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The central tenet of ecomorphological theory holds that there is a correlation between design (morphological traits) and ecology of organisms. The sigmodontine rodents (Rodentia, Cricetidae, Sigmodontinae) exhibit a remarkably high diversity of locomotory types, allowing them to occupy different environments and ecological niches. The main aims of our work were to test whether the internal morphology of the forelimb of 26 species of sigmodontines, as assessed through the analysis of 32 characters, differs among taxa that exhibit different types of locomotion (saltatorial, ambulatory, fossorial, scansorial, and natatorial), and whether such patterns also can be explained by the phylogenetic affinities of the species examined. Our results show that phylogeny explains an important part of the observed morphological variation in sigmodontine rodents. This phylogenetic inertia could be responsible for the homogeneity in the overall muscle forelimb morphology in this group. Tendon variables seem to be better descriptors of locomotory types than muscle variables. Twelve tendon variables of the forelimb exhibit distinct differences between fossorial and scansorial sigmodontines. No particular morphological variables are associated with ambulatory, saltatorial, and natatorial taxa. Additionally, 3 muscles (triceps longus, extensor digitorum, and flexor digitorum profundus) exhibit a greater anatomical cross-sectional area in fossorial and natatorial taxa than in other locomotory types.

Key words: locomotion, morphofunctional analysis, muscles, sigmodontine, tendons

Ecomorphological theory stresses that there is a correlation between design (morphological traits) and ecology of the organisms. In other words, mechanical demands imposed by ecological traits should be reflected in morphological changes of the system involved (Darwin 1859; Lauder 1981; Arnold 1983; Losos et al. 1998, 2002; Huey et al. 2003; Schulte et al. 2003, 2004; Vanhooydonck et al. 2006, 2009, 2010; Herrel et al. 2008; Russell and Higham 2009; Grizante et al. 2010; Tulli et al. 2011). In many ecomorphological and ecophysiological studies, locomotion is thought to be an intermediary step between form and function (Clemente et al. 2009). In this context, mammals exhibit a variety of body shapes that are often considered specific adaptations to particular environments and particular modes of life, all of which affect locomotion (e.g., Slijper 1946; Hildebrand 1985; Biewener 2003).

The muscle anatomy of the limbs of mammals is well known and has been studied in detail in several groups (e.g., carnivores, rodents, primates, marsupials, and xenarthrans—Slijper 1946; Lehmann 1963; Goldstein 1971; Woods 1972; McConathy et al. 1983; Hildebrand 1985; Kesner 1986; Spoor and Badoux 1986; Thorington et al. 1997; Biewener 1998; Elissamburu and Vizcaíno 2004; Hudson et al. 2011a, 2011b; Alvarez et al. 2012; Moore et al. 2013). These investigations, based on external and internal architecture of muscles, have demonstrated that muscle anatomy is linked with particular functional demands and the locomotory type of the species. For example, fossorial taxa present enlarged forelimb extensor muscles with an elevated proportion of fast oxidative–

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Table 1.—List of the muscles and tendons of the forelimb examined in this study.

Muscle	Abbreviation	Tendon	Muscle group
Extensor			
Teres major	Tm		Subscapular
Clavo-acromiodeltoideus	MCA		Deltoid
Spinodeltoideus	MSD		Deltoid
Tricep brachii, caput longus	TLg		Triceps
Tricep brachii, caput lateralis	TLat		Triceps
Tricep brachii, caput medialis	TMd		Triceps
Dorsoepitrochlearis	MD		Triceps
Extensor carpi radialis	ECR	X	Extensor of the forearm
Extensor carpi ulnaris	ECU	X	Extensor of the forearm
Extensor digitorum	ED	X	Extensor of the forearm
Abductor pollicis longus	Pl		Extensor of the forearm
Flexor			
Biceps brachii	BB		Flexor of the arm
Brachialis	B		Flexor of the arm
Flexor carpi radialis	FCR	X	Flexor of the forearm
Flexor carpi ulnaris	FCU	X	Flexor of the forearm
Flexor digitorum profundus	FDP	X	Flexor of the forearm
Flexor digitorum sublimis	FDSub	X	Flexor of the forearm
Palmaris longus	Pm	X	Flexor of the forearm
Pronator teres	Pr		Flexor of the forearm

glycolytic fibers, characteristics linked to rapid, powerful movements during excavations (Lehmann 1963; Goldstein 1971; Alvarez et al. 2012). Previous studies also have noted some relationship between the length of the tendons of some limb muscles and the mechanical constraints imposed by the environments in which they are used: the flexor carpi ulnaris tendon in didelphid mammals has been shown to be related to habitat use (Abdala et al. 2006).

In rodents, the subfamily Sigmodontinae is one of the most taxonomically diverse components of the Neotropical mammal fauna (Reig 1980). Sigmodontines also are diverse in terms of their ecology and lifestyles and exhibit a great variety of locomotory types, allowing them to occupy a wide range of environments, such as wet and dry forests, steppes, grasslands, savannas, deserts, paramo, and puna (Hershkovitz 1962; Voss 1988; Rivas and Linares 2006; Weksler 2006; Rivas et al. 2010).

Despite this extraordinary ecological diversity, only 2 studies have previously described the myology of some genera of sigmodontine rodents (e.g., Howell 1926; Rinker 1954), but neither quantified architectural properties of the muscles or their ecomorphological aspects. In this work, we examined for the 1st time the forelimb muscles and tendon morphology of specimens belonging to 26 species of sigmodontines that

exhibit different forms of locomotion. Our main aims are to test whether the internal morphology of the sigmodontine forelimb, as assessed through the analysis of 32 characters, differs among taxa that exhibit different types of locomotion and whether such patterns can be explained solely by the phylogenetic affinities of the species examined or by another underlying factor. Taking into account that muscles used in burrowing tend to be short (Gambaryan 1960; Hildebrand 1985) and that the forelimbs are the primary digging tools in the species we studied, we predict that fossorial sigmodontines will have forelimb muscles that are significantly shorter than those of the other locomotory groups. Considering that muscles used in digging tend to be more massive than others (Hildebrand 1985), we predict that fossorial sigmodontines will have muscles with greater cross-sectional areas than those of other locomotory groups. Muscles having short, pennate fibers and attached to long tendons evolve to act as force generators for elastic strain energy storage and recovery within the tendon (Biewener 1998), and we predict that saltatorial, scansorial, and natatorial sigmodontines will present short muscles branches and long tendons. We predict that extensor muscles of the forelimb used by natatorial sigmodontines to paddle should have large cross-sectional areas to generate a higher force to thrust. We predict that part of the variability of our data set will be explained by phylogeny instead of adaptation, because of the different degrees of relatedness shown by our selected species.

Materials and Methods

We examined 97 adult specimens from 26 sigmodontine species. These species belong to several tribes and display different locomotory types (see Appendix I).

Morphology.—The right forelimb was dissected and 19 muscles and 9 tendons (Table 1; Supporting Information S1, DOI: 10.1644/13-MAMM-A-232.S1) were removed intact and measured (Figs. 1a and 1b). Muscle and tendon lengths were measured between the origin and insertion points, and we also recorded tendon width. Muscle and tendon names follow Rinker (1954) and Diogo et al. (2009). When we refer to muscles we add the abbreviation "m." before muscle names; otherwise names refer to tendons associated with those muscles. To remove the effects of body size from the morphometric variables, we used residuals from regressions between body size and each variable. The resultant untransformed residuals were used as variables in subsequent statistical analyses (Borcard et al. 1992; ter Braak 1995; Giannini 2003). All measurements were taken in millimeters using a digital caliper (± 0.01 mm; Mitutoyo Corp., Kure, Japan).

