features have been suggested as consistent with terrestrial or cursorial habits. Robustness of the ungual phalanges (Sinclair, 1906), an inferred distal musculature reduction, extended and semidigitigrade or even digitigrade limbs (but see Forasiepi, 2009), and a relatively low lumbar flexibility (Muizon, 1998; Argot, 2003a) are in agreement with terrestrial locomotion. The morphology of humeral and ulnar attachment areas, and the anteriorly projected coronoid process of the ulna suggest the presence of strong digital and carpal flexors and extensors (Muizon, 1998) and important participation of the ulna in body support. This is more characteristic of nonspecialized habits (e.g. occasionally scansorial) than cursorial ones. However, it is necessary to consider the functional constraints on forelimb morphology in metatherians (Sears, 2004), which may obscure the interpretation. Moreover, the generalized morphology of the femur, tibia, and autopodials (Muizon, 1998), and appendicular proportions (e.g. not elongated ulna and metacarpals; Argot, 2003a), amongst other features, do not support fully cursorial habits. These features do not preclude climbing abilities for *B. tuberata*. In both RW and RRW analyses of the humerus and ulna, *B. tuberata* shares positions with some felids (e.g. *Panthera leo*) and *Gulo gulo*, which are scansorial and open-habitat ambulatory forms.

To sum up, the shape and discriminant analyses agree in classifying *B. tuberata* as a mainly terrestrial mammal, with some degree of cursorial abilities; it was probably a long-distance traveller but not a fast runner, and some potential climbing abilities cannot be ignored.

Cladosictis patagonica

This taxon has generalized humerus and ulna shapes, with a large humeral medial epicondyle, a high lateral epicondylar crest, and a moderately proximally projected olecranon with a convex posterior margin. A prominent feature of the proximal tibia is the anteriorly located and relatively narrow tibial tuberosity (Figs 2, 4, 5; see also Supporting Information Fig. S2).

All these features are consistent with moderate climbing and manipulation capabilities, a slightly flexed habitual posture of the forelimbs, and powerful and extended hindlimbs. This is in partial agreement with previous works (Muizon, 1998; Argot, 2003b). Muizon (1998) pointed out that this taxon showed some degree of cursorial capabilities, inferred because of the restricted movements of the shoulder and elbow joints. By contrast, Argot (2003b) suggested a striking combination of terrestrial (e.g. constraints on elbow joint movements) and scansorial features (e.g. convex posterior ulnar margin), with short plantigrade or semidigitigrade limbs. All discriminant analyses agreed in assigning *C. patagonica* to the scansorial habit category and, secondarily in most cases, to the semifossorial group. The restricted range of elbow and shoulder movements, and the radial robustness and straightness pointed out by Muizon (1998) and Argot (2003b), increased the moment arms of the flexors and extensors of forelimb joints (shoulder, elbow, and wrist) inferred here (from the shape analyses of the humerus and ulna). These are consistent with the functional requirements for some degree of digging activity (see Polly, 2007). In the forelimb autopodium (as seen in Argot, 2003b: fig. 6), the proximal phalanx of the fifth digit, the metacarpals, and the only known ungual phalanx (from the first digit) of *C. patagonica* seem to be relatively robust, at least in comparison with the autopodial bones of *S. gracilis* (Argot, 2003b), which is phylogenetically close. Strong ungual phalanges are concordant with fossorial habits because they allow exertion of great forces against the substrate (MacLeod & Rose, 1993). The hindlimb features of *C. patagonica* do not preclude this possibility: the anteriorly located and narrow tibial tuberosity, and well-developed gluteal fossa and greater trochanter (Argot, 2003b) are typical features of semifossorial mammals (e.g. *Meles meles*). These features increase moment arms and extend the attachment areas of knee extensors for body mass support and stabilization.

A scansorial–semifossorial interpretation reconciles morphology and function of the forelimbs as a tradeoff between free movement in climbing and stability in digging. The semifossorial abilities of *C. patagonica* are only potential, and are not as evident as in the Sparassodonta *Callistoe vincei* (Babot, Powell & Muizon, 2002; Argot & Babot, 2011). Our analyses suggest scansorial habits for *C. patagonica*, agreeing with Marshall (1977a) and Argot (2003b), and add the possibility of some digging capabilities although without great specialization in this sense.

'Lycopsis' longirostrus

In this species, the analyses of the humerus and ulna show moderate muscular attachment areas on these forelimb elements, and a slight concavity of the posterior margin of the ulna (Figs 2, 4; see also Supporting Information Fig. S2).

