MORPHOLOGICAL DIVERSITY OF THE HUMERUS OF THE SOUTH AMERICAN SUBTERRANEAN RODENT *CTENOMYS* (RODENTIA, CTENOMYIDAE)

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Humeral variation associated with digging ability in the subterranean rodent *Ctenomys* was analyzed through 6 functionally significant indexes. The humerus of some extinct and living species was slightly more specialized than that of fossorial octodontoids †*Actenomys* and *Octodon*, whereas it was highly specialized in some living species. The constant occurrence of greater epicondyles suggests a hierarchical pattern in the acquisition of scratch-digging specializations. A possible relationship between humeral morphological diversity and environments is preliminarily discussed.

Key words: Ctenomyidae, morphofunctional humeral diversity, rodents, scratch-digging adaptations

The family Ctenomyidae comprises a group of caviomorph rodents endemic to southern South America, including 1 living and at least 6 extinct genera (Verzi et al. 2004:796, figure 1) with diverse burrowing adaptations (Fernández et al. 2000; Quintana 1994; Reig et al. 1990; Verzi 2002). The only extant genus, *Ctenomys*, is 1st recorded in the Pliocene (Verzi et al. 2004), and includes the tuco-tucos, the living South American rodents with most markedly subterranean habits (Reig 1970), along with *Spalacopus* of the sister family Octodontidae (Honeycutt et al. 2003).

Ctenomys is the most polytypic genus of subterranean rodents worldwide, including more than 60 extant species (Cook et al. 2000; Reig et al. 1990; about 85 named species [Woods and Kilpatrick 2005]). Currently, tuco-tucos are widely distributed in South America, ranging between 15°S and 55°S latitude, and from the Andes to the Atlantic coast. Within this range they inhabit a wide variety of habitats with diverse soils and vegetational characteristics, including the Puna desert at 4,000 m elevation, sand dunes at the Atlantic coast, humid plains, and open areas in subtropical forests (Reig et al. 1965, 1990).

Ctenomys species are considered to be scratch-diggers that secondarily use their incisors for burrowing, according to substrate requirements (De Santis et al. 1998 and references therein; Stein 2000; Ubilla and Altuna 1990; Vassallo 1998). Scratch-digging is primarily achieved by means of forelimb actions in which the humerus (and associated muscles) plays a major role; thus, this postcranial bone is rich in functional–adaptive information (Szalay and Sargis 2001). Compared to nondigging rodents, the humerus of scratch-diggers shows greater robustness, which provides resistance to the loads imposed by the soil; greater articular surface area for elbow stabilization; and more-distal deltoid process and wider epicondyles, which give greater mechanical advantage to forelimb muscles (Argot 2001; Hildebrand 1985; Szalay and Sargis 2001; Vassallo 1998).

Humeral adaptations of *Ctenomys* are known only for a few species (*C. australis* and *C. talarum*—Vassallo 1998), even though it is a highly speciose genus. General data also can be found in comparative analyses of *Ctenomys* with respect to extinct ctenomyid genera (Casinos et al. 1993; Fernández et al. 2000; Quintana 1994; Reig and Quintana 1992), other subterranean rodent taxa (Dubost 1968; Lessa 1990, 1993), or other caviomorphs (Biknevicius 1993). In this paper we perform a quantitative analysis of the morphofunctional diversity of the humerus in 26 species of *Ctenomys*, including both living and extinct Pliocene and Pleistocene representatives of the genus. Morphological disparity and changes in humeral features associated with digging ability are discussed.

MATERIALS AND METHODS

The humeri of 2 specimens of the extinct †*Ctenomys chapalmalensis* (late Pliocene, Argentina—Ameghino 1908; Reig and Quintana 1992), 5 specimens of 4 undescribed species from the Pleistocene of Argentina (as †*Ctenomys* in Tonni et al. [1996]), and 67 adult specimens belonging to 21 living species from Argentina, Bolivia, Uruguay, and Brazil (Appendix I) were studied. All the fossil humeri were associated with skull or mandibular remains, or both. The comparative analysis included the Pliocene monotypic genus †*Actenomys* (†*A. priscus*, 10
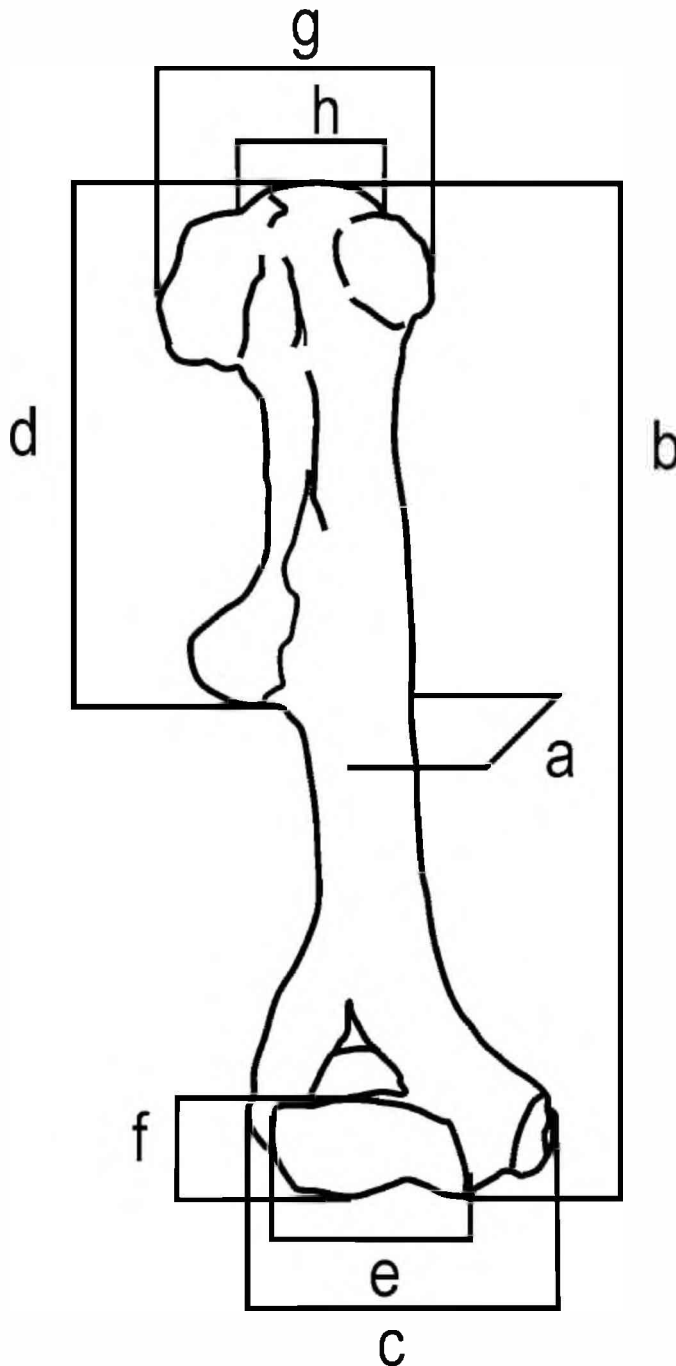
FIG. 1.—Linear measurements of the humerus: a, anteroposterior diameter at diaphysis; b, total humeral length; c, width at epicondyles; d, humeral head–distal origin of deltoid process length; e, distal articular surface width; f, length of trochlea; g, humeral width at tuberosities; h, humeral head width.