Determination of locomotory types.—Although we are aware that the average sigmodontine rodent is capable of a wide range of locomotory modes, we assigned the different locomotory types based on what the species most frequently do. The assignment of locomotory types in the rats studied was mainly based on Polly (2007), information from the literature,
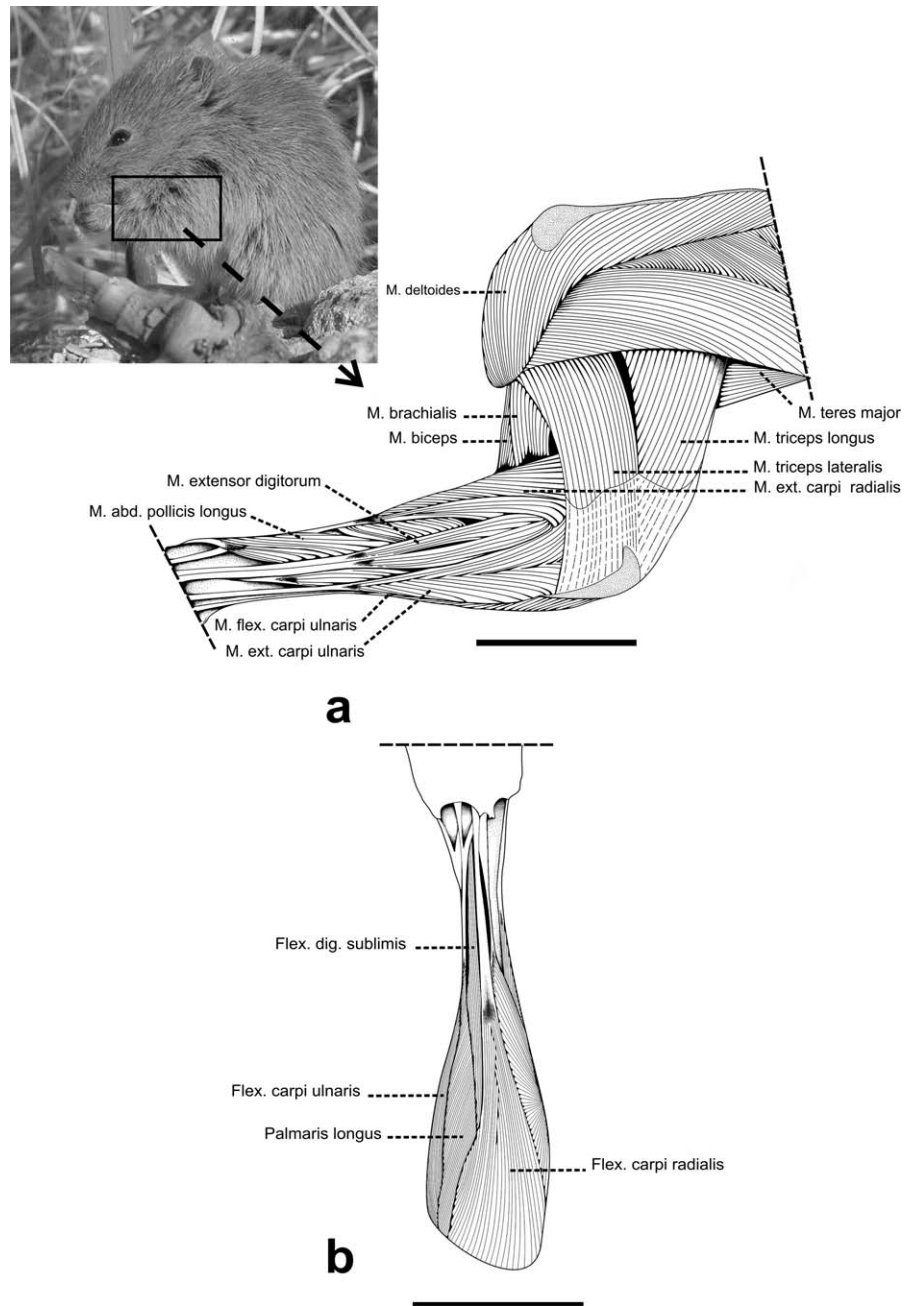
Fig. 1.—Superficial muscles of the forelimb of a sigmodontine rodent (*Akodon spegazzinii*): a) lateral view, and b) ventral view. The arrow indicates a detail of the dissected muscles and tendons of the forelimb (in the box).

and field observations (Table 2). Species were classified into categories as follows: saltatorial, species in which progression is composed of a series of leaps in which both limbs extend simultaneously, lifting the body completely from the ground and forward; scansorial, species that climb vertical surfaces by pulling their forefeet toward the substrate, while the hind feet push on the substrate; ambulatory, species that usually use the ground to move about and do not have specializations that limit any particular activity; natatorial, species that regularly swim for dispersal, escape, or foraging, using the limbs as their primary means of propulsion; and fossorial, species that regularly dig to build simple burrows as shelters or for foraging underground, using mainly their forelimbs.

Statistical analysis.—To reduce the dimensionality of morphometric variation, we performed a principal component analysis (PCA) based on a variance–covariance matrix of size-corrected morphological data for all 97 specimens. We carried out 2 PCAs separately, one of them using muscle traits and the other tendon traits (Tables 3a and 3b). The number of principal component (PC) axes used in subsequent analyses was determined from a scree plot of the eigenvalues (Jackson 1993).

TABLE 2.—Locomotor types of the species examined in this study based on literature data.

Species	Locomotor type	Reference
Abrothrix lanosus	Ambulatory	Rodríguez-Serrano et al. (2008)
Abrothrix longipilis	Ambulatory	Rodríguez-Serrano et al. (2008)
Akodon caenosus	Ambulatory	Emmons and Feer (1999)
Akodon simulator	Ambulatory	Ojeda and Tabeni (2007)
Akodon spegazzinii	Ambulatory	Ojeda and Tabeni (2007)
Calomys callosus	Ambulatory	Rivas et al. (2010)
Calomys musculinus	Ambulatory	Corbalán and Debandi (2009)
Calomys tener	Ambulatory	Mares et al. (1986)
Chelemys macronyx	Fossorial	Alarcón et al. (2011)
Eligmodontia puerulus	Saltatorial	Hershkovitz (1962)
Eligmodontia typus	Saltatorial	Taraborelli et al. (2003)
Graomys griseoflavus	Ambulatory	Hershkovitz (1962)
Holochilus brasiliensis	Natatorial	Weksler (2006)
Holochilus chacarius	Natatorial	Weksler (2006)
Necromys obscurus	Ambulatory	Rivas et al. (2010)
Nectomys squamipes	Natatorial	Santori et al. (2008)
Oligoryzomys brendae	Scansorial	Weksler (2006)
Oligoryzomys chacoensis	Scansorial	Myers and Carleton (1981)
Oligoryzomys delticola	Scansorial	Miller and Anderson (1977)
Oligoryzomys flavescens	Scansorial	Miller and Anderson (1977)
Oligoryzomys longicaudatus	Scansorial	Myers and Carleton (1981)
Oxymycterus rufus	Fossorial	Hershkovitz (1994)
Phyllotis osilae	Ambulatory	Hershkovitz (1962)
Phyllotis xanthopygus	Ambulatory	Hershkovitz (1962)
Reithrodon auritus	Ambulatory	Pardiñas et al. (2008)
Scapteromys aquaticus	Natatorial	Miller and Anderson (1977)

Morphology–locomotory types.—To test the correlation among morphological traits and ecological groups, we ran redundancy analysis (RDA—Rao 1964; ter Braak 1995). RDA is an ordination technique deriving from PCA, with a linear constraint represented by explanatory variables of an external matrix (see details in ter Braak [1995]). Thus, the main matrix includes morphological data (length and width of forelimb muscles and tendons); a 2nd data set includes ecological data (the 5 locomotory type categories). For all these analyses, calculations were done using a covariance matrix, because our variables were measured in the same units (Legendre and Legendre 1998). Significance was evaluated using 4,999 unrestricted Monte Carlo permutations for individual locomotory categories, using forward stepwise addition when appropriate. In all cases the alpha level of significance was set to 0.05 (see Morales and Giannini 2010). Analyses such as RDA are useful when trying to relate a matrix of variables (commonly a species matrix, main matrix) to another matrix (environmental matrix or explanatory variables matrix—Legendre and Legendre 1998). This analysis allowed us to constrain all the variation in the analysis to the explanatory variable matrix.