These features suggest moderate to little pronation–supination, carpal and digital flexion-extension, and a semicrouched or extended forelimb. Argot (2004c) arrived at similar conclusions through analyses of ulnar and phalangeal morphology. She listed several postcranial features supporting a primarily terrestrial (and secondarily scansorial) classification, including: quadrangular morphology of the scapula, great development of the coronoid process, and restricted movements in the hip but not the knee joints, amongst others. Our humerus discriminant analyses assigned this taxon to the scansorial category, whereas the ulna analysis supported an assignment to the terrestrial group, in agreement with Argot's (2004c) conclusions.

Prothylacynus patagonicus

Prothylacynus patagonicus has a humerus with a shallow trochlea and rounded capitulum, and an ulna with a well-developed coronoid process, a laterally orientated radial notch, and a convex posterior margin of the proximal ulna. In both the humerus and ulna, the muscular areas for attachment of elbow and wrist flexor and extensor muscles are very well developed. The tibial shape analysis shows great development of the cranial intercondyloid area and a moderate to narrow base of the tibial tuberosity anteriorly located (Figs 2, 4, 5; see also Supporting Information Fig. S2).

The features of the humerus and ulna of *Pr. patagonicus* suggest high elbow mobility (also in the wrist; see Argot, 2003a), and a powerful, semiflexed habitual posture of the forelimbs. These features also suggest that *Pr. patagonicus* had climbing abilities, agreeing with previous studies (Muizon, 1998; Argot, 2003a; *contra* Sinclair, 1906; Marshall, 1977b). Argot (2003a) inferred strong climbing abilities for this taxon, elbow mobility, semidigitigrade feet, and a muscular tail (as a balancing appendage). Humeral and ulnar discriminant analyses agreed in assigning this species to scansorial and arboreal habits. However, all features observed in our tibia analyses suggest a habitually extended position of the hindlimbs and knee movements restricted to the parasagittal plane, ruling out a highly arboreal specialization. These conclusions agree with Muizon (1998), who inferred movement restrictions at the knee and especially ankle joints, and they only partially agree with the inferences stated by Sinclair (1906) and Argot (2003a).

The strong and anteriorly located tibial tuberosity was interpreted by Muizon (1998) as an indicator of jumping or running abilities. Another possible function of this feature is knee stabilization, linked to the need to transport large prey, as in the case of *H. hyaena* (Spoor, 1985). This analogy is conceivable if we consider the strong attachments for the mandibular, neck, and forelimb muscles (Argot, 2003a, 2004a; Forasiepi, 2006).

Ulna and tibia discriminant analyses tended to secondarily associate *Pr. patagonicus* with semifossorial habits because of its olecranon and tibial tuberosity development and shape. However, the shallow humeral trochlea, ungual phalanx morphology (Argot, 2003a), the inferred great pronation–supination mobility at the elbow (Muizon, 1998; Argot, 2003a), and a great lumbar mobility (Argot, 2003a) disagree with this assignment. It is noteworthy that in the ulna and humerus analyses, some scansorial species with high forelimb manipulatory capabilities or strength were incorrectly assigned to arboreal or semifossorial categories (e.g. *Lutreolina crassicaudata* in ulna analysis). The case of *Pr. patagonicus* could result from a similar process.

In summary, we infer that *Pr. patagonicus* was a scansorial predator that travelled on land, with moderate climbing capabilities. Its peculiar combination of features in the forelimb could be explained by its hunting strategy rather than by fully arboreal locomotion (but see Argot, 2003a).

Pseudonotictis pusillus

The specimen of *Ps. pusillus* was included only in the humerus analyses, in which its morphology was similar to that of arboreal and scansorial forms (Fig. 2; see also Supporting Information Fig. S2), as was previously pointed out by Argot (2003b). Taking into account the state of preservation of the humeral mediodistal margin, its medial epicondyle may actually be more projected than was inferred in this study. In any case, a great number of features support the arboreal group assignment, including a well-developed lateral epicondylar crest, lateral epicondyle, and entepicondylar foramen. Radial morphology (Argot, 2003b) also suggests an important range of movement in the elbow joint, consistent with arboreal or scansorial locomotion.

Sipalocyon gracilis

The morphology of the elbow bones and lateral margin of the humerus are very similar to those of *C. patagonica* and *'L.' longirostrus*, whereas the medial epicondyle and medial epicondylar bridge are very similar to those of *C. patagonica*, but with a more slender shape. The ulnar proximal shaft is robust, and compared to *C. patagonica* and *'L.' longirostrus*, *S. gracilis* has a more laterally tilted radial notch of the ulna (Figs 2, 4; see also Supporting Information Fig. S2).

