

Forelimb proportions and fossorial adaptations in the scratch-digging rodent *Ctenomys* (Caviomorpha)

A. ELISSAMBURU* AND L. DE SANTIS

Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Calle 64 N°3 e/119 y 120, 1900 La Plata, Argentina

* Correspondent: aelissamburu@gmail.com

Members of the genus *Ctenomys* (tuco-tuco; Rodentia: Caviomorpha: Octodontidae) are considered scratch diggers. We compared the forelimbs of adult *C. azarae* with those of 13 species within other genera of caviomorph rodents to identify morphofunctional variation in osseous elements related to fossorial habits. Eight measurements of the humerus and ulna were used to construct five functional indices that were subjected to principal components analysis and simple comparisons among means. *Ctenomys* has a general morphology similar to that of terrestrial caviomorph rodents but exhibits some features that reflect its specialized fossorial condition, such as its comparatively large epicondyles. These features indicate greater muscular development and capacity for force production in the pronators and supinators of the forelimb and manus and flexors of the manus. The deltoid complex is well developed, indicating a large moment arm for the deltoid and latissimus dorsi muscles, which increases the capacity for force production on humeral flexion. Humeral indices are the best for differentiating fossorial forms from diggers, occasional diggers, generalized, and cursorial forms. Limb bone segments are used differently by highly fossorial and scratch-digging forms.

Key words: *Ctenomys*, forelimb, fossorial adaptations, morphometry

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Tuco-tucos (*Ctenomys*) are South American rodents of the family Octodontidae. This genus diversified rapidly beginning in the Pleistocene. More than 70 species are known, and >60 of those are extant (Reig et al. 1990). Species of the genus *Ctenomys* occur over a wide geographical and environmental range, but they all share fossorial adaptations, similar ecological niches, and common behaviors. Body mass ranges from 100 g (*C. talarum*) to 700 g (*C. tucumanus*; Nowak 1999).

Ctenomys is adapted to terrestrial and underground activity (Camín et al. 1995). Like most other caviomorphs, it is a highly fossorial scratch digger that digs by extending the forefeet into the earth and then drawing the claws downward toward, or under, the body (Hildebrand 1985). First, the manus is pronated and slightly rotated in the direction of the 5th digit. Then the forelimb is retracted and flexed from the extended position while the forearm and manus are rotated laterally (Lehmann 1963). *Ctenomys* concludes a digging cycle by sweeping the soil out of the tunnel with its hind feet (Pearson 1959) on which a pad that moves the accumulated soil has evolved (Hildebrand 1985).

According to Hildebrand (1988), different functional adaptations of the appendicular skeleton or skull are found

in scratch-digging, chisel-toothed, and head-lift digging forms. Highly fossorial rodents exhibit many of the same features seen in semifossorial species but to a greater degree (Hildebrand 1985; Nevo 1999). In addition, fossorial rodents possess elongate claws on the manus and manual bones that are extremely reduced (Hildebrand 1985; Stein 2000). The principal musculoskeletal characteristics of scratch diggers are short limbs and necks, radii that are shorter than humeri, short and heavy autopodia, and muscular insertions that are distant from articulations. For example, the deltoid muscle inserts on more than one-half of the humeral diaphysis, and its extensive muscular development is exemplified by large origin and insertion areas (Hildebrand 1985). These modifications increase strength in flexing the digits and wrist, extending the elbow, flexing the humerus on the scapula, and stabilizing the shoulder (Hildebrand 1985).

In addition to scratch digging with the forelimbs, *Ctenomys* also uses its teeth to cut roots and branches and to break soil (Lessa 1993). Different digging behaviors can be seen in

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different *Ctenomys* species—e.g., *C. australis* cuts roots with its teeth, and *C. talarum* breaks soil with its teeth (Vassallo 1998)—and sometimes in the same species on different soils, as in *C. pearsoni* (Altuna et al. 1993; Giannoni et al. 1996). Although fossorial adaptations are present in both the forelimbs and the skulls of *Ctenomys* (Mora et al. 2003; Reig 1989; Vassallo 1998), digging with the teeth is considered to be secondary to scratch digging (De Santis 1986; De Santis et al. 1998).