Morphology–phylogeny.—Comparative methods, such as canonical phylogenetic ordination (CPO—Giannini 2003), are used to determine the morphological variation explained by historical factors (phylogeny) and its covariation with other factors (locomotory types). Additionally, we used a Monte Carlo permutation test based on 4,999 random permutations to calculate the statistical significance ($P = 0.05$) of every external variable (Manly 1997). CPO is a phylogenetically based comparative method by which the set of species is codified in a phylogenetic structure matrix (assigning 0s and 1s based on whether species belong to a monophyletic group or not). This matrix can then be employed as an external or covariate matrix in statistical tests (Giannini 2003). Thus, in our study the main matrix includes morphological data (length and width of forelimb muscles and tendons). A 2nd data set includes phylogenetic data (the phylogenetic matrix) constructed using different topologies based on a metatree from the available topologies that depict the pattern of relationships of the species studied (see Morales and Giannini 2010). That tree (Fig. 2) is based on the results of several morphological and molecular studies (e.g., D'Elía 2003; Weksler 2006; Lanzone et al. 2007; Rivera et al. 2007; Feijoo et al. 2008; Bonvicino et al. 2010; Jayat et al. 2010; Salazar-Bravo et al. 2013).

Ecomorphological relationships: partial canonical phylogenetic ordination.—To test the relationships among morphology, ecological categories, and phylogeny, we performed a partial canonical phylogenetic ordination (pCPO—Giannini 2003). We used 3 variable matrices for this analysis: a main matrix including morphological variables, an external matrix of ecological data (the 5 locomotory categories after RDA), and an external matrix of phylogenetic data (after CPO). Thus, the variation explained is partitioned into 3 components: locomotory types alone (ecology), clades alone (phylogeny), and their covariation. This technique ordinates the 1st set or main matrix on axes that are linear combinations of variables of the 2nd set or explanatory variables matrix. Thus, the analysis extracts the major gradients in the data that can be accounted for by explanatory variables. When a 2nd external matrix is included (phylogenetic matrix) variation can be partitioned and percentages exclusive to, and shared by, each external matrix are obtained. pCPO is a modification of a unimodal canonical correspondence analysis (ter Braak 1986) or an RDA (ter Braak and Smilauer 1998). A pCPO was performed by adding variables successively (forward stepwise), which yielded an economic model to explain the variation in the main matrix with a minimum number of variables. Using the same multivariate approach as pCPO, we tested for the possible covariation of locomotory types and phylogeny using partial RDA (Borcard et al. 1992). In this technique, the phylogenetic matrix can be used as the covariable to estimate covariation of external factors. The ecomorphological correlations are shown as a triplot (Figs. 3 and 4; ter Braak and Smilauer 1998), where the angle between vectors indicates their correlation to each axis and the lengths indicate the magnitude of influence of each variable on the canonical axis (large vectors indicate more-influential variables).

Statistical analyses were carried out using Canoco 4.0 (ter Braak and Smilauer 1998) and Statistica 6.0 (StatSoft, Inc. 2004).

Anatomical cross-sectional area.—Given that the force that a muscle can develop is largely proportional to its cross-

TABLE 3.—Component scores resulting from a principal component analysis (PCA) performed on a) muscle morphometric characters and b) tendon morphometric characters. All traits were log-transformed, and the effects of body size were removed. Traits contributing most to each component are indicated in boldface type. Extracted axes from the PCA accounted for 61.7% of the total variation considered for muscle morphometric characters and 69.76% of the total variation considered for tendon morphometric characters.

Trait	Axis 1	Axis 2
a) Muscle		
Spinodeltoideus (MSD)	**−0.76729**	−0.036168
Clavo-acromiodeltoideus (MCA)	−0.32657	−0.651019
Dorsoepitrochlearis (MD)	−0.68586	−0.189958
Tricep brachii, caput longus (TLg)	**−0.79845**	0.012410
Tricep brachii, caput lateralis (TLat)	**−0.77173**	−0.005006
Tricep brachii, caput medialis (TMd)	**−0.70198**	−0.450575
Teres major (Tm)	−0.40151	0.544883
Insertion of teres major (Ti)	−0.44584	**−0.711888**
Biceps brachii (BB)	−0.66522	−0.035265
Brachialis (B)	**−0.81741**	0.103603
Extensor digitorum (ED)	**−0.78100**	0.147382
Extensor carpi ulnaris (ECU)	**−0.82328**	0.025464
Extensor carpi radialis (ECR)	−0.65469	0.408317
Abductor pollicis longus (Pl)	**−0.71309**	0.202702
Flexor digitorum profundus (FDP)	**−0.72284**	0.512692
Flexor carpi ulnaris (FCU)	**−0.89374**	0.131474
Flexor carpi radialis (FCR)	**−0.88833**	0.074441
Flexor digitorum sublimis (FDSub)	**−0.75885**	−0.400286
Palmaris longus (Pm)	**−0.72963**	−0.181719
Pronator teres (Pr)	−0.58137	0.090233
Eigenvalues	10.14	2.19
Cumulative variance	50.71	**61.7**
b) Tendon		
Length of the tendon of m. extensor digitorum (TEDl)	**−0.92777**	0.020396
Width of the tendon of m. extensor digitorum (TEDa)	**−0.82812**	0.161924
Length of the tendon of m. extensor carpi ulnaris (TECUl)	**−0.89151**	0.148152
Width of the tendon of m. extensor carpi ulnaris (TECUa)	**−0.90686**	0.035666
Length of the tendon of m. extensor carpi radialis (TECRl)	**−0.89883**	−0.072400
Width of the tendon of m. extensor carpi radialis (TECRa)	**−0.86302**	−0.143238
Length of the tendon of m. flexor palmaris longus (TPl)	**−0.85608**	−0.053714
Width of the tendon of m. flexor palmaris longus (TPa)	**−0.86457**	0.126377
Length of the tendon of m. flexor digit. profundus (TFDPl)	0.22606	**−0.738850**
Width of the tendon of m. flexor digit. profundus (TFDPa)	0.28765	**−0.791636**
Length of the tendon of m. flexor carpi ulnaris (TFCUl)	−0.32162	**−0.728297**
Width of the tendon of m. flexor carpi ulnaris (TFCUa)	−0.06104	−0.042420
Length of the tendon of m. flexor carpi radialis (TFCRl)	**−0.91846**	−0.041862
Width of the tendon of m. flexor carpi radialis (TFCRa)	**−0.88545**	−0.104061
Length of the tendon of m. flexor digit. sublimis (TSubl)	**−0.79094**	0.104575
Width of the tendon of m. flexor digit. sublimis (TSuba)	**−0.77475**	−0.176055

TABLE 3.—Continued.

Trait	Axis 1	Axis 2
Length of tendon of the m. palmaris longus (TPml)	**−0.94093**	−0.050487
Width of tendon of the m. palmaris longus (TPma)	**−0.70509**	−0.167577
Eigenvalues	10.67	1.88
Cumulative variance	59.29	**69.76**

sectional area (Biewener 1998), we tested for differences in anatomical cross-sectional areas among muscles of different locomotory types of sigmodontines. We selected the following muscles: m. triceps longus (important in forearm extension); m. extensor digitorum (important in wrist extension); and m. flexor digitorum profundus (important in wrist flexion and digit movement—Vassallo 1998; Moore et al. 2013). All 3 muscles consist of fibers packed in parallel. We also measured the cross-sectional area of the tendon of the m. flexor digitorum (important for digit flexion—Manzano et al. 2008; Abdala et al. 2009). The muscles and tendon were transversally cut across their maximum diameter and photographed in dorsal view with a high-resolution digital camera (Sony DSC-H 5; Sony Corp., Tokyo, Japan). Each image was taken using the same magnification and from the same distance. Captured images were measured and analyzed using Image Tool 3.0 (Wilcox et al. 2002). Image analysis function used included a dimensional variable measurement (area, in mm^2).

All cross-sectional areas and body size were standarized to comparable scales. The resultant values of these regressions were used in a univariate analysis of variance (ANOVA), using the locomotory types as categorical variables.

RESULTS

The total data set, with body size and muscle and tendon measurements for each individual, is presented in Supporting Information S1. The first 2 axes from the PCA of muscle data explained 61.7% of the variability (Table 3). All variables are negatively correlated with PC1. The first 2 axes from PCA of the tendon data explained 69.76% of the variance (Table 3). Most variables were negatively correlated with PC1. The 14 variables that contributed most to the first 2 components of the muscle PCA (Table 3) and the 17 variables that contributed most to the first 2 components of the tendon PCA (Table 3) were significantly correlated with their respective PC ($P = 0.0001$) and were used for subsequent analysis combined in only 1 morphological matrix.

