An ecomorphological analysis of forelimb musculotendinous system in sigmodontine rodents (Rodentia, Cricetidae, Sigmodontinae)

Author(s): Luz V. Carrizo, María J. Tulli, and Virginia Abdala
Published By: American Society of Mammalogists
DOI: http://dx.doi.org/10.1644/13-MAMM-A-232

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne’s Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.
An ecomorphological analysis of forelimb musculotendinous system in sigmodontine rodents (Rodentia, Cricetidae, Sigmodontinae)

LUZ V. CARRIZO,* MARÍA J. TULLI, AND VIRGINIA ABDALA

Caátedra de Biología General, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Miguel Lillo 205, 4000 San Miguel de Tucumán, Argentina (LVC, VA)
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)—Instituto de Herpetología—Fundación Miguel Lillo, Miguel Lillo 251, 4000 San Miguel de Tucumán, Argentina (MJT, VA)
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)—Instituto de Biodiversidad Neotropical, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Miguel Lillo 205, 4000 San Miguel de Tucumán, Argentina (VA)

* Correspondent: luzvaleria.carrizo@gmail.com

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

© 2014 American Society of Mammalogists

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 muscule 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; Spoors 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—
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 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,

### Table 1

<table>
<thead>
<tr>
<th>Muscle Abbreviation</th>
<th>Tendon Abbreviation</th>
<th>Muscle group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Teres major Tm</td>
<td>Subscapular</td>
<td></td>
</tr>
<tr>
<td>Clavo-acromiodeltoideus MCA</td>
<td>Deltid</td>
<td></td>
</tr>
<tr>
<td>Spinodeltoideus MSD</td>
<td>Deltid</td>
<td></td>
</tr>
<tr>
<td>Triceps brachii caput longus TLg</td>
<td>Triceps</td>
<td></td>
</tr>
<tr>
<td>Triceps brachii caput lateralis TLat</td>
<td>Triceps</td>
<td></td>
</tr>
<tr>
<td>Abductor pollicis longus MD</td>
<td>Triceps</td>
<td></td>
</tr>
<tr>
<td>Extensor carpi radialis ECR X</td>
<td>Extensor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Extensor carpi ulnaris ECU X</td>
<td>Extensor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Extensor digitorum ED X</td>
<td>Extensor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Flexor pollicis longus Pl</td>
<td>Extensor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Biceps brachii BB</td>
<td>Flexor of the arm</td>
<td></td>
</tr>
<tr>
<td>Brachialis B</td>
<td>Flexor of the arm</td>
<td></td>
</tr>
<tr>
<td>Flexor carpi radialis FCR X</td>
<td>Flexor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Flexor carpi ulnaris FCU X</td>
<td>Flexor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Flexor digitorum profundus FDP X</td>
<td>Flexor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Flexor digitorum sublimis FDSub X</td>
<td>Flexor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Palmaris longus Pm X</td>
<td>Flexor of the forearm</td>
<td></td>
</tr>
<tr>
<td>Pronator teres Pr</td>
<td>Flexor of the forearm</td>
<td></td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locomotor type</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abrothrix lanosus</td>
<td>Ambulatory</td>
<td>Rodríguez-Serrano et al. (2008)</td>
</tr>
<tr>
<td>Abrothrix longipilis</td>
<td>Ambulatory</td>
<td>Rodríguez-Serrano et al. (2008)</td>
</tr>
<tr>
<td>Akodon caesnus</td>
<td>Ambulatory</td>
<td>Emmons and Feer (1999)</td>
</tr>
<tr>
<td>Akodon simulanud</td>
<td>Ambulatory</td>
<td>Ojeda and Tabeni (2007)</td>
</tr>
<tr>
<td>Akodon speczazinii</td>
<td>Ambulatory</td>
<td>Ojeda and Tabeni (2007)</td>
</tr>
<tr>
<td>Calomys callosus</td>
<td>Ambulatory</td>
<td>Rivas et al. (2010)</td>
</tr>
<tr>
<td>Calomys musculinus</td>
<td>Ambulatory</td>
<td>Corbalán and Debandi (2009)</td>
</tr>
<tr>
<td>Calomys tener</td>
<td>Ambulatory</td>
<td>Mares et al. (1986)</td>
</tr>
<tr>
<td>Chelenmys macronyx</td>
<td>Fossorial</td>
<td>Alarcón et al. (2011)</td>
</tr>
<tr>
<td>Eligmodonta prueralis</td>
<td>Saltatorial</td>
<td>Hershkovitz (1962)</td>
</tr>
<tr>
<td>Eligmodonta typus</td>
<td>Saltatorial</td>
<td>Taraborelli et al. (2003)</td>
</tr>
<tr>
<td>Graomys griseoflavus</td>
<td>Ambulatory</td>
<td>Hershkovitz (1962)</td>
</tr>
<tr>
<td>Holochilus brasiliensis</td>
<td>Natatorial</td>
<td>Weksler (2006)</td>
</tr>
<tr>
<td>Holochilus chacarius</td>
<td>Natatorial</td>
<td>Weksler (2006)</td>
</tr>
<tr>
<td>Necromys obscurus</td>
<td>Ambulatory</td>
<td>Rivas et al. (2010)</td>
</tr>
<tr>
<td>Nectomys squamipes</td>
<td>Natatorial</td>
<td>Santori et al. (2008)</td>
</tr>
<tr>
<td>Oligoryzomys brendae</td>
<td>Scansorial</td>
<td>Weksler (2006)</td>
</tr>
<tr>
<td>Oligoryzomys chacoensis</td>
<td>Scansorial</td>
<td>Myers and Carleton (1981)</td>
</tr>
<tr>
<td>Oligoryzomys delticola</td>
<td>Scansorial</td>
<td>Miller and Anderson (1977)</td>
</tr>
<tr>
<td>Oligoryzomys flavescens</td>
<td>Scansorial</td>
<td>Miller and Anderson (1977)</td>
</tr>
<tr>
<td>Oligoryzomys longicudatus</td>
<td>Scansorial</td>
<td>Myers and Carleton (1981)</td>
</tr>
<tr>
<td>Oxymycterus rufus</td>
<td>Fossorial</td>
<td>Hershkovitz (1994)</td>
</tr>
<tr>
<td>Phyllotis osilae</td>
<td>Ambulatory</td>
<td>Hershkovitz (1962)</td>
</tr>
<tr>
<td>Phyllotis xanthophyus</td>
<td>Ambulatory</td>
<td>Hershkovitz (1962)</td>
</tr>
<tr>
<td>Reithrodon aurita</td>
<td>Ambulatory</td>
<td>Pardinas et al. (2008)</td>
</tr>
<tr>
<td>Scapteromys aquaticus</td>
<td>Natatorial</td>
<td>Miller and Anderson (1977)</td>
</tr>
</tbody>
</table>