specimens), the only extinct ctenomyid genus for which complete humeri are known, and the living *Octodon* (4 specimens) of the sister family Octodontidae. Both are assumed to have more generalized fossorial habits than *Ctenomys* (Fernández et al. 2000; Lessa et al. 2004; Verzi 2002). The sister taxon of *Ctenomys* (Verzi 2002), †*Praectenomys rhombidens* (Pliocene of Umala Formation, Bolivia—Villarroel 1975), was analyzed qualitatively by means of illustrations (C. A. Quintana, unpublished illustrations; Quintana 1994).

Six indexes with assumed functional significance, calculated from linear measurements, were selected for quantitative analysis on the basis of a qualitative assessment and previous proposals (Casinos et al. 1993; Elissamburu and Vizcaíno 2004; Fernández et al. 2000; Hildebrand 1985; Sargis 2003; Stein 2000). These indexes are (Fig. 1): HDEWI, relative width at epicondyles (width at epicondyles [c] divided by humeral length [b]), an estimator of development of carpal and digital flexor muscles. HWL, humeral robustness (anteroposterior diameter at diaphysis [a] divided by humerus length [b]), an indicator of general bone resistance. RDP, relative position of the deltoid process (humeral head–distal base of deltoid process distance [d] divided by humeral length [b]), an estimator of in-lever arm for deltoid and pectoral muscles. Given that these muscles (especially the spinodeltoid) insert onto the entire surface of the deltoid process, we measured the relative position of the distal margin of the process (following Elissamburu and Vizcaíno 2004). RDSW, relative width of distal articular surface (distal articular surface width [e] divided by humeral length [b]), estimator of stabilization of the elbow joint. RTD, relative development of tuberosities (relative size of tuberosities [g/h] divided by humeral length [b]), an indicator of development of stabilizing shoulder muscles. TLI, relative length of the trochlea (trochlear length [f] divided by humeral length [b]), another estimator of elbow joint stabilization. Descriptions and illustrations of forelimb ctenomyid musculature are available in Woods (1972), Vassallo (1998), and Fernández et al. (2000).

Indexes were log 10 transformed and analyzed by factor analysis (principal component analysis) of the correlation matrix. Nonparametric analysis of variance (ANOVA; Kruskal–Wallis test, $\alpha = 0.05$) was used to evaluate character differences among selected species (see "Results"). Statistical significance of differences among these species for each index was analyzed using Dunn's post hoc test (Zar 1984). Statistical analyses were performed using PAST version 1.34 (Hammer et al. 2001). We evaluated the possible influence of body size (allometry) on the studied indexes for *Ctenomys* species through regression analysis (major axis method, *Model II Regression—User's Guide*—P. Legendre 2001, available from Département de Sciences Biologiques, Université de Montréal, http://www.bio.umontreal.ca/legendre/index.html). Given that body weight data were not available for most of the studied specimens, we used length of molariforms DP4–M2 as an estimator of body mass. In an assessment of specimens belonging to 16 living species, for which body mass and skulls (but not postcranial skeleton) were available, DP4–M2 length showed the best adjustment with respect to body mass ($r = 0.86$; $P < 0.001$; $n = 61$; data not shown but available from the authors). The total humeral length of †*C. chapalmalensis* MACN 19249 (humeral head missing) was estimated by means of the regression equation obtained from measurements of complete humeri from *Ctenomys* species. The width at epicondyles of the left humerus of †*Ctenomys* sp. 1 MLP 91-IV-25-212, better preserved but with damaged distal portion, was estimated from a reconstruction based on the right humerus (Fig. 2b).