Studies of humeral morphology suggest that *Ctenomys* has moderate skeletal specializations for digging compared with extremely specialized fossorial forms from other families (Morgan and Verzi 2006). However, it has not been compared with more generalized digging caviomorphs. A comparison of *Ctenomys* with scratch diggers that do not exhibit extreme fossorial specializations could help to elucidate bone and muscular variations associated with fossorial specialization within caviomorphs.

Limb morphology reflects limb function and, as in many mechanical systems, a trade-off exists between force and speed (Hildebrand 1985). Distal limb bone elongation and short muscular insertions (moment arms) are found in limbs adapted for speed, and short distal limb bone segments and long moment arms are found in limbs adapted for force (Hildebrand 1985). Morphometric studies of the limbs of *Ctenomys* are scarce (Morgan and Verzi 2006; Vassallo 1998), and comparisons of this fossorial genus with nonfossorial, scratch-digging caviomorph rodents are lacking. A study of limb morphology and function in caviomorph rodents that did not include *Ctenomys* demonstrated a continuous morphofunctional sequence from diggers to more cursorial forms (Elissamburu and Vizcaíno 2004). Among the functional types digger, occasional digger, generalist, and cursor, diggers have relatively large forelimb muscles and long muscle moment arms that are consistent with Hildebrand's (1985) analyses of anatomical specializations for high force production during digging. In general, caviomorph diggers are characterized by indices that represent humeral and ulnar robustness, deltoid and epicondylar development, and increased olecranon size.

We compared the highly fossorial *Ctenomys* with other caviomorphs to identify aspects of variation in bone morphology associated with fossorial habits and to help determine whether digging specializations of *Ctenomys* are unique or fall within a continuation of the observed sequence from cursorial to scratch-digging forms. We hypothesized that fossorial forms will exhibit morphofunctional characteristics similar to those of diggers but with additional specializations related to powerful digging.

This study focuses on *Ctenomys azarae*, which is smaller (193–585 g body mass of the specimens examined) than other caviomorph scratch diggers such as the vizcacha, *Lagostomus maximus* (female 2–4.5 kg, male 5–8 kg—Nowak 1999) and the paca, *Agouti paca* (6.3–12 kg—Nowak 1999). Variation in limb bones exists in *Ctenomys*, but morphometric measurements of different species (Morgan and Verzi 2006)

TABLE 1.—Species included in this study, their locomotor and digging habits (from Nowak 1999), and sample size (*n*).

Species	Locomotor and digging habits	<i>n</i>
<i>Ctenomys azarae</i> (tuco-tuco)	Fossorial	27
<i>Lagostomus maximus</i> (vizcacha)	Digging	10
<i>Agouti paca</i> (paca)	Digger-swimming	3
<i>Myocastor coypus</i> (nutria)	Occasional digger	5
<i>Galea musteloides</i> (cuis)	Occasional digger	1
<i>Microcavia</i> sp. (mountain cavy)	Occasional digger	11
<i>Dinomys branickii</i> (pacarana)	Occasional digger	1
<i>Cavia aperea</i> (cavy)	Generalized	9
<i>Dasyprocta punctata</i> (agouti)	Cursorial	9
<i>Myoprocta</i> sp. (acouchis)	Cursorial	1
<i>Dolichotis patagonum</i> (mara)	Cursorial	6
<i>Hydrochoeris hydrochaeris</i> (capybara)	Cursorial-swimming	2
<i>Lagidium viscacia</i> (mountain vizcacha)	Jumper	3
<i>Chinchilla</i> sp. (chinchilla)	Jumper	5

demonstrate that the variation among them is not significant and that *C. azarae* is representative of the genus. The objectives of this study are to compare morphometric variation in the bones of the forelimb in *C. azarae* and other caviomorph rodents and to analyze the morphometric variation among fossorial forms in a functional context.