These features suggest that *S. gracilis* had moderate to important manipulation, pronation–supination capabilities, and a semicrouched habitual posture, features typical of scansorial species, and also suggested by previous authors (Sinclair, 1906; Argot, 2003b), who in turn included observations on radial and autopodial morphology of this taxon shared with extant scansorial species. The moderate to important development of carpal and digital flexors and extensors, inferred from the development of the muscular attachment areas, is a trait shared with arboreal, scansorial, and semifossorial living forms, and in agreement with the assignments from discriminant analyses.

In some classification instances, *S. gracilis* was assigned to semifossorial habits, but its high elbow mobility and slender forelimb morphology disagree with this interpretation. Thus, we infer scansorial habits for *S. gracilis*, but without extreme arboreal specialization.

Thylacosmilus atrox

The distal articular surface shape of the humerus of *T. atrox* is moderately developed. By contrast, this taxon shows a great proximal development of the lateral epicondylar crest, with a proximally located and little-developed medial epicondyle on the humerus. The ulna has a strong, short, and straight olecranon, but is not especially robust in its remaining proximal diaphysis, and the radial notch is laterally orientated. The tibial tuberosity of *T. atrox* is anteriorly located and its articular surface shows poor development in comparison to the cranial intercondylar area (Figs 2, 4, 5; see also Supporting Information Fig. S2).

The features observed in the elbow suggest moderate elbow stabilization, whereas the position of the radial notch and medial epicondyle (site of origin of the pronator muscle), and the well-developed and high lateral epicondylar crest of the humerus (origin of supinator muscles) suggest marked pronation–supination abilities. The morphology of the ulna and medial sector of the humerus suggest no remarkable development of the digital and carpal flexors and extensors, and an extended forelimb posture. Some of these features, added to shoulder mobility and strong forelimb adductors, have been interpreted as indicators of prey manipulation hunting strategies (e.g. Simpson, 1941; Argot, 2004b). The shape of the proximal tibia suggests a habitually extended posture of the hindlimbs and strong extensor musculature, but not a wide range of movement at the knee. Our discriminant analyses of the humerus precluded clear assignment of *T. atrox*, given the low probabilities assigned to semifossorial, terrestrial, and scansorial groups, suggesting that the morphology of the humerus of *T. atrox* cannot be considered diagnostic of any locomotory category here contemplated. The discriminant analyses of both ulna and tibia suggest terrestrial habits for cf. *Thylacosmilus*, with the specimen MACN-Pv 10956 placed amongst the cursorials, and for *T. atrox*, with the specimen FMNH 14344 amongst the semifossorial and fully terrestrial taxa. Riggs (1934) and Argot (2004b) described *T. atrox* as digitigrade or semidigitigrade in the forelimbs, and semidigitigrade in the hindlimbs, suggesting the use of the terrestrial substrate and use of an ambush hunting strategy (Riggs, 1934; Simpson, 1941; Marshall, 1977a; Goin & Pascual, 1987; Argot, 2004a, b).

Shared features between hyaenids and *T. atrox* include: short lumbar region, robust hindlimbs, underdeveloped greater trochanter, and short tibia relative to the femur. Other attributes observed in hyaenids and inferred for *T. atrox* are: restricted movements in lumbar region, stabilized and restricted movements at the knee and ankle, forelimbs more elongated than hindlimbs (see Riggs, 1934; Goin & Pascual, 1987; Argot, 2004b), and a strong and powerful musculature of the neck and cranium. Argot (2004b) interpreted some of these features as indicators of stable support during hunting, and precluding fast or persistent running. However, these features are also present in living hyaenids, which are heavy cursorial carnivorans and include species capable of persistent running and travelling slowly but over long distances (Rieger, 1981; Garland & Janis, 1993; Hofer & Mills, 1998). The anterior location of the centre of gravity, inferred for *T. atrox*, has been related to transport of large prey (such as in *H. hyaena*; Spoor, 1985; Spoor & Belterman, 1986) and a transverse gallop gait when running (Spoor & Belterman, 1986; Spoor & Badoux, 1988; Turner & Antón, 1996; Wroe, Lowry & Antón, 2008). Ursids, which are ambulatory mammals that travel long distances, share many of these features, but their tibial tuberosity is not anteriorly located as in *T. atrox* and hyaenids (Fig. 5A). By contrast, some authors (Churcher, 1985; Argot, 2004b) have mentioned the presence of a reduced metatarsal in *T. atrox*, and for this reason they have attributed to this taxon some degree of cursoriality (Churcher, 1985). A recent revision suggested that the bone in question would be a parafibula (Forasiepi, 2006, 2009). If so, then the palaeontological inferences based on this material have to be reconsidered. It is important to note that the analyses of ulna and tibia shape, after removing the effects of phylogeny, agreed in placing *T. atrox* near the hyaenids, and secondarily, close to other long-distance ambulatory taxa.