In order to show patterns of change of the characters studied, the index values were separated into 3 or 4 unordered character states by establishing equal-sized intervals for each index range and mapped onto a partial phylogeny (see "Discussion") under maximum-parsimony criterion.

RESULTS

The 1st axis (PC-1) of the principal component analysis, which explained 51.28% of the total variation, expressed primarily the variation in robustness (HWL), relative width at epicondyles (HDEWI), relative position of the deltoid process
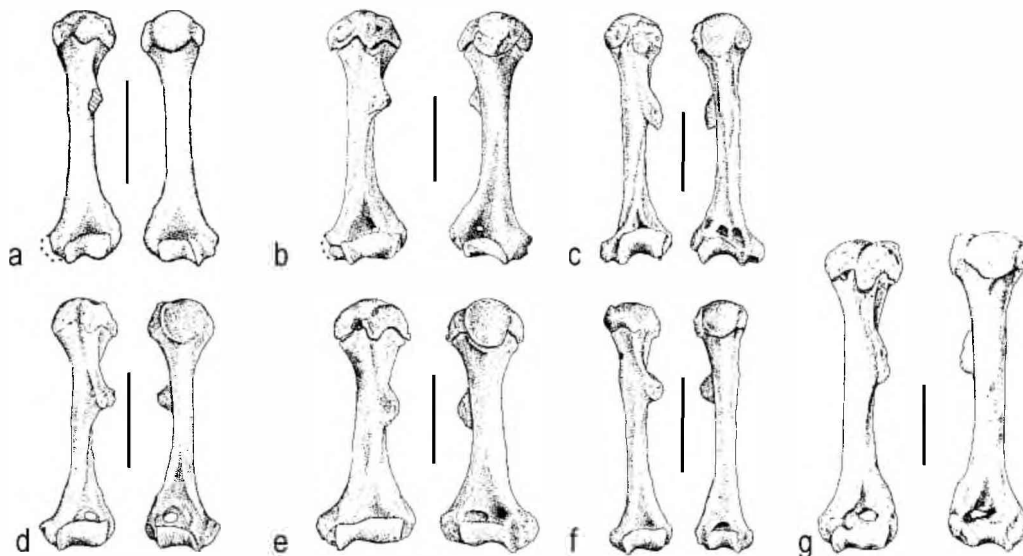
FIG. 2.—Anterior (left) and posterior (right) view of left humeri of species examined (inverted right humeri in c, and d–f): a) †*Ctenomys chapalmalensis* MMP 358-S; b) †*Ctenomys* sp. 1 MLP 91-IV-25-212; c) †*Ctenomys* sp. 2 MLP 91-IV-25-96; d) *Ctenomys flamarioni* MLP 28.V.01.5; e) *Ctenomys lewisi* CBF 00926; f) *Octodon* MLP 12.VIII.88.6; g) †*Actenomys priscus* MLP 91-IV-5-255. Dotted lines in a and b indicate parts reconstructed from other specimens (see "Materials and Methods" and Appendix I). Scale bar = 1 cm.

(RDP), and relative width of distal articular surface (RDSW) and, to a lesser extent, relative trochlear length (TLI; Fig. 3; Table 1). The variables RDSW, HDEWI, and HWL had the highest loadings on this axis. Although PC-1 is often a size vector, the contiguous position of unequally sized species (e.g., †*C. chapalmalensis*, DP4–M2 length = 6.9–8.7 mm compared to †*Actenomys priscus*, DP4–M2 length = 10.8–12.1 mm) on this axis suggests that PC-1 expressed shape independent of size. Moreover, the regressions performed for allometric analyses in *Ctenomys* resulted in very low correlation coefficients for all indexes ($r \leq 0.35$), with the exception of relative development of tuberosities (RTD; Table 2). This suggests that variables that loaded significantly in PC-1 are not influenced by size.

There was clear discrimination on PC-1 between *Octodon* and *Ctenomys*. †*Actenomys* occupied an intermediate position. This can be interpreted as a morphofunctional gradient in which *Octodon* exhibited the most generalized morphology (Fig. 2), with less humeral robustness, less development of epicondyles, and smaller distal articular surface. *Ctenomys* species were distributed on this axis over a considerable range, in which the living *C. flamarioni*, the Pliocene †*C. chapalmalensis*, and the Pleistocene †*Ctenomys* sp. 1 and †*Ctenomys* sp. 4 presented the lowest values for these variables within the genus. The living *C. lewisi* had the highest values of humeral robustness, epicondyle width, and distal articular surface width of all the species analyzed (Figs. 2 and 3; Table 3).

Principal component 2 explained 20.82% of the total variation, and was due mostly to variation in relative development of tuberosities (Table 1); this axis separated *Octodon* and *Ctenomys*, both with more-developed humeral tuberosities, from †*Actenomys*. However, the arrangement of species along this axis could be influenced by body size, because tuberosity

development showed negative allometry with respect to DP4–M2 (Table 2). The largest species, †*A. priscus*, had the lowest RTD values. *Ctenomys* species were spread widely along this axis.

To test for significance of the differences, the 2 *Ctenomys* species that occupied extreme positions in the principal component analysis, that is, *C. flamarioni* and *C. lewisi*, were compared with †*Actenomys* and *Octodon*. The nonparametric ANOVA indicated significant differences between species for all indexes ($P < 0.05$; Kruskal–Wallis *H*). In the post hoc multiple comparisons analysis (Dunn's test; Table 4), the ctenomyids †*Actenomys* and *Ctenomys* differed significantly from *Octodon* in relative position of the deltoid process. *C. flamarioni* differed significantly from *Octodon* also in relative width at epicondyles, but none of its indexes were significantly different from those of †*Actenomys*. In contrast, all the indexes of *C. lewisi* differed significantly with respect to those of *Octodon* and *Actenomys*. Moreover, *C. lewisi* also differed significantly from *C. flamarioni* in all morphofunctional indexes with the exception of HDEWI.