MATERIALS AND METHODS

We collected data from 93 adult specimens of caviomorph rodents belonging to 14 extant species housed in the Museo Municipal de Ciencias Naturales “Lorenzo Scaglia,” Mar del Plata, Argentina; Museo de Ciencias Naturales de La Plata, La Plata, Argentina; Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo de La Plata, La Plata, Argentina; Museo de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; and American Museum of Natural History, New York. Species were categorized as digging, occasional digging, generalized, cursorial, cursorial-swimming, and jumping functional types (Elissamburu and Vizcaíno 2004; Table 1).

We took 9 measurements (to the nearest 0.01 mm) from the humerus and ulna of each specimen using digital calipers (Elissamburu and Vizcaíno 2004; Fig. 1). Some of these measurements were combined to calculate 5 functional indices that represent attributes of the bones and mechanical efficiency of principal muscles related to forelimb function. These indices were shown to be relevant for interpreting limb function in caviomorph rodents in previous works, and are considered good indicators of digging activity within this group (Elissamburu 2001; Elissamburu and Vizcaíno 2004). A detailed explanation of each index is given in Elissamburu and Vizcaíno (2004).

Shoulder moment index (SMI) is the deltoid length of the humerus divided by the functional length of the humerus (DLH/HL × 100). This index provides an indication of the mechanical advantage of the deltoid and pectoralis major muscles (hereafter called the deltoid complex) that insert in

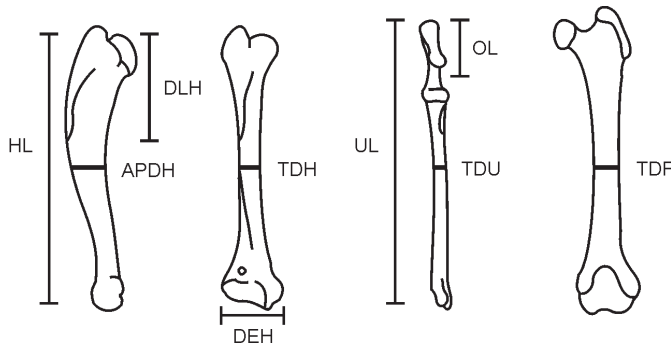


FIG. 1.—Measurements of the limbs. HL, functional humerus length; DLH, deltoid length of the humerus; TDH, transverse diameter of the humerus at the diaphyseal midpoint; APDH, anteroposterior diameter of the humerus at a distance of 35% from the distal articular surface; DEH, diameter of the epicondyles; UL, total ulna length; OL, olecranon length from the tip of the olecranon process to the center of the trochlear notch; TDU, transverse diameter of the ulna at the diaphyseal midpoint; TDF, transverse diameter of the femur at the diaphyseal midpoint. Adapted from Elissamburu and Vizcaíno (2004).

the deltoid crest and act across the shoulder joint. The deltoid muscle is both a shoulder stabilizer and flexor of the arm, and the pectoralis major acts as a limb protractor during locomotion. The shape and position of the deltoid tuberosity probably reflect a compromise in response to multiple factors, including the force exerted on the substratum for digging, shoulder stabilization, support of body mass, and, to a lesser degree, recovery speed of steps (Elissamburu and Vizcaíno 2004).

The humerus robustness index (HRI) is the transverse diameter of the humerus divided by functional length of the humerus ($\text{TDH}/\text{HL} \times 100$). The HRI is an indication of the robustness of the humerus. Robustness of the bones can be related to the need to support body mass during locomotion or to the development of forces required for more specific functions of the limb, such as digging activity. This index is related to digging function in generalized caviomorphs, and in occasional diggers it is related to supporting the body (Elissamburu and Vizcaíno 2004).