The short and semirigid lumbar zone of *T. atrox* suggests that this species was unable to achieve the fast acceleration required for ambush strategies (Hildebrand, 1961, 1984; Garland & Janis, 1993; Janis & Wilhelm, 1993; Hofer & Mills, 1998; Andersson, 2004; Wroe *et al*., 2008). The wide effective angle of gape measured in *T. atrox* (Churcher, 1985), the relatively poor development of digital and carpal flexors and extensors, and the lack of retractile claws (Argot, 2004b), have been proposed by Churcher (1985) and Goin & Pascual (1987) as evidence of a hunting strategy different from ambush (but see Argot, 2004b).

In summary, the power and dexterity of the forelimbs of *T. atrox* suggest prey manipulation during hunting, as pointed out in previous work (Simpson, 1945; Churcher, 1985; Goin & Pascual, 1987; Argot, 2004b). However, the proportions, shape and postures inferred for its limbs, added to its lumbar morphology, could have precluded climbing or fast running, but are consistent with some degree of cursoriality. *Thylacosmilus atrox* may have been capable of persistent galloping, as in the case of living hyaenids, some ursids, and large mustelids, amongst others (Hildebrand, 1977; Spoor & Belterman, 1986; Spoor & Badoux, 1988; Turner & Antón, 1996).

CONCLUSIONS

The application of geometric morphometric techniques and phylogenetic comparative methods to study the postcranial shape variation of extant predators and extinct Sparassodonta species offers a comparative and quantitative framework that has permitted the analysis of the association between shape and locomotory categories, as well as a review of shape–function relationships previously established through other approaches.

The shape of the humerus, ulna, and tibia was influenced by phylogeny, partitioning many of the locomotory groups in the morphospace according to higher taxonomic level, and obscuring shape–function relationships and locomotory group discrimination. This effect decreased after the application of comparative methods. The cursorial locomotory group was clearly defined in all morphospaces, with morphological features opposed to those observed in the arboreal group.

With respect to fossil species, *B. tuberata* and *T. atrox* could have reached some degree of cursoriality, being persistent runners rather than fast ones. Many of the fossil taxa analysed, such as *B. tuberata*, *C. patagonica*, '*L.*' *longirostrus*, *Ps. pusillus*, *Pr. patagonicus*, and *S. gracilis* may have been able to climb, but none of them seem to be tree-dwelling specialist forms. *Arctodictis sinclairi* was probably a terrestrial predator, with no cursorial or scansorial specializations. The Sparassodonta species were shown to be a diverse group with respect to locomotory habits, although they did not reach the high degree of specialization observed in some extant predators.

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SUPPORTING INFORMATION

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

Appendix S1. Sparassodonta specimens analysed, indicating collection number, species, skeletal elements included, provenance, and a short description of postcranial remains.
Appendix S2. Extant specimens studied and institutions where they are stored.
Appendix S3. Datasets for Sparassodonta specimens and extant species, indicating locomotory habits (Loc. Hab.), centroid size (CS), and first four relative warps (RW) for each analysed element.
Appendix S4. Confusion matrix and correct reclassification percentages of humerus, ulna, and tibia analyses, including as explanatory variables: relative warps (RWs), residual components of Phylogenetic Autoregression analyses (RRWs PA), and residual components of Phylogenetic Eigenvector Regression (RRWs PVR).
Figure S1. Combined phylogenetic tree used to build the connectivity matrices for comparative methods.
Figure S2. Sparassodonta postcranial elements included in shape analyses (one for each species): A–H, anterior view of distal part of humerus; I–O, lateral view of proximal part of ulna; and P–S, proximal view of tibia. A, I, *Arctodictis sinclairi*; B, J, P, *Borhyaena tuberata*; C, K, Q, *Cladosictis patagonica*; D, L, '*Lycopsis*' *longirostrus*; E, M, R, *Prothylacynus patagonicus*; F, *Pseudonotictis pusillus*; G, N, *Sipalocyon gracilis*; H, O, S, *Thylacosmilus atrox*.