Figure 4 shows characters that resulted in significance in the principal component analysis (loads higher than 0.7; Table 1) mapped onto a partial phylogeny of taxa studied (see "Materials and Methods"). Relationships of *Ctenomys* are based on recent data of combined intron sequences of 2 nuclear genes (Fig. 4; Castillo et al. 2005), although only 9 of the 21 living *Ctenomys* species analyzed could be included because of poor knowledge of the phylogeny of this highly polytypic genus (Lessa and Cook 1998; Woods and Kilpatrick 2005). Nevertheless, the cladogram is used here to depict possible changes, while acknowledging that any analysis of pattern through phylogeny is a biased representation of processes occurring at lower hierarchical levels (Cracraft 1990; Verzi
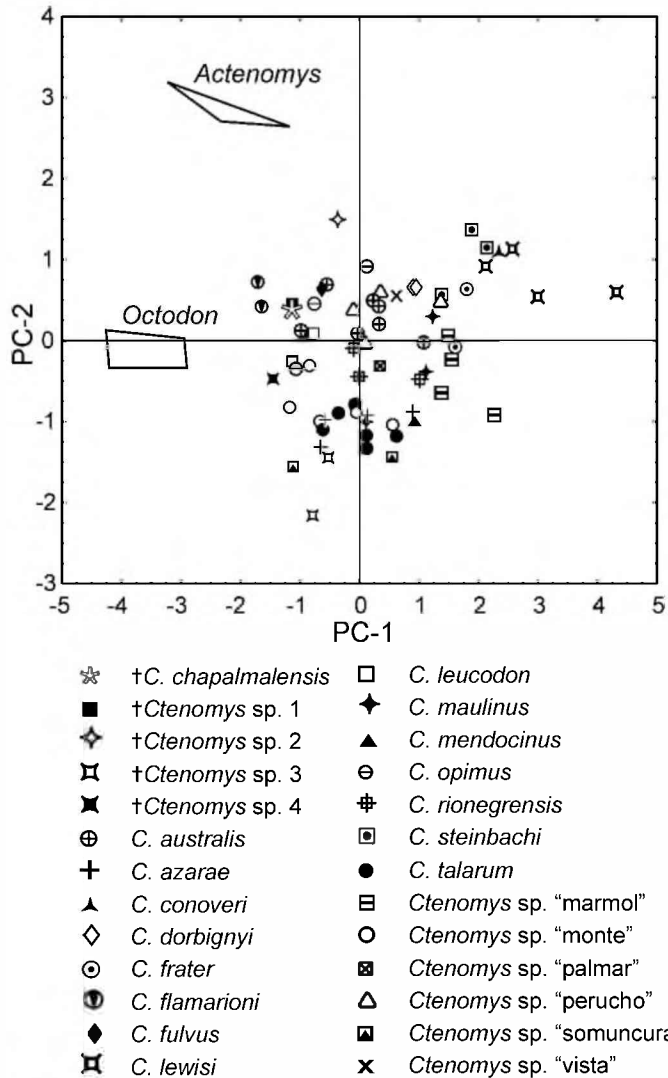
Fig. 3.—Plot of scores on principal component axes 1 and 2 from principal component analysis of humeral variables of 75 specimens belonging to †*Actenomys priscus* (*n* = 3), *Octodon* (*n* = 4), and *Ctenomys* (26 species).

2001). The featured topology includes the Pliocene †*C. chapalmalensis* and the living species that occupied extreme positions in the principal component analysis. In addition, other species belonging to distant lineages such as the "*mendocinus*"

TABLE 1.—Principal component analysis of humeral indexes of South American octodontoids. Component loading pattern on the first 2 principal component analysis axes, eigenvalues, and percent of total explained variance are given. Asterisks indicate loads > 0.7.

Variable	PC-1	PC-2
Log HWL (humeral robustness)	0.81*	0.30
Log HDEWI (relative width at epicondyles)	0.87*	−0.04
Log RDP (relative position of deltoid process)	0.70*	−0.04
Log TLI (relative length of trochlea)	0.64	−0.10
Log RDSW (relative width of distal articular surface)	0.90*	−0.05
Log RTD (relative development of tuberosities)	0.13	−0.97*
Eigenvalue	2.39	0.97
Total variance explained (%)	51.28	20.82

TABLE 2.—Allometric equations (Model II regression, major axis method) of morphofunctional indexes of *Ctenomys*, regressed against length of molariforms DP4–M2. Abbreviations as in Table 1.

Regression	Equation (y = ax^b)	*n*	*r*	*P*	Confidence intervals
HWL	$y = -1.76x^{0.82}$	68	0.35	0.002	$a = -2.46 - -1.36$ $b = 0.38 - 1.61$
HDEWI	$y = -0.71x^{0.24}$	66	0.25	0.023	$a = -0.93 - -0.51$ $b = 0.02 - 0.48$
RDP	$y = -0.33x^{0.04}$	68	0.08	0.26	$a = -0.44 - -0.21$ $b = -0.08 - 0.17$
TLI	$y = -1.08x^{0.17}$	68	0.09	0.24	$a = -1.59 - -0.64$ $b = -0.32 - 0.75$
RTD	$y = 0.18x^{-1.51}$	67	−0.81	0.001	$a = -0.03 - 0.44$ $b = -1.82 - -1.28$
RDSW	$y = -0.74x^{0.09}$	61	0.10	0.209	$a = -0.95 - 0.53$ $b = -0.14 - 0.33$

group, that is, *C. flamarioni*, *C. rionegrensis*, and *C. mendocinus* (see Castillo et al. 2005; Massarini et al. 1991), and at least 2 different clades of Bolivian taxa, that is, *C. steinbachi* of the "*boliviensis*" group and *C. lewisi–C. frater–C. conoveri*, also are included. The phylogenetic position of *C. leucodon* and *C. opimus* is controversial (see Castillo et al. 2005; Lessa and Cook 1998).