The epicondyle index (EI) is the epicondylar width of the humerus divided by functional length of the humerus ($\text{DEH}/\text{HL} \times 100$). The EI is an indicator of the relative width available for the origin of the flexor, pronator, and supinator muscles of the forearm. These muscles act in the pronation and supination of the zeugopodium and manus and flexion of the manus—functions that are important during scratch digging. The relative mass of flexor, pronator, and supinator musculature of the middle and distal forelimb segments and associated musculature increases as the manus increases in size from cursorial to digging forms. These muscles are associated with digging rather than locomotion, but in occasional diggers the relative mass of these muscles is correlated with body mass (Elissamburu and Vizcaíno 2004).

The index of fossorial ability (IFA) is the length of the olecranon process (OL) divided by the functional ulna length

(FUL, the difference between total ulna length and olecranon length), i.e., $\text{OL}/\text{FUL} \times 100$. This index provides a measure of the mechanical advantage of the triceps and dorsoepitrochlearis muscles in elbow extension. Triceps and dorsoepitrochlearis muscles insert on the olecranon process and extend the zeugopodia to impart force on the substrate. The IFA is considered a good indicator of fossoriality (Hildebrand 1985; Vizcaíno and Milne 2002; Vizcaíno et al. 1999). It is correlated with the functional sequence from cursorial to digging forms in caviomorph rodents and reflects force development for digging or speed among specialized cursorial forms (Elissamburu and Vizcaíno 2004).

The ulna robustness index (URI) is the transverse diameter of the ulna (TDU) divided by the functional ulna length ($\text{TDU}/\text{FUL} \times 100$). It gives an indication of the robustness of the forearm and the relative width available for the insertion of muscles involved with pronation and supination of the forearm and flexion of the manus and digits. Like the HRI, it is related to the ability to support body mass. Besides, robustness is related to the forces imparted on the bones by the action of pronators and supinators of the zeugopodium and flexors of the manus and digits that act during scratch digging and other activities. The URI increases from cursorial to digging forms and can be used to distinguish among the different specializations of cursorial forms (Elissamburu and Vizcaíno 2004).

A principal components analysis (PCA) on a correlation matrix of these indices was conducted to explore their variation among *Ctenomys* (represented by *C. azarae*) and 13 other caviomorph species (Table 1). Body masses were included as a variable in the PCA to evaluate whether the indices vary with size. When body mass data were missing, estimations were calculated as the average of several allometric equations of the anteroposterior diameter of the humerus and transverse diameter of the femur (Biknevicius 1999; Biknevicius et al. 1993). The significance of the indices and body mass relative to the principal components was evaluated using the standard Kaiser–Guttman criterion ($\lambda > 1$) and comparison with broken stick models (Legendre and Legendre 1998). Analysis of variance (ANOVA) and post hoc multiple-comparison Tukey tests (Zar 1984) were used to compare mean values of the indices between *C. azarae* and each of the other caviomorph species. Normality was tested with the Kolmogorov–Smirnov test (Zar 1984) and homogeneity of variance with the Brown–Forsythe test (Brown and Forsythe 1974). Distributions were normal except for EI ($P < 0.05$). Variances were homogeneous except for IFA ($P < 0.05$). However, ANOVA is robust and operates well even with considerable deviations from normality and homoscedasticity (Zar 1984), so data were not transformed.

RESULTS

In the PCA 2 eigenvalues were >1 and explained 74% of the total variance among the species, which was greater than that predicted by the broken stick model (65%). PC1 separated