Locomotory types: redundance analysis.—The results of the RDA performed on the ecological data set, using body size as a covariable with the remaining 32 morphological variables, are summarized in the biplots of Fig. 3. The angle between the vectors in the biplots indicates the correlation of each variable to each axis, and the lengths of the vectors indicate the magnitude of influence of each variable on the canonical axis (large vectors indicate more-influential variables). In the RDA,
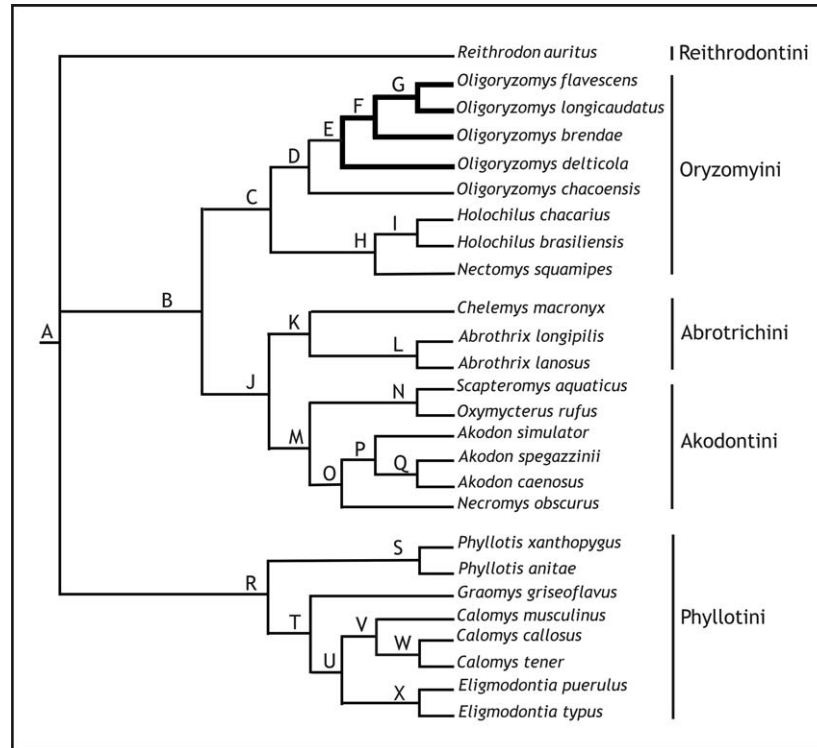
FIG. 2.—Composite cladogram of Neotropical sigmodontines in our study (based on D'Elía 2003; Weksler 2006; Lanzone et al. 2007; Rivera et al. 2007; Feijoo et al. 2008; Bonvicino et al. 2010; Jayat et al. 2010; Salazar-Bravo et al. 2013). Groups used in canonical phylogenetic ordination analyses are noted on the tree as nodes A through X.

the first 2 axes explain 86.3% of the variance in the data set. After a Monte Carlo permutations test, the morphological matrix was reduced because some of the variables had no significant variance, and the analysis excluded them automatically. The variables retained were 12 tendon and 3 muscule variables. In the ecological matrix, scansorial and fossorial groups were retained (Fig. 3). Thus, the 1st axis separates fossorial taxa ($F = 3.13$, $P = 0.02$), and it is defined by longest pollici longus, extensor carpi radialis and ulnaris, and flexor carpi radialis tendons; longer and wider extensor digitorum tendon; and wider palmaris longus tendon (Fig. 3). On the 2nd axis, scansorial species ($F = 3.43$, $P = 0.02$) have high values, and they are defined by the longest m. triceps lateralis, m. extensor carpi ulnaris, and m. flexor digitorum profundus, and the widest tendons (extensor carpi ulnaris and radialis, flexor sublimis, flexor carpi radialis, and flexor pollici). The tendon of m. flexor digitorum sublimis was the longest in scansorial species compared to all other species examined. The rest of the locomotory groups were not recovered by this analysis (Fig. 3).

Phylogeny: canonical phylogenetical ordination.—In the phylogenetic matrix using body size as covariable, only 2 groups (defined by nodes G and E; Fig. 4) inside the *Oligoryzomys* clade were significant, and these accounted for 41% of the total variation (node G, $F = 3.81$, $P = 0.006$; node E, $F = 5.41$, $P = 0.00$; Fig. 4). Within Oryzomyini, scansorial species form a monophyletic group composed of most of the

Oligoryzomys clade (node E). Thus, when the phylogeny is taken into account (CPO) the longest m. palmaris and m. triceps medialis and the tendon of m. flexor digitorum profundus explain a significant proportion of the variation (at node G). The monophyletic group defined by node E is correlated with the lengths of the m. extensor carpi ulnaris and m. flexor carpi radialis; lengths of the flexor carpi radialis, pollicis longus, and palmaris longus tendons; and widths of the extensor carpi ulnaris, extensor digitorum, flexor carpi radialis, flexor sublimis, and palmaris longus tendons (Fig. 4).

Ecomorphological consideration.—After a Monte Carlo permutations test, the number of variables in the ecological and phylogenetic matrices was reduced because some of the variables had no significant variance. A pCPO using the ecological and phylogenetic matrices showed that variance in the morphological matrix was partitioned into variances unique to ecological variables (11%), variance unique to phylogeny (13%; $F = 2.61$, $P = 0.03$), and the shared variance (28%). Regarding ecology, only the fossorial group is significant in morphological ordination. The variance shared by phylogeny and ecology indicates that the variation attributable to historical processes contains an ecomorphological component (Giannini 2003) related, in this case, to longer m. palmaris, m. triceps medialis, and flexor digitorum profundus tendon.

Anatomical cross-sectional area.—The ANOVA of cross-sectional areas of muscles (Fig. 5) showed that fossorial and natatorial taxa have significantly greater muscle areas those that
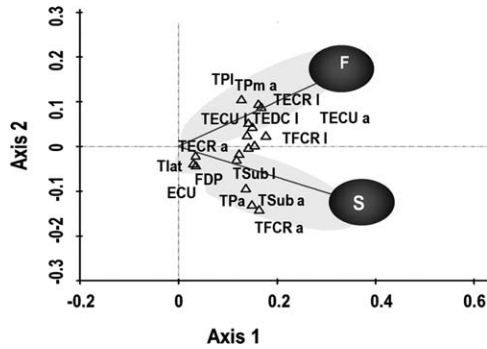
FIG. 3.—Correlation among morphological traits and ecological groups as shown by redundancy analysis (RDA). The RDA indicated that the first 2 axes explain 86.3% of the variance in the ecological variables. The 1st axis separates fossorial taxa. It is defined by longer pollici longus, extensor carpi radialis and ulnaris, and flexor carpi radialis tendons; longer and wider extensor digitorum tendon; and wider palmaris longus tendon. On the 2nd axis, scansorial species are defined by the longest muscles (m. triceps lateralis, m. extensor carpi ulnaris, and m. flexor digitorum profundus), and the widest tendons (extensor carpi ulnaris and radialis, flexor sublimis, flexor carpi radialis, and flexor pollici). The tendon of m. flexor digitorum sublimis was the longest. The rest of the groups were not recovered by our analysis. Abbreviations for locomotory types: F, fossorial; S, scansorial. Abbreviations for muscle and tendon variables: ECU, m. extensor carpi ulnaris length; FDP, m. flexor digitorum profundus length; TPl, length of the tendon of m. palmaris longus; TPma, width of the tendon of m. palmaris longus; TECRl, length of the tendon of m. extensor carpi radialis; TEDl, length of the tendon of m. extensor digitorum; TFCRl, length of the tendon of m. flexor carpi radialis; TECRa, width of the tendon of m. extensor carpi radialis; TECUa, width of the tendon of m. extensor carpi ulnaris; Tlat, m. triceps lateralis length; TSubl, length of the tendon of m. flexor digitorum sublimis; TPa, width of the tendon of m. abductor pollicis longus; TSuba, width of the tendon of m. flexor digitorum sublimis; TFCRa, width of the tendon of m. flexor carpi radialis.
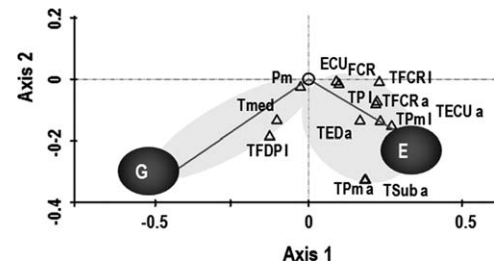