Character mapping (Fig. 4) shows that *Ctenomys* as a genus differs from the fossorial *Octodon* and †*Actenomys* only by its greater epicondyle development (even though, as stated above, this difference is not always statistically significant). *C. steinbachi* and the *C. lewisi–C. frater* clade show the highest degree of specialization in humeral morphology. An increase of all the values mentioned occurs independently at least in the 1st species and the latter clade (and also partially in *C. conoveri*). Even so, beyond the pattern shown by these species, shifts in different humeral features seem to be uncoupled, as shown by the character states in *C. leucodon* (Table 3; Fig. 4).

DISCUSSION

Within the radiation of South American rodents, the octodontoids of families Ctenomyidae and Octodontidae have developed the greatest adaptations for digging and subterranean life. Given that *Ctenomys* has been primarily characterized as a fully subterranean scratch-digger, several humeral specializations classically related to these habits would be expected (Elissamburu and Vizcaíno 2004; Hildebrand 1985; Hill 1937; Laville 1989; Lehmann 1963; Lessa and Stein 1992; Stalheim-Smith 1984; Stein 2000; Vassallo 1998). However, our analysis of humeral morphology shows that, at least in some species, greater development of the epicondyle represents the only scratch-digging specialization with respect to the fossorial †*Actenomys* and *Octodon*. These results partially support the statement of Reig et al. (1990) that *Ctenomys* has moderate skeletal specializations for digging. Moreover, this is in agreement with the inferred habits of the extinct representatives of the major clade that includes *Ctenomys*, which exhibit only moderate digging adaptations (Lessa et al. 2004; Verzi 2002). Fragmentary materials known for the sister genus of *Ctenomys*,

TABLE 3.—Values of humeral morphofunctional indexes of South American octodontoids. Data are expressed as mean $\pm$ *SD*. Abbreviations as in Table 1.

Species	Sample size (n)	HWL	HDEWI	RDP	TLI	RDSW	RTD
Living *Ctenomys*							
C. australis	7	0.09 ± 0.007	0.33 ± 0.017	0.48 ± 0.011	0.12 ± 0.004	0.22 ± 0.009	0.06 ± 0.003
C. azarae	4	0.09 ± 0.007	0.31 ± 0.011	0.50 ± 0.012	0.12 ± 0.010	0.23 ± 0.004	0.08 ± 0.004
C. conoveri	1	0.09	0.36	0.55	0.14	0.27	0.05
C. dorbignyi	2	0.11 ± 0.000	0.33 ± 0.002	0.52 ± 0.017	0.11 ± 0.012	0.22 ± 0.011	0.06 ± 0.000
C. flamarioni	2	0.09 ± 0.000	0.28 ± 0.005	0.48 ± 0.010	0.11 ± 0.007	0.19 ± 0.009	0.06 ± 0.003
C. frater	2	0.11 ± 0.006	0.34 ± 0.021	0.55 ± 0.002	0.12 ± 0.005	0.23 ± 0.002	0.06 ± 0.005
C. fulvus	3	0.09 ± 0.003	0.29[a]	0.49 ± 0.010	0.12 ± 0.005	0.22 ± 0.006	0.05 ± 0.003
C. leucodon	2	0.08 ± 0.005	0.30 ± 0.006	0.53 ± 0.029	0.11 ± 0.000	0.21 ± 0.002	0.06 ± 0.001
C. lewisi	4	0.12 ± 0.008	0.37 ± 0.021	0.56 ± 0.016	0.13 ± 0.013	0.25 ± 0.012	0.06 ± 0.005
C. maulinus	3	0.10 ± 0.010	0.34 ± 0.005	0.50 ± 0.006	0.12 ± 0.007	0.23 ± 0.008	0.07 ± 0.007
C. mendocinus	1	0.09	0.32	0.51	0.13	0.23	0.08
C. opimus	3	0.09 ± 0.005	0.30 ± 0.005	0.51 ± 0.006	0.11 ± 0.009	0.21 ± 0.003	0.06 ± 0.008
C. rionegrensis	3	0.10 ± 0.004	0.33 ± 0.005	0.51 ± 0.017	0.11 ± 0.002	0.22 ± 0.009	0.07 ± 0.004
C. steinbachi	3	0.11 ± 0.008	0.33 ± 0.005	0.56 ± 0.012	0.13 ± 0.006	0.23 ± 0.004	0.05 ± 0.003
C. talarum	9	0.09 ± 0.006	0.30 ± 0.011	0.52 ± 0.008	0.12 ± 0.008	0.21 ± 0.008	0.08 ± 0.007
C. "marmol"	4	0.11 ± 0.004	0.34 ± 0.008	0.53 ± 0.017	0.12 ± 0.008	0.24 ± 0.009	0.08 ± 0.007
C. "monte"	6	0.09 ± 0.012	0.29 ± 0.010	0.50 ± 0.023	0.12 ± 0.011	0.20 ± 0.013	0.10 ± 0.005
C. "palmar"	1	0.10	0.32	0.52	0.10	0.23	0.07
C. "perucho"	4	0.10 ± 0.008	0.29 ± 0.016	0.52 ± 0.009	0.13 ± 0.002	0.22 ± 0.009	0.06 ± 0.001
C. "somuncura"	2	0.09 ± 0.011	0.31 ± 0.010	0.51 ± 0.001	0.12 ± 0.000	0.21 ± 0.019	0.09 ± 0.004
C. "vista"	1	0.10	0.32	0.53	0.11	0.24	0.06
Plio–Pleistocene *Ctenomys*							
C. chapalmalensis	2	0.09 ± 0.008	0.30 ± 0.019	0.45 ± 0.005	0.10 ± 0.003	0.20 ± 0.008	0.06[a]
Ctenomys sp. 1	1	0.12	0.35	0.46	0.10	0.22	0.06
Ctenomys sp. 2	1	0.10	0.30	0.48	0.11	0.22	0.05
Ctenomys sp. 3	2	0.08 ± 0.011	0.31 ± 0.010	0.51 ± 0.025	0.11 ± 0.020	0.21 ± 0.004	0.09 ± 0.001
Ctenomys sp. 4	1	0.08	0.32	0.56	0.09	0.20	0.07
Octodon sp.	4	0.08 ± 0.008	0.24 ± 0.010	0.44 ± 0.010	0.11 ± 0.022	0.17 ± 0.011	0.06 ± 0.002
Actenomys priscus	10	0.09 ± 0.005	0.26 ± 0.016	0.47 ± 0.005	0.11 ± 0.009[b]	0.19 ± 0.011[c]	0.04 ± 0.001[d]