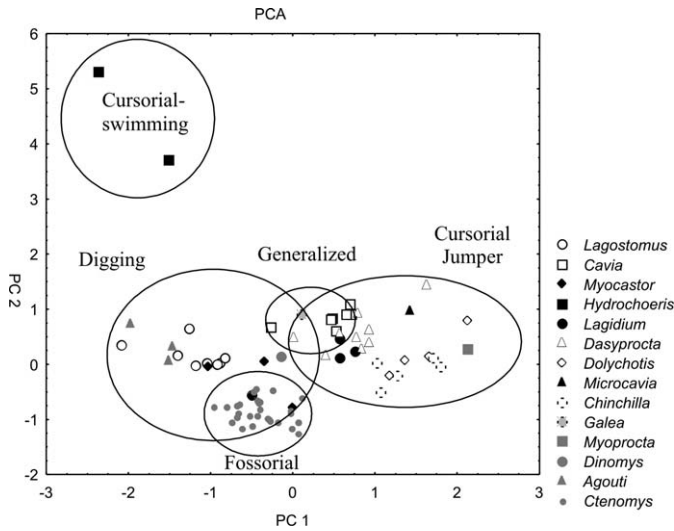


FIG. 2.—Scatter plot of principal components PC1 and PC2 scores for *Ctenomys* and other caviomorph rodents. Locomotor and digging habits are indicated on the figure.

taxa into cursorial, generalist, occasional digging, and digging functional types (Fig. 2). The loadings of the variables (Table 2) showed that PC1 had a strong association with decreases in humeral and ulnar robustness and development of the deltoid spine, epicondyles of the humerus, and the olecranon. Body mass had no significant loading on PC1; variation along this component can be used to interpret form–function variation rather than size. Digging (*Lagostomus*) and digging-swimming (*Agouti*) forms had low values on PC1, followed by occasional digging (*Myocastor*) and fossorial (*Ctenomys*) forms. Cursorial (*Dolichotis*, *Myoprocta*) and jumping nondigging forms (*Chinchilla*) had high values on PC1. The generalized (*Cavia*), less specialized cursorial forms (*Dasyprocta*), and jumping forms (*Lagidium*) were intermediate. The occasional diggers *Galea* and *Dinomys* had values that were similar to *Cavia*, and *Microcavia* had high values. Values for *Galea*, *Dinomys*, *Myoprocta*, and *Microcavia* are based on a single individual and so do not adequately represent the range of variation within these genera.

PC2 did not show separation of taxa by functional types and was strongly linked to body mass (factor loading = 0.79). Lowest values were observed for *Ctenomys* and the highest values for *Hydrochoeris*, with other taxa intermediate (Fig. 2). Among *Ctenomys* and *Hydrochoeris* were *Chinchilla*, *Myocastor*, *Dolichotis*, *Lagostomus*, *Myoprocta*, *Lagidium*, *Dinomys*, *Agouti*, *Dasyprocta*, *Galea*, *Microcavia*, and *Cavia*.

Ctenomys had greater epicondylar development of the humerus and lower humeral robustness and body mass values than did the digger *Lagostomus* and the digging-swimming *Agouti* (Table 3); *Lagostomus* had greater relative olecranon size and *Agouti* had greater ulna robustness. The occasional digger *Myocastor* had lower deltoid development and greater body mass values than did *Ctenomys*, and *Microcavia* had lower deltoid development, humeral robustness, epicondylar development, and body mass. The generalist *Cavia* had lower epicondylar and deltoid development of the humerus.

TABLE 2.—Eigenvalues, explained variance, and factor loadings for principal components 1 and 2 in principal components analysis (PCA) used to explain variation among caviomorph rodents in the following indices: HRI, humerus robustness index; SMI, shoulder moment index; EI, epicondyle index; URI, ulna robustness index; IFA, index of fossorial ability.

Variable	PC 1	PC 2
Mass	0.32	0.79*
HRI	−0.84*	0.27
SMI	−0.73*	−0.35
EI	−0.70*	−0.53
URI	−0.78*	0.37
IFA	−0.79*	0.39
Eigenvalues	3.07	1.38
% explained variance	51	23

* Highlights variables with loadings >0.7.