FIG. 4.—Canonical phylogenetic ordination (CPO) results. The letters E and G correspond to the 2 groups in the *Oligoryzomys* clade retained by the CPO (Fig. 2, nodes E and G). The longest palmaris and triceps medialis muscles and the tendon of the flexor digitorum profundus explain a significant proportion of the variation in clade G. Monophyletic group E is correlated with the lengths of the m. extensor carpi ulnaris and m. flexor carpi radialis; lengths of the flexor carpi radialis, pollicis longus, and palmaris longus tendons; and widths of the extensor carpi ulnaris, extensor digitorum, flexor carpi radialis, flexor sublimis, and palmaris longus tendons. Abbreviations for morphological variables: ECU, m. extensor carpi ulnaris length; FCR, m. flexor carpi radialis length; TFCRl, length of the tendon of m. flexor carpi radialis; TPl, length of the tendon of m. flexor palmaris longus; TFCRa, width of the tendon of m. flexor carpi radialis; TECUa, width of the tendon of m. extensor carpi ulnaris; TPml, length of the tendon of m. palmaris longus; TEDa, width of the tendon extensor digitorum; TPma, width of the tendon of m. palmaris longus; TSuba, width of the tendon of m. flexor digitorum sublimis; TFDPl, length of the tendon of m. flexor digitorum profundus; Tmed, m. triceps medialis length; Pm, m. palmaris longus length.

of the other groups ($F_{(16,52.573)} = 2.41$, $P = 0.008$). Results of the ANOVA of tendon cross-section results yielded no significant differences among locomotory types (Fig. 5).

DISCUSSION

The main aims of this work were to test whether the internal morphology of the sigmodontine forelimb, as assessed through the analysis of 32 characters, differs among taxa that exhibit different types of locomotion and whether such patterns also can be explained by the phylogenetic affinities of the species examined. Our results show the effect of phylogeny in explaining an important part of the observed morphological variation in sigmodontine rodents. This phylogenetic inertia could be responsible for the homogeneity in the overall muscle forelimb morphology in this group.

The main outcome of our analysis is the finding that tendon variables seem to be better descriptors of locomotory types than muscle variables. Bobbert (2001) previously called attention to one intriguing design aspect of the musculoskeletal

system in humans: distal muscle–tendon complexes span the large distance between origin and insertion with long tendon structures and very short muscle fibers. This pattern supports the importance of the role of the tendons in force transmission.

Fossorial species have longer pollici longus, extensor carpi radialis, extensor carpi ulnaris, and extensor digitorum tendons than are present in the other locomotory types, highlighting the predominance of wrist and digit extension in digging. Lehmann (1963) showed that the arm extensor muscles, such as m. triceps brachii, m. dorsoepitrochlearis, and m. teres major are enlarged in the subterranean rodents of the genera *Geomys* and *Ctenomys* (see also Alvarez et al. 2012). Examination of our data indicates that extension of the wrist and hand also are important in this energetically expensive mode of locomotion, suggesting that the greatest force is reached through forelimb extension during excavation. Our data are consistent with the broader, more robust insertion tendons of the extensor digitorum reported by Lessa and Stein (1992) in fossorial geomyid rodents. All of these fossorial taxa share postcranial variables, such as a long medial humerus epicondyle; a long olecranon process, with a well-developed medial process; and low neural processes of the lumbar vertebrae (Hildebrand 1985; Lessa and Stein 1992; Vassallo 1998; Stein 2000; Lagaria and Youlatos 2006; Carrizo et al. 2014). Although almost all rodents exhibit burrowing behavior (Deacon 2006), few characteristics of their musculotendinous system have been
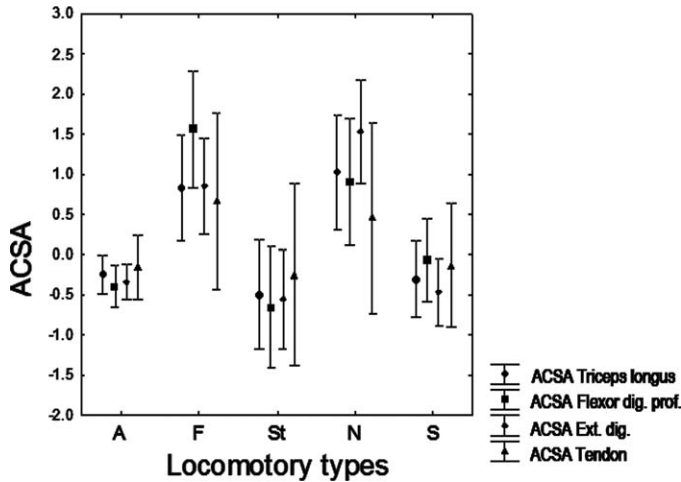
Fɪɢ. 5.—Box-and-whisker plot of anatomical cross-sectional areas (ACSAs) of muscles and tendons. Symbols indicate mean values; whiskers represent variances for each muscle or tendon. Note that fossorial and natatorial groups have significantly greater muscle areas than those of the other locomotor groups. Abbreviations for locomotory types: A, ambulatory; F, fossorial; St, saltatorial; N, natatorial; S, scansorial.

identified as adaptations for digging (see Hildebrand 1985; Lessa and Stein 1992).

Scansorial sigmodontines exhibit the longest m. triceps lateralis. According to Taylor (1974), this muscle is probably used for resisting movement of the animal's body past its forefeet in downward vertical locomotion. Argot (2001) stressed that, in scansorial didelphids, the m. triceps complex as a whole acts during the propulsive phase, to provide powerful axial thrust to the limb by the extension of the elbow. Electromyographical studies indicate that this muscle initiates extensions (Pauly et al. 1967), but it also may act as an efficient stabilizer of the elbow joint during flexed stances, when the elbow is abducted, and the distal parts of the forelimb are pressed against the medially lying arboreal substrate (Argot 2001). Our results also show that the m. carpi ulnaris is another extensor important in climbing, because it is the longest extensor muscle in the scansorial locomotory types. It could be inferred that both the m. carpi ulnaris and m. triceps complex are synchronously extended during the powerful axial thrust of the forelimbs, with the triceps producing larger out-forces than in, for example, semifossorial taxa (Stalheim-Smith 1984). Scansorial sigmodontines have longer tendons of the m. flexor digitorum sublimis, which indicates the importance of wrist and digit flexion in climbing (Cartmill 1985). Our results suggest that releasing the claws from the rough substrate also should be considered in analyzing climbing, because the m. extensor carpi ulnaris and m. radialis have the widest tendons. Rodents tend to climb using "interlocking grasping," the simplest and most familiar of the nonfrictional grip mechanisms (Cartmill 1985). This form of climbing is achieved through the use of claws, which penetrate into the surface of the substrate (Cartmill 1985). The claws are maintained against

the substrate and released mainly as a result of the force exerted by the digits through the tendons of the forearm muscles (Manzano et al. 2008; Abdala et al. 2009; Tulli et al. 2011; Sustaita et al. 2013), many of which are the longest and widest in scansorial sigmodontine rodents. However, taking phylogeny into account, our pCPO analysis shows that morphological shifts associated with scansorial taxa (node G) have occurred only in phylogenetically related species, suggesting an origin much deeper in the evolutionary history of this particular group. Our analysis indicates that the speciation event that originated the *Oligoryzomys* clade significantly explains almost half (41%) of the morphological variation observed in the musculotendinous systems of the genus (Fig. 4). As in other ecomorphological studies based on internal anatomical traits (Morales and Giannini 2010; Tulli et al. 2011) the history of these species accounts for most of the variation considered. This result indicates that the relationships in the morphospace represent inherited phylogenetic structure (*Oligoryzomys* clade) that covaries with ecological features such as climbing (see also Morales and Giannini 2010).

The other locomotory types do not have obvious muscle or tendon specializations in their forelimb. Thus, for example, the forelimbs of saltatorial forms often resemble those of generalized, ambulatory, or scansorial species, because saltatorial species use mainly the hind limb for propulsion, weight support, and maneuverability (Maynard Smith and Savage 1956; Emerson 1985; Polly 2007). Examination of our data suggests that sigmodontines do not specialize in climbing or digging, but retain an all-purpose musculotendinous pattern that allows them to use a variety of habitats. It should be noted that the average sigmodontine rodent is capable of a wide range of locomotory modes, opportunistically shifting habits to facilitate foraging or to escape predators. This morphological inertia also was revealed in our previous study about the ecomorphological descriptors of the postcranial skeleton of sigmodontines (Carrizo et al. 2014).