[a] $n = 1$.
[b] $n = 9$.
[c] $n = 8$.
[d] $n = 3$.

†*Praectenomys*, preclude a reliable estimation of its habits (Quintana 1994; Villarroel 1975). However, the other members of this clade, †*Actenomys–Xenodontomys*, are fossorial ctenomyids that would have spent an important fraction of time on the surface (De Santis and Moreira 2000; Verzi 2002).

If epicondyle increase is assumed to be the only humeral specialization accompanying the differentiation of the subterranean *Ctenomys*, this suggests the existence of a certain hierarchical pattern in the acquisition of biomechanical specializations for scratch-digging. In this hierarchy, increase

of the forearm flexor and extensor muscles that originate on the epicondyles would have been a primary requirement. This increase provides more powerful flexion to the wrist and digits, which is necessary for the forelimb to overcome soil resistance in the power stroke during scratch-digging (Argot 2001; Hildebrand 1985; Sargis 2003).

Among the living species, further specializations occur, comprising greater robustness (HWL), more extensive contact area between the trochlea and longer trochlear notch (higher RDSW and TLI), increased distalization of the deltoid process (higher

TABLE 4.—Results of Dunn's post hoc test for multiple nonparametric comparisons of South American octodontoids, showing Q-value calculated for each comparison (1s-row taxon versus each 2nd-row taxon in headings). Asterisk indicates significant differences ($Q = 2.639$, $d.f. = 4$, 0.05). Abbreviations as in Table 1.

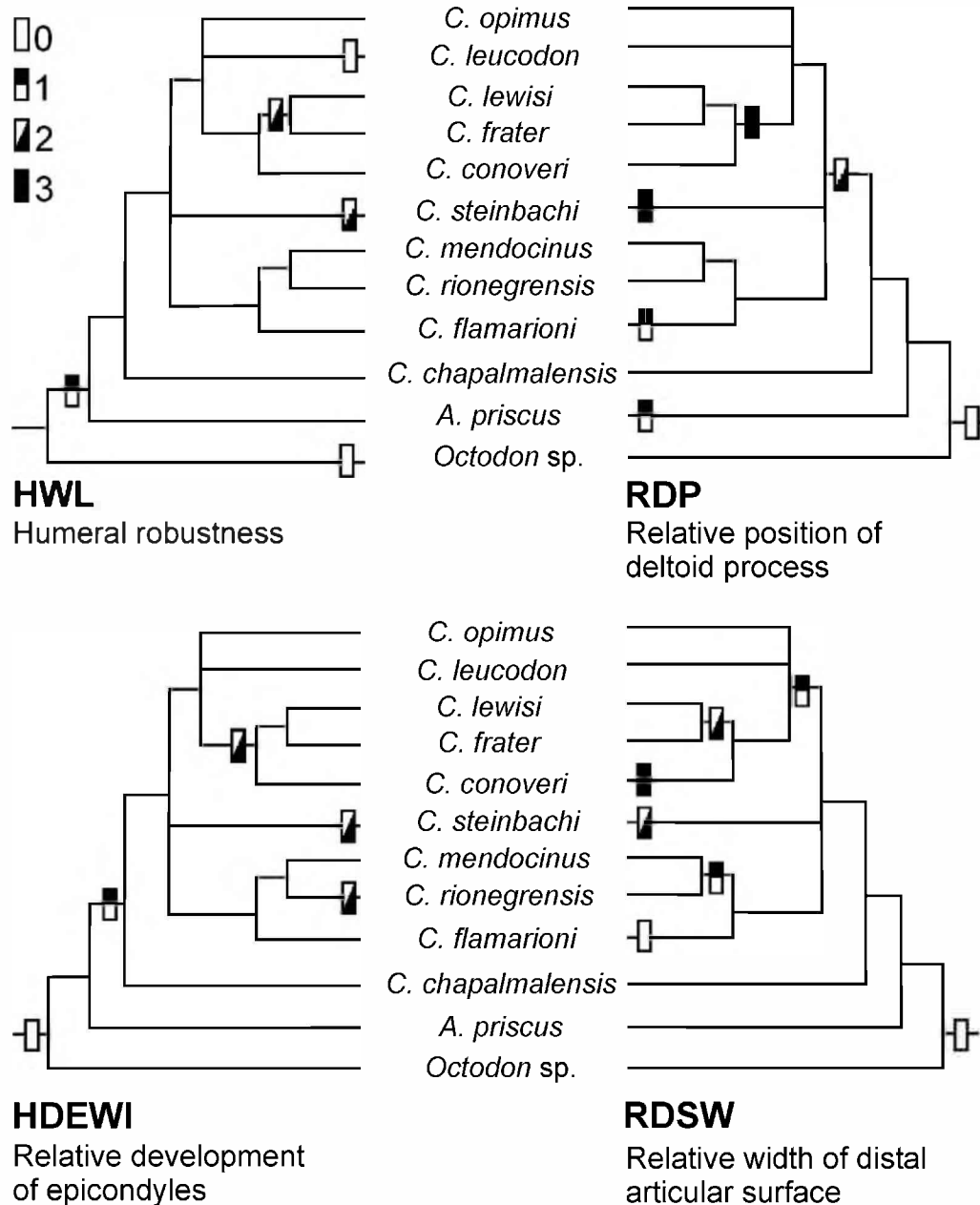| Index	Octodon			Actenomys		Ctenomys lewisi
	Actenomys	*C. flamarioni*	*C. lewisi*	*C. flamarioni*	*C. lewisi*	*C. flamarioni*
HWL	3.22*	1.23	8.28*	1.89	3.71*	3.10*
HDEWI	1.54	4.85*	8.00*	2.44	5.17*	2.32
RDP	3.25*	4.55*	8.42*	0.68	3.80*	6.19*
RDSW	0.36	0.58	5.87*	0.89	5.15*	4.65*