Compared with the more specialized cursorial forms *Dasyprocta* and *Dolychotis*, *Ctenomys* had high values in epicondylar and deltoid development, robustness of the humerus, and relative olecranon size; *Dolychotis* had lower ulna robustness. *Dasyprocta* and *Dolychotis* have great body mass. Compared with the jumper *Chinchilla*, *Ctenomys* had high values, except for the similar value of ulna robustness, and compared with *Lagidium*, high degree of epicondylar development. *Hydrochoeris* had greater relative olecranon size and ulna robustness than *Ctenomys*. Mean comparisons with *Galea*, *Dinomys*, and *Myoprocta* were not possible because of small sample sizes.

DISCUSSION

As suggested previously (Elissamburu and Vizcaíno 2004), the PCA illustrated variation among taxa along a cursorial to digging functional continuum that reflects a decrease in the speed and increase in the force capacities in forelimb through the cursorial, generalist, occasional digger, to digger sequence. From the cursorial to the digging extreme, humeral and ulnar robustness increase, as do the relative size of the epicondyles and olecranon process and the relative length of the deltoid spine. Cursorial forms have a slimmer forelimb, with a less robust humerus and ulna, and reduced development of the pronator and supinator muscles of the limb and manus and flexor muscles of the manus, as do the moment arm of the deltoids and latissimus dorsi muscles (flexors of the humerus) and the moment arm of triceps and dorsoepitrichlearis muscles (extensors of the ulna). These arrangements are consistent with a more speed-adapted forelimb and lower force production.

On the other end of the continuum digging forms have more robust forelimbs, with strong humeri and ulnae, great development of the musculature that pronates and supinates the limb and manus and flexes the manus, and longer moment arms for the muscles that flex the humerus and extend the ulna. These morphologies are consistent with powerful forelimb and high capacity for force production.

TABLE 3.—Means \pm SDs (n) for functional indices for forelimb function used in this study. HRI, humerus robustness index; SMI, shoulder moment index; EI, epicondyle index; URI, ulna robustness index; IFA, index of fossorial ability. Results of ANOVAs (made without *Galea*, *Dinomys*, and *Myoprocta*; and without *Microcavia* for URI and IFA) comparing genera for each index are presented at the bottom of the table.

Species	Indices				
	HRI	SMI	EI	URI	IFA
<i>Ctenomys</i>	9.4 \pm 0.7 (27)	52.0 \pm 1.7 (27)	30.4 \pm 1.5 (27)	5.7 \pm 0.7 (27)	23.6 \pm 2.1 (27)
<i>Agouti</i>	11.9* \pm 0.6 (3)	59 \pm 3.5 (3)	25.6* \pm 0.9 (3)	8.8* \pm 1.3 (3)	27.5 \pm 1.1 (3)
<i>Lagostomus</i>	11.0* \pm 0.9 (10)	53.0 \pm 2.5 (10)	26.0* \pm 2.0 (10)	7.1 \pm 2.1 (9)	28.8* \pm 1.8 (10)
<i>Myocastor</i>	11.0 \pm 1.3 (5)	44.5* \pm 2.5 (5)	30.2 \pm 0.4 (5)	6.2 \pm 2.4 (4)	24.2 \pm 2.2 (4)
<i>Galea</i>	8.2 (1)	45.4 (1)	16.6 (1)	6.6 (1)	28.7 (1)
<i>Microcavia</i>	7.4* \pm 0.5 (11)	37.9* \pm 3.9 (11)	19.3* \pm 1.5 (11)	4.7 (1)	23.4 (1)
<i>Dinomys</i>	9.8 (1)	43.9 (1)	28.3 (1)	5.5 (1)	23.9 (1)
<i>Cavia</i>	8.3 \pm 1.0 (9)	35.3* \pm 13.7 (8)	19.7* \pm 2.5 (9)	5.9 \pm 0.8 (8)	26.1 \pm 2.4 (8)
<i>Dasyprocta</i>	7.5* \pm 1.0 (9)	45.9* \pm 6.1 (9)	17.9* \pm 1.7 (9)	6.1 \pm 0.5 (9)	20.6* \pm 0.8 (9)
<i>Myoprocta</i>	4.4 (1)	40.0 (1)	18.8 (1)	2.8 (1)	17.1 (1)
<i>Dolichotis</i>	7.5* \pm 0.8 (5)	44.1* \pm 6.2 (5)	17.4* \pm 0.3 (5)	1.1* \pm 0.3 (6)	17.4* \pm 0.8 (6)
<i>Hydrochoeris</i>	8.6 \pm 0.7 (2)	49.2 \pm 0.7 (2)	26.3 \pm 0.5 (2)	10.7* \pm 1.3 (2)	34.7* \pm 2.5 (2)
<i>Lagidium</i>	7.9 \pm 0.3 (3)	45.8 \pm 1.7 (3)	20.2* \pm 0.6 (3)	5.2 \pm 0.1 (3)	22.4 \pm 1.0 (3)
<i>Chinchilla</i>	7.3* \pm 1.1 (5)	42.4* \pm 3.0 (5)	19.8* \pm 0.8 (5)	3.6 \pm 0.6 (5)	18.0* \pm 1.4 (5)
<i>F</i>	25.85	24.98	100.59	23.47	35.45
<i>d.f.</i>	10, 78	10, 77	10, 78	9, 66	9, 67
<i>P</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