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 a random 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-
b) Tendon

The PCA accounted for 61.7% of the total variation considered for b) tendon morphometric characters. All traits were log-transformed, analysis (PCA) performed on a) muscle morphometric characters and

August 2014

847CARRIZO ET AL.—ECOMORPHOLOGY OF SIGMODONTINE RODENTS

<table>
<thead>
<tr>
<th>Trait</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of tendon of the m. palmaris longus (TPml)</td>
<td>-0.94093</td>
<td>-0.050487</td>
</tr>
<tr>
<td>Width of tendon of the m. palmaris longus (TPma)</td>
<td>-0.70509</td>
<td>-0.167577</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>10.67</td>
<td>1.88</td>
</tr>
<tr>
<td>Cumulative variance</td>
<td>59.29</td>
<td>69.76</td>
</tr>
</tbody>
</table>

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.

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: redundancy 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, 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 digit extension); and m. flexor digitorum profundus (important in digit flexion and 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

### Table 3.—Continued.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of tendon of the m. palmaris longus (TPml)</td>
<td>-0.94093</td>
<td>-0.050487</td>
</tr>
<tr>
<td>Width of tendon of the m. palmaris longus (TPma)</td>
<td>-0.70509</td>
<td>-0.167577</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>10.67</td>
<td>1.88</td>
</tr>
<tr>
<td>Cumulative variance</td>
<td>59.29</td>
<td>69.76</td>
</tr>
</tbody>
</table>

Table 3.—Continued.
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 muscle 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...
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 Geomyos 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 epicondyyle; 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
The extensor carpi ulnaris and m. radialis have the widest tendons. These should be considered in analyzing climbing, because the m. digitorum sublimis, which indicates the importance of wrist and digit flexion in climbing (Cartmill 1985). Our results 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 muscule 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 1955; 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

![Graph showing anatomical cross-sectional areas (ACSAs) of muscles and tendons across different locomotory types.](image-url)
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 muscular-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 descriptoros 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.

**ACKNOWLEDGMENTS**

We especially thank D. Verzi (Museo de La Plata), D. Flores (Museo Argentino de Ciencias Naturales), and U. Pardiñas (Colección de Mamíferos del Centro Nacional Patagónico) for allowing access to mammal collections. We thank Mariano Sánchez (Facultad de Ciencias Naturales, FCN), Pablo Jayat (Instituto de Ecología Regional, IER), Pablo Teta (Centro Nacional Patagónico, CENPAT), A. Novillo and A. Ojeda (Instituto Argentino de Investigaciones de las Zonas Aridas, IADIZA) for allowing access to the study material. We thank P. Jayat for sharing photography of *Akodon spegazzinii*. We thank R. Sánchez for helping with production of the figures. Thanks to J. Samuels and D. Polly for their valuable comments that improved the quality of this work. This work was partially financed by grants BID-PICT 0616 and PIP CONICET 0284.

**SUPPORTING INFORMATION**

**SUPPORTING INFORMATION S1.**—Body size and muscle and tendon measurements of species of sigmodontines, reported as mean ± SE. Found at DOI: 10.1644/13-MAMM-A-232.S1

**LITERATURE CITED**


ASSOCIATE EDITOR was Neal Woodman.