Anatomical cross-sectional area.—Examination of our data indicates that fossorial and natatorial sigmodontines present greater anatomical cross-sectional area of the m. triceps longus, m. extensor digitorum, and m. flexor profundus than do the other locomotory types. The anatomical cross-sectional area of a muscle is a measure of its potential force output (Nauwelaerts et al. 2007), which indicates that digging and swimming are 2 highly demanding physical activities. It has already been stressed that both locomotory types present similar specializations in regard to the forelimb (Polly 2007). Digging requires the ability to generate and transmit great forces to loosen and remove resistant material (Hildebrand 1985; Nevo 1999; Alvarez et al. 2012), whereas swimming requires powerful forelimb extension for pushing through the dense medium of water (Polly 2007; Santori et al. 2008). Our analysis reveals that the m. triceps is a key muscle in digging, because it presents the greatest area (see also Hildebrand 1985; Lessa and Stein 1992; Gambaryan and Gasc 1993; Stein 2000; Lagaria and Youlatos 2006). Zhao-Can et al. (2007) also stressed that the

whole m. triceps brachii of *Myospalax cansus* is well developed, indicating adaptation to the fossorial life.

Fossorial sigmodontines do not have shorter muscles than the other locomotory types, contradicting our 1st prediction. Our 2nd prediction proposing that fossorial sigmodontines will exhibit greater cross-sectional areas than the other taxa is supported by our data; fossorial taxa do exhibit the greater anatomical cross-sectional area, although natatorial taxa also share this characteristic. Contrary to our 3rd prediction, only scansorial taxa exhibit the longest muscles and widest tendons. Our 4th prediction, proposing that natatorial species should have extensor muscles of the arm with large cross-sectional areas, was generally supported by our data. Natatorial species have greater anatomical cross-sectional area in all selected muscles than species with other locomotorial classification, with the exception of fossorial species. Our analyses also indicate that about 13% of morphological variability is explained by common ancestry.

RESUMEN

La idea central de la teoría ecomorfológica plantea que existe una correlación entre los requisitos ecológicos y el diseño (morfología) de los organismos. Los roedores sigmodontinos presentan una amplia variedad de tipos locomotores que les permiten explorar distintos hábitats. Dada la escasez de estudios sobre aspectos ecomorfológicos del sistema músculo-tendinoso del miembro anterior, en este trabajo se propone investigar la relación entre los tipos locomotores y los rasgos morfológicos del miembro anterior en especies de sigmodontinos que exploran diferentes hábitats en un contexto filogenético. Se analizaron 32 caracteres en 26 especies de sigmodontinos exhibiendo distintos tipos de locomoción (cavador, trepador, saltador, terrestre y nadador) usando análisis de ordenamiento canónico. Nuestros resultados muestran que la filogenia explica una importante parte de la variación morfológica observada en los roedores sigmodontinos. Esta inercia filogenética podría ser la responsable de la homogeneidad morfológica general de los músculos del miembro anterior de este grupo. Se encontró que varios rasgos del sistema tendinoso fueron más informativos que los del sistema muscular, siendo aquellos los mejores descriptores para especies cavadoras y trepadoras. Doce rasgos del sistema tendinoso del miembro anterior de las especies cavadoras y trepadoras señalan interesantes diferencias entre estas dos actividades. Las especies saltadoras, terrestres y nadadoras no presentaron variables particulares asociadas con su tipo locomotor. Además, se observó que los cavadores y nadadores exhiben una mayor área de sección transversal anatómica de los tres músculos seleccionados (triceps longus, extensor digitorum, y flexor digitorum profundus) que el resto de las categorías locomotoras consideradas.

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SUPPORTING INFORMATION

LITERATURE CITED

ABDALA, V., A. MANZANO, AND S. MORO. 2006. The flexor tendons in the didelphid manus. Mastozoología Neotropical 13:193–204.

ABDALA, V., A. MANZANO, M. J. TULLI, AND A. HERREL. 2009. The tendinous patterns in the palmar surface of the lizard manus: tests of functional consequences for grasping ability. Anatomical Record 292:842–853.

ALARCÓN, O., G. D'ELIA, E. P. LESSA, AND U. F. J. PARDIÑAS. 2011. Phylogeographic structure of the fossorial long-clawed mouse *Chelemys macronyx* (Cricetidae: Sigmodontinae). Zoological Studies 50:682–688.

ALVAREZ, G. I., A. O. DÍAZ, M. V. LONGO, F. BECERRA, AND A. I. VASSALLO. 2012. Histochemical and morphometric analyses of the musculature of the forelimb of the subterranean rodent *Ctenomys talarum* (Octodontoidea). Anatomia, Histologia, Embryologia 41:317–325.

ARGOT, C. 2001. Functional–adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. Journal of Morphology 247:51–79.

ARNOLD, S. J. 1983. Morphology, performance and fitness. American Zoologist 23:347–361.

BIEWENER, A. A. 1998. Muscle function in vivo: a comparison of muscles used for elastic energy savings versus muscles used to generate mechanical power. American Zoologist 38:703–717.

BIEWENER, A. A. 2003. Animal locomotion. Oxford University Press, Oxford, United Kingdom.

BOBBERT, M. F. 2001. Dependence of human squat jump performance on the series elastic compliance of the triceps of the triceps surae: a simulation study. Journal of Experimental Biology 204:533–542.

BONVICINO, C. R., J. A. OLIVEIRA, AND R. GENTILE. 2010. A new species of *Calomys* (Rodentia: Sigmodontinae) from eastern Brazil. Zootaxa 2336:19–25.

BORCARD, D., P. LEGENDRE, AND P. DRAPEAU. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045–1055.

CARRIZO L. V., M. J. TULLI, D. A. DOS SANTOS, AND V. ABDALA. 2014. Interplay between postcranial morphology and locomotor types in Neotropical sigmodontine rodents. Journal of Anatomy 224:469–481.

CARTMILL, M. 1985. Climbing. Pp. 73–88 in Functional vertebrate morphology (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Belknap Press, Cambridge, United Kingdom.

CLEMENTE, C. J., P. C. WITHERS, AND G. G. THOMPSON. 2009. Metabolic rate and endurance capacity in Australian varanid lizards (Squamata: Varanidae: *Varanus*). Biological Journal of the Linnean Society 97:664–676.

CORBALÁN, V., AND G. DEBANDI. 2009. Evaluating microhabitat selection by *Calomys musculinus* (Rodentia: Cricetidae) in western Argentina using luminous powders. Mastozoología Neotropical 16:205–210.

DARWIN, C. 1859. The origin of species by means of natural selection. 1st ed. John Murray, London, United Kingdom.

DEACON, M. J. 2006. Burrowing in rodents: a sensitive method for detecting behavioral dysfunction. Nature Protocols 1:118–121.

D'ELÍA, G. 2003. Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307–323.

DIOGO, R., V. ABDALA, M. A. AZIZ, N. LONERGAN, AND B. A. WOOD. 2009. From fish to modern humans—comparative anatomy, homologies and evolution of the pectoral and forelimb musculature. Journal of Anatomy 214:694–716.

ELISSAMBURU, A., AND S. F. VIZCAÍNO. 2004. Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). Journal of Zoology (London) 262:145–159.

EMERSON, S. B. 1985. Jumping and leaping. Pp. 58–72 in Functional vertebrate morphology (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Belknap Press, Cambridge, United Kingdom.

EMMONS, L., AND F. FEER. 1999. Mamíferos de los bosques húmedos de América tropical: una guía de campo. 2nd ed. Editorial Fundación Amigos de la Naturaleza—Noel Kempff, Santa Cruz, Bolivia.

FEIJOO, M., G. D'ELÍA, U. F. J. PARDIÑAS, AND E. P. LESSA. 2008. Systematics of the southem Patagonian–Fueguian endemic *Abrothrix lanosus* (Rodentia: Sigmodontinae): phylogenetic position, karyotypic and morphological data. Mammalian Biology 75:122–137.

GAMBARIAN, P. P., AND J. P. GASC. 1993. Adaptive properties of the musculoskeletal system in the mole-rat *Myospalax myospalax* (Mammalia, Rodentia), cinefluorographical anatomical, and biomechanical analyses of burrowing. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tierre 123:363–401.