FIG. 4.—Morphofunctional indexes mapped onto a partial phylogeny of living *Ctenomys* modified from Castillo et al. (2005). Position of the other species included follows Verzi (2002). Only unambiguous apomorphies are shown. Characters and character states (ranges coded into discrete character states, in parentheses): HWL, 0 (0.061–0.08), 1 (0.081–0.10), 2 (0.101–0.12). RDP, 0 (0.42–0.46), 1 (0.461–0.50), 2 (0.501–0.54), 3 (0.541–0.60). HDEWI, 0 (0.20–0.26), 1 (0.261–0.32), 2 (0.321–0.38). RDSW, 0 (0.17–0.20), 1 (0.201–0.23), 2 (0.231–0.26), 3 (0.261–0.29).

RDP), and greater epicondyle development (higher HDEWI). Greater robustness provides resistance to the loads imposed by muscular action and substrate resistance. Greater contact area between the trochlea and the trochlear notch, as well as a longer trochlea, stabilize the elbow joint without restricting movement range (Argot 2001) and allow efficient dissipation of the loads acting at this joint during digging (Szalay and Sargis 2001). A more-distal deltoid process gives greater mechanical advantage (increased in-lever arm, i.e., distance from muscle attachment to joint) to the deltoid and pectoral muscles that contribute to forelimb retraction (Fernández et al. 2000; Hildebrand 1985;

Stein 2000). Finally, increased epicondyle development offers more extensive surface for the origin of carpal and digital flexor and pronator muscles (medial epicondyle), and extensor and supinator muscles (lateral epicondyle—e.g., Hildebrand 1985; Vassallo 1998).

Greater development of the humeral tuberosities is related to increased development of stabilizing shoulder muscles, allowing the limb to withstand the stresses applied across the joint during scratch-digging (Argot 2001; Sargis 2003). In our analysis, the relative development of the humeral tuberosities (RTD) was the only index correlated with size. Further analyses

are necessary to test if its negative allometry is related to the existence of a size threshold or other constraint for this feature.

The strong specialization in some of the living species examined (i.e., *C. lewisi*, *C. frater*, *C. steinbachi*, *C. conoveri*, and *Ctenomys* sp. "marmol") occurs in a context of strong morphological disparity that is already present among Pleistocene representatives (Figs. 2–4; Table 3). Although environmental data for the species studied are often incomplete or nonexistent, the available information allows some preliminary considerations concerning this disparity.

The humeri of †*C. chapalmalensis* (the oldest species of the genus for which postcranial remains are known) and *C. flamarioni* are morphologically similar to that of the fossorial †*Actenomys*, except for the slight difference in epicondyle development (Fig. 2). The skull morphology of these *Ctenomys* species does not exhibit remarkable tooth-digging adaptations (Quintana 1994; Verzi 2002; D. H. Verzi, pers. comm.). Conceivably, †*C. chapalmalensis* required very friable soils to perform primarily as a scratch-digger. Indeed, this species, recorded in the latest Pliocene of central Argentina, is part of the extinct caviomorph fauna most clearly indicative of arid environments that has been recorded so far (Verzi and Quintana 2005); thus, this species could have inhabited immature, friable soils. Concurrently, the distribution of the living *C. flamarioni* is restricted to the 1st line of coastal sand dunes in Rio Grande do Sul, southeastern Brazil (Freitas 1995). In contrast, *C. lewisi* and *C. frater*, which showed the most specialized humeral morphology, inhabit deep soils, often near creeks or rivers (Anderson 1997; Cook et al. 1990). *C. lewisi* is found in Tarija, in southwestern Bolivia (Cook et al. 1990). *C. frater* inhabits humid meadows and forests from southwestern Bolivia to northwestern Argentina and builds galleries in deep, humus, and presumably compact soils (Eisenberg and Redford 1999; Mora et al. 2003). No accurate data on the habitat of the also specialized *C. steinbachi*, *C. conoveri*, and *Ctenomys* sp. "marmol" are available (Anderson 1997; Eisenberg and Redford 1999).