* Denotes significant differences ($P < 0.05$) in comparison with the mean index values of *Ctenomys*.

The analyses demonstrate that *Ctenomys* resembles occasional diggers and digging forms, which have forelimbs adapted to digging activity and force development. Although it has a highly specialized forelimb related to its fossorial behavior, analysis of the forelimb indices as a whole places *Ctenomys* in a position along PC1 that indicates muscular development and force capacity that is similar to the digging forms *Lagostomus*, *Agouti*, and *Myocastor*. Its position on PC1 could be associated with a fossorial adaptation different from the principal variation present in the scratch-diggers sequence. In comparison with the cursorial-digging sequence, a conformation for force development is detected for *Ctenomys*. However, fossorial forms/specializations showed a different trend from that of nonfossorial scratch-digger specializations. Fossorial forms (represented by *Ctenomys*) seem to have high force specializations in the proximal and distal segments of the forelimb (humerus and hand), different from nonfossorial scratch-digger forms, which show specialization for force production in the medial segment of the limb (olecranon proportion, ulna robustness—Elissamburu and Vizcaíno 2004). Force applied to the substrate and body position for digging can produce different muscle and bone trends in fossorial specializations.

On the basis of comparison of the epicondyle index, *Ctenomys* has even greater epicondylar development than digging forms (*Lagostomus*, *Agouti*), indicating greater muscular development and capacity for force production in pronators and supinators of the limb and hand and flexors of the hand (Elissamburu and Vizcaíno 2004; Hildebrand 1985). This is concordant with the digging behavior of *Ctenomys*, in which the hand and fingers are used to break up the substrate (Hildebrand 1985), and the limb and hand are pronated and supinated during digging (Lehmann 1963). Woods (1972) observed that the pronator teres, which

originates on the medial epicondyle, is large in *Ctenomys* compared with other caviomorph rodents and that the insertion is more distal on the radius. He attributed this morphology to a more powerful forelimb in general. Epicondylar development could be an early specialization of the *Ctenomys* clade (Morgan and Verzi 2006) and is one of the principal characters that can be used to identify fossorial digging forms. Lehmann (1963) also observed increased epicondyle development in fossorial rodents. Epicondyle development suggests that in *Ctenomys* morphological specializations in the forelimb are for force production in digging rather than in locomotion, as seen in the nonfossorial caviomorph rodents (Elissamburu and Vizcaíno 2004).

A second important index is the SMI. The SMI of *Ctenomys* is similar to that of the digging forms (*Lagostomus*, *Agouti*) and greater than in occasional diggers, generalists, and cursorials. Large values of this index reflect large moment arms of the deltoid complex and latissimus dorsi muscle, which increase the capacity of force production in humeral flexion (Hildebrand 1985). Interpretation of this index varies according to limb function, but its significance in digging forms is clear (Elissamburu and Vizcaíno 2004). In diggers the teres major is robust and inserts more distally than in nonfossorial rodents, and the attachments of the subscapularis muscle are positioned to produce powerful flexion of the shoulder (Lehmann 1963). The low body mass of *Ctenomys* in comparison with the other digging forms, coupled with its EI and SMI, suggests a functional relationship between muscle and force development for fossorial activity rather than body support.