GAMBARYAN, P. P. 1960. Adaptative features of the locomotory organs in fossorial mammals. Izdatel'stvo AN Armyanskoi SSR, Erevan, Russia.

GIANNINI, N. P. 2003. Canonical phylogenetic ordination. Systematic Biology 52:684–695.

GOLDSTEIN, B. 1971. Heterogeneity of muscle fibers in some burrowing mammals. Journal of Mammalogy 52:515–527.

GRIZANTE, M. B., C. A. NAVAS, T. GARLAND, JR., AND T. KOHLSDORF. 2010. Morphological evolution in Tropidurinae squamates: an integrated view along a continuum of ecological settings. Journal of Evolutionary Biology 23:98–111.

HERREL, A., B. VANHOOYDONCK, J. PORCK, AND D. IRSCHICK. 2008. Anatomical basis of differences in locomotory behavior in *Anolis* lizards: a comparison between 2 ecomorphs. Bulletin of the Museum of Comparative Zoology 159:213–238.

HERSHKOVITZ, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana: Zoology 46:1–524.

HERSHKOVITZ, P. 1994. The description of a new species of South American hocicudo, or long-nose mouse genus *Oxymycterus* (Sigmodontinae, Muroidea), with a critical review of the generic content. Fieldiana: Zoology (New Series) 79:1–40.

HILDEBRAND, M. 1985. Digging of quadrupeds. Pp. 90–108 in Functional vertebrate morphology (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Belknap Press of Harvard University, Cambridge, Massachusetts.

HOWELL, A. B. 1926. Anatomy of the wood rat. Monographs of the American Society of Mammalogists. The Williams & Wilkins Company, Baltimore, Maryland.

HUDSON, P. E., S. A. CORR, R. C. PAYNE-DAVIS, S. N. CLANCY, E. LANE, AND A. M. WILSON. 2011a. Functional anatomy of the cheetah (*Acinonyx jubatus*) hindlimb. Journal of Anatomy 218:363–374.

HUDSON, P. E., S. A. CORR, R. C. PAYNE-DAVIS, S. N. CLANCY, E. LANE, AND A. M. WILSON. 2011b. Functional anatomy of the cheetah (*Acinonyx jubatus*) forelimb. Journal of Anatomy 218:375–385.

HUEY, R. B., P. E. HERTZ, AND B. SINERVO. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. American Naturalist 161:357–366.

JACKSON, D. A. 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. Ecology 74:2201–2214.

JAYAT, J. P., P. E. ORTIZ, J. SALAZAR-BRAVO, U. F. J. PARDIÑAS, AND G. D'ELÍA. 2010. The *Akodon boliviensis* species group (Rodentia: Cricetidae: Sigmodontinae) in Argentina: species limits and distribution, with the description of a new entity. Zootaxa 2409:1–61.

KESNER, M. H. 1986. Myology of the manus of microtine rodents. Journal of Zoology (London) 210:1–22.

LAGARIA, A., AND D. YOULATOS. 2006. Anatomical correlates to scratch digging in the forelimb of European ground squirrels (*Spermophilus citellus*). Journal of Mammalogy 87:563–570.

LANZONE, C., R. A. OJEDA, AND M. H. GALLARDO. 2007. Integrative taxonomy, systematics, and distribution of the genus *Eligmodontia* (Rodentia, Cricetidae, Sigmodontinae) in the temperate Monte Desert of Argentina. Mammalian Biology 72:299–312.

LAUDER, G. V. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology 7:430–442.

LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical ecology. 2nd ed. Elsevier, Amsterdam, Netherlands.

LEHMANN, W. H. 1963. The forelimb architecture of some fossorial rodents. Journal of Morphology 113:59–76.

LESSA, E. P., AND B. R. STEIN. 1992. Morphological constraints in the digging apparatus of pocket gophers (Mammalia: Geomyidae). Biological Journal of the Linnean Society 47:439–453.

LOSOS, J. B., D. CREER, AND J. SCHULTE II. 2002. Cautionary comments on use of maximal sprint performance. Journal of Zoology (London) 258:57–61.

LOSOS, J. B., T. R. JACKMAN, A. LARSON, K. DE QUEIROZ, AND L. RODRÍGUEZ-SCHETTINO. 1998. Historical contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.

MANLY, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. 2nd ed. Chapman & Hall, London, United Kingdom.

MANZANO, A., V. ABDALA, AND A. HERREL. 2008. Morphology and function of the forelimb in arboreal frogs: specializations for grasping ability? Journal of Anatomy 213:296–307.

MARES, M. A., A. K. ERNEST, AND D. D. GETTINGER. 1986. Small mammal community structure and composition in the Cerrado province of central Brazil. Journal of Tropical Ecology 2:289–300.

Maynard Smith, J. R., and J. G. Savage. 1956. Some locomotory adaptations in mammals. Zoological Journal of the Linnean Society 42:603–622.

McConathy, D., C. J. Giddings, and W. J. Gonyea. 1983. Structure–function relationships of the flexor carpi radialis muscle compared among four species of mammals. Journal of Morphology 175:279–292.

Miller, L. M., and S. Anderson. 1977. Bodily proportions of Uruguayan myomorph rodents. American Museum Novitates 2615:1–10.

Moore, A. L., J. E. Budny, A. P. Russell, and M. T. Butcher. 2013. Architectural specialization of the intrinsic thoracic limb musculature of the American badger (Taxidea taxus). Journal of Morphology 274:35–48.

Morales, M., and N. P. Giannini. 2010. Morphofunctional patterns in Neotropical felids: species co-existence and historical assembly. Biological Journal of the Linnean Society 100:711–724.

Myers, P., and M. D. Carleton. 1981. The species of Oryzomys (Oligoryzomys) in Paraguay and the identity of Azara's "Rat sixieme ou Rat a Tarse Noir." Miscellaneous Publications, Museum of Zoology, University of Michigan 161:1–41.

Nauwelaerts, S., J. Ramsay, and P. Aerts. 2007. Morphological correlates of aquatic and terrestrial locomotion in a semi-aquatic frog, Rana esculenta: no evidence for a design conflict. Journal of Anatomy 210:304–317.

Nevo, E. 1999. Mosaic evolution of subterranean mammals: regression, progression and global convergence. Oxford University Press, Oxford, United Kingdom.

Ojeda, R., and S. Tabeni. 2007. The mammals of the Monte Desert revisited. Journal of Arid Environments 73:173–181.

Pardiñas, U. F. J., P. Jayat, and G. F. D'Elia. 2008. Reithrodon auritus. In IUCN 2013. IUCN Red list of threatened species. Version 2013.2. www.iucnredlist.org. Accessed 30 June 2008.

Pauly, J. E., J. L. Rushing, and L. E. Scheving. 1967. An electromyographic study of some muscles crossing the elbow joint. Anatomical Record 159:47–53.

Polly, D. 2007. Limb in mammalian evolution. Pp. 245–268 in Fins into limbs: evolution, development, and transformation (B. K. Hall, ed.). University of Chicago Press, Chicago, Illinois.

Rao, C. R. 1964. The use and interpretation of principal components analysis in applied research. Sankhya Analytics 26:329–358.

Reig, O. A. 1980. A new fossil genus of South American cricetid rodents allied to Weidomys, with an assessment of the Sigmodontinae. Journal of Zoology (London) 192:257–281.

Rinker, G. C. 1954. The comparative myology of the mammalian genera Sigmodon, Oryzomys, Neotoma, and Peromyscus (Cricetinae), with remarks on their intergeneric relationships. Miscellaneous Publications, Museum of Zoology, University of Michigan 83:1–125.

Rivas, B. A., G. D'Elia, and O. Linares. 2010. Diferenciación morfológica en sigmodontinos (Rodentia: Cricetidae) de las Guayanas venezolanas con relación a su locomoción y hábitat. Mastozoología Neotropical 17:97–109.

Rivas, B. A., and O. J. Linares. 2006. Cambios en la forma de la pata posterior entre roedores sigmodontinos según su locomoción y hábitat. Mastozoología Neotropical 13:205–215.

Rivera, C. P., R. E. Ittig Gonzalez, J. Rossi Fraire, S. Levis, and C. Gardenal. 2007. Molecular identification and phylogenetic relationships among the species of the genus Oligoryzomys (Rodentia: Cricetidae) present in Argentina, putative reservoirs of hantaviruses. Zoologica Scripta 36:231–239.