Examination of these partial data suggests a possible relationship between humeral morphology and soil characteristics. Within the profuse cladogenesis of *Ctenomys*, characterized by very early and rapid split of major clades (Castillo et al. 2005; Lessa and Cook 1998), both dissimilar selective pressures, derived from diverse habitats, and historical factors differentially affecting each of the early major lineages, could have promoted the extensive diversity of humeral morphology. However, further ecological, systematic, and phylogenetic studies are necessary to allow testing of adaptive hypotheses while controlling for phylogenetic effects.

RESUMEN

Se analizó la diversidad morfológica del húmero asociada con la capacidad excavatoria en el roedor sudamericano *Ctenomys*, a través de la evaluación de 6 índices funcionalmente significativos. La morfología humeral de algunas especies extintas y vivientes resultó sólo ligeramente más especializada que la de los octodontoideos fosoriales †*Actenomys* y *Octodon*.

Una marcada especialización se detectó en algunas especies vivientes. La presencia constante de epicóndilos bien desarrollados sugiere cierto patrón jerárquico de adquisición de especializaciones para la braquioexcavación. Se discute preliminarmente la posible relación entre la diversidad morfológica del húmero y los ambientes habitados.

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APPENDIX I

Specimens examined.—The specimens of Octodontoidea (22 extant and 6 extinct species) studied in this work belong to the following mammalogical or paleontological collections: Colección Boliviana de Fauna, Bolivia (CBF); Museo de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia," Argentina (MMP); Museo de La Plata, Argentina (MLP); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Argentina (MACN); and Laboratorio de Evolución, Facultad de Ciencias, Universidad de la República, Uruguay (CA and EV).

Extant species.—*Ctenomys australis*: MLP 3.XI.95.5, MLP 7.XI.95.1, MLP 7.XI.95.3, MLP 7.XI.95.5, MLP 7.XI.95.6, MLP 10.XI.95.2, MLP Prov 99-VII-14-03. *Ctenomys azarae*: MLP 2.IV.02.7, MLP 20.V.02.7, MLP 20.V.02.8, MLP 20.V.02.9. *Ctenomys conoveri*: CBF 00939. *Ctenomys dorbignyi*: MLP 5.VI.00.1, MLP 5.VI.00.6. *Ctenomys flamarioni*: MLP 28.V.01.5, MLP 28.V.01.6. *Ctenomys frater*: CBF 00940, CBF 2307. *Ctenomys fulvus*: MLP 7.XI.95.8, MLP 7.XI.95.10, MLP 9.XI.95.2. *Ctenomys leucodon*: CBF 3658, CBF 3659. *Ctenomys lewisi*: CBF 926, CBF 2280, CBF 2281, CBF 2282. *Ctenomys maulinus*: MLP 1.X.01.2, MLP 1.X.01.3, MLP 1.X.01.4. *Ctenomys mendocinus*: MLP 8.X.02.1. *Ctenomys opimus*: MLP 12.XI.02.16, MLP 12.XI.02.17, MLP 12.XI.02.18. *Ctenomys rionegrensis*: CA 393, CA 412, EV1137. *Ctenomys steinbachi*: CBF 00942, CBF 00943, CBF 00944. *Ctenomys talarum*: MLP 26.VIII.01.5, MLP 1.XI.95.8, MLP 1.XI.95.15, MLP 2.V.00.1, MLP 1.VIII.00.7, MLP 1.VIII.00.8, MLP 1.VIII.00.12, MLP 1.VIII.00.13, MLP 3.XI.95.2. *Ctenomys* sp. "marmol" (Mármol Creek, Entre Ríos Province, Argentina): MLP 1.X.01.6, MLP 1.X.01.8, MLP 1.X.01.9, MLP 1.X.01.10. *Ctenomys* sp. "monte" (Monte Hermoso, Buenos Aires Province, Argentina): MLP 27.XII.01.47, MLP 27.XII.01.50, MLP 27.XII.01.55, MLP 27.XII.01.58, MLP 13.VI.02.1, MLP 8.X.02.17. *Ctenomys* sp. "palmar" (Arroyo El Palmar, Entre Ríos Province, Argentina): MLP 4.VII.02.5. *Ctenomys* sp. "perucho" (Perucho Verna Creek, Entre Ríos Province, Argentina): MLP 31.III.99.2, MLP 31.III.99.5, MLP 31.III.99.6, MLP 31.III.99.7. *Ctenomys* sp. "somuncura" (Somuncurá, Río Negro Province, Argentina): MLP 15.III.96.2, MLP 15.III.96.5. *Ctenomys* sp. "vista" (Bella Vista, Corrientes Province, Argentina): MLP 7.X.92.6. *Octodon* sp. (Lanín National Park, Neuquén Province, Argentina): MLP 12.VII.88.1, MLP 12.VII.88.2, MLP 12.VII.88.6, MLP 12.VII.88.7.

Extinct species.—†*Ctenomys* sp. 1 (Costa Bonita, Buenos Aires Province, Argentina; middle Pleistocene): MLP 91.IV.25.212, left humerus with damaged medial