The HRI in *Ctenomys* was intermediate compared with the other species. This index alone is not a good indicator of fossorial activity. Robustness of the humerus is correlated with body mass in some groups of caviomorph rodents (Elissam-

buru and Vizcaíno 2004). However, this character might be relevant for interpreting intergeneric variation; an increase in the robustness of the humerus and deltoid distance has occurred from origin of the genus to extant *Ctenomys* (Morgan and Verzi 2006).

The IFA in *Ctenomys* was lower than in *Lagostomus*, similar to that of *Agouti* and only higher than the cursorial forms *Dolichotis* and *Dasyprocta* and the jumping *Chinchilla*. It was not a good indicator of fossorial activity within the caviomorph rodents sampled here. The URI also was not a good indicator of fossorial activity.

These observations conflict with the relatively large olecranon, deltooids, epicondylar development, and robustness of the humerus and ulna observed by Samuels and Van Valkenburgh (2008) in fossorial rodents. However, the only terrestrial caviomorph rodents included in their analysis were *Myocastor* and *Dinomys*. Within a larger sample that was limited to caviomorph rodents, specific suites of bone and muscular arrangements characterize arboreal and fossorial forms (Elissamburu 2001). These patterns provide valuable information about the family. Caviomorph rodents are a highly diverse group in terms of locomotor strategies and therefore are good candidates for morphofunctional studies of the limb. This study shows that olecranon and ulnar characters associated with fossorial activity in *Ctenomys* might not characterize fossorial rodents in general.

Overall, morphological features of the humerus and manus are the principal characters that differ between fossorial and nonfossorial caviomorph rodents. Humeral flexion and flexion and pronation of the hand function to produce force during highly specialized fossorial activity. In addition, highly specialized characters of the humerus and manus indicate that they serve different functions in digging and fossorial activity. Lehmann (1963) gives a short description of digging activity in *Ctenomys*, and Vassallo (1998) described digging in 2 species, *C. talarum* and *C. australis*. Unfortunately, movement of limb bone segments is not described in detail in either study. A kinematic study of limb use during digging activity is needed for a more complete analysis of digging behavior in *Ctenomys*.

RESUMEN

Los miembros del género *Ctenomys* (tuco-tuco; Rodentia, Caviomorpha, Octodontidae) son considerados cavadores "scratch-digger". Comparamos la extremidad anterior de adultos de *C. azarae* con 13 especies de otros géneros de roedores caviomorfos para interpretar la variación morfofuncional de los elementos óseos en relación con los hábitos fosoriales. Ocho medidas del húmero y ulna se usaron para construir cinco índices funcionales, que se analizaron con análisis de componentes principales (PCA) y de diferencia de medias. *Ctenomys* tiene una conformación general similar a la de los roedores caviomorfos cavadores epigeos, aunque presenta caracteres particulares propios de su condición fosorial especializada, como los epicóndilos comparativamente desarrollados. Estas características indican gran desa-

rollo muscular y capacidad de producción de fuerzas en la pronación y supinación del zeugopodio y la mano y flexión de la mano. El complejo deltoideo está bien desarrollado, indicativo de un arma de momento grande para el complejo muscular deltoideo y el músculo latissimus dorsi, que incrementan la capacidad de producción de fuerza en la flexión del húmero. Los índices del húmero son los más indicados para diferenciar las formas fosoriales de las cavadoras, cavadoras ocasionales, generalistas y cursoriales. Se supone un uso diferente de los segmentos de la extremidad en los roedores altamente fosoriales en comparación con scratch-digger epigeos.

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