Rodríguez-Serrano, E., R. E. Palma, and C. E. Hernández. 2008. The evolution of ecomorphological traits within the Abrothrichini (Rodentia: Sigmodontinae): a Bayesian phylogenetics approach. Molecular Phylogenetics and Evolution 48:473–480.

Russell, A. P., and T. E. Higham. 2009. A new angle on clinging in geckos: incline, not substrate, triggers the deployment of the adhesive system. Proceeding of the Royal Society, B. Biological Sciences 276:3705–3709.

Salazar-Bravo, J., U. F. J. Pardiñas, and G. D'Elía. 2013. A phylogenetic appraisal of Sigmodontinae (Rodentia, Cricetidae) with emphasis on phyllotine genera: systematics and biogeography. Zoologica Scripta 42:250–261.

Santori, R. T., V. Vieira, O. Rocha-Barbosa, J. A. Magnan-Nieto, and N. Gobbi. 2008. Water absorption of the fur and swimming behavior of semiaquatic and terrestrial oryzomine rodents. Journal of Mammalogy 89:1152–1161.

Schulte, J. A., II, J. B. Losos, F. B. Cruz, and H. Núñez. 2004. The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade Liolaemus (Iguanidae: Tropidurinae: Liolaemini). Journal of Evolutionary Biology 17:408–420.

Schulte, J. A., II, J. Valladares, and A. Larson. 2003. Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. Herpetologica 59:399–419.

Slijper, E. J. 1946. Comparative biologic–anatomical investigations on the vertebral column and spinal musculature of mammals. Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen 42:1–128.

Spoor, C. F., and D. M. Badoux. 1986. Descriptive and functional myology of the neck and forelimb of the striped Hyena (Hyaena hyaena, L. 1758). Anatomischer Anzeiger, Jena 161:375–387.

Stalheim-Smith, A. 1984. Comparative study of the forelimbs of the semifossorial prairie dog, Cynomys gunnisoni, and the scansorial fox squirrel, Sciurus niger. Journal Morphology 180:55–68.

StatSoft, Inc. 2004. Statistica (data analysis software system), version 7. www.statsoft.com. Accessed 12 August 2004.

Stein, B. R. 2000. Morphology of subterranean rodents. Pp. 19–61 in Life underground: the biology of subterranean rodents (E. A. Lacey, J. L. Patton, and G. N. Cameron, eds.). University of Chicago Press, Chicago, Illinois.

Sustaita, D., E. Pouydebat, A. Manzano, V. Abdala, F. Hertel, and A. Herrel. 2013. Getting a grip on tetrapod grasping: form, function, and evolution. Biological Reviews 88:380–405.

Taraborelli, P., V. Corbalán, and S. Giannoni. 2003. Locomotion and escape modes in rodents of the Monte Desert (Argentina). Ethology 109:475–485.

Taylor, M. E. 1974. The functional anatomy of the forelimbs of some African Viverridae (Carnivora). Journal of Morphology 143:307–336.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

ter Braak, C. J. F. 1995. Ordination. Pp. 91–173 in Data analysis in community and landscape ecology (R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, eds.). Cambridge University Press, Cambridge, United Kingdom.

ter Braak, C. J. F., and P. Smilauer. 1998. Canoco reference manual and user's guide to Canoco for Windows: software for canonical community ordination. Version 4. Microcomputer Power, Ithaca, New York.

THORINGTON, R. W., K. DARROW, AND A. D. K. BETTS. 1997. Comparative myology of the forelimb of squirrels (Sciuridae). Journal of Morphology 234:155–182.

TULLI, M. J., V. ABDALA, AND F. B. CRUZ. 2011. Relationships among morphology, clinging performance and habitat use in *Liolaemini* lizards. Journal of Evolutionary Biology 24:843–855.

VANHOOYDONCK, B., F. B. CRUZ, C. S. ABDALA, D. L. MORENO AZÓCAR, M. F. BONINO, AND A. HERREL. 2010. Sex-specific evolution of bite performance in *Liolaemus* lizards (Iguania: Iguanidae): the battle of the sexes. Biological Journal of the Linnean Society 101:461–475.

VANHOOYDONCK, B., A. HERREL, AND D. IRSCHICK. 2006. Out on a limb: the differential effect of substrate diameter on acceleration capacity in *Anolis* lizards. Journal of Experimental Biology 209:4515–4523.

VANHOOYDONCK, B., ET AL. 2009. Ecomorphological analysis of aerial performance in a non-specialized lacertid lizard, *Holaspis guentheri*. Journal of Experimental Biology 212:2475–2492.

VASSALLO, A. I. 1998. Functional morphology, comparative behaviour, and adaptation in two sympatric subterranean rodents genus *Ctenomys* (Caviomorpha: Octodontidae). Journal of Zoology (London) 244:415–427.

VOSS, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History 188:259–493.

WEKSLER, M. 2006. Phylogenetic relationships of oryzomyine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. Bulletin of the American Museum of Natural History 296:1–149.

WILCOX, C. D., S. B. DOVE, W. D. MCDAVID, AND D. B GREER. 2002. UTHSCSA image tool. Version 3.0. University of Texas Health Center, San Antonio.

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

ZHAO-CAN, C., L. JIN-GANG, AND L. YUE-MING. 2007. Analysis of digging efficiency of the forelimbs of three rodents. Chinese Journal of Zoology 2:17–20.

APPENDIX I

Material examined

Institutional abbreviations where voucher specimens of the species studied are deposited. CNP, Colección de Mamíferos—Colección de material de egagrópilas y afines "Elio Massoia," Centro Nacional Patagónico (CENPAT-CONICET), Puerto Madryn, Chubut, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; CMLP, Museo de La Plata, La Plata; W/D, without data.

Tribe Phyllotini.—*Calomys callosus* (3): MACN (2921, 32235), W/D; *Calomys musculinus* (3): MACN (14580, 2111, 32242); *Calomys tener* (1): MACN (5139); *Eligmodontia typus* (7): MACN (13536, 13539, 14561, 14562, 14564, 25886), CMLP (3X.70.81); *Eligmodontia puerulus* (1): MACN (25887); *Graomys griseoflavus* (6): MACN (3613, 3691, 3694, 3695, 40118, 16356); *Phyllotis osilae* (4): MACN (21019, 25883, 42145, 42144); *Phyllotis xanthopygus* (2): MACN (25884, 25885).

Tribe Akodontini.—*Akodon caenosus* (2): MACN (25866, 25867); *Akodon simulator* (11): MACN (25881, 25868, 25882, 25869, 25870, 25871, 25872, 25873, 25874, 25876, 25875); *Akodon spegazzinii* (3): MACN (25879, 25878, 25877); *Necromys obscurus* (3) MACN (13824, 13926, 13927); *Oxymycterus rufus* (6): MACN (14959, 1505), CMLP (3X.00.09, 3X.00.10, 7X.70.62, 19.VI.02.17); *Scapteromys aquaticus* (5): CMLP (3X.00.7, 12XI.02.19, 12XI.02.20, 12XI.02.21, 12XI.02.22).

Tribe Abrotrichini.—*Abrothrix longipilis* (7): MACN (19249, 19250, 19258), CMLP (16.VIII.96.11, 16.VIII.16.32, 16.VIII.96.16), CNP (3644); *Abrothrix lanosus* (1): MACN (32230); *Chelemys macronyx* (1): CNP (3647).

Tribe Oryzomyini.—*Holochilus brasiliensis* (2): MACN (5190), CMLP (18.XI.02.3); *Holochilus chacarius* (7): MACN (14450, 14453, 4176, 29774, 40139), CMLP (18.XI.02.3, 19.VI.02.23); *Oligoryzomys brendae* (1): MACN (25880); *Oligoryzomys chacoensis* (2): MACN (21304, 24275); *Oligoryzomys delticola* (1): MACN (22872); *Oligoryzomys flavescens* (5): MACN (13359, 13360, 19237, 2588, 39809); *Oligoryzomys longicaudatus* (1): MACN (23331); *Nectomys squamipes* (7): MACN (13057, 49387, 49420, 49421, 49450, 49451, 5154).

Tribe Reithrodontini.—*Reithrodon auritus* (5): MACN (13820, 15348, 31304), CMLP (2.X.70.31, 2.X.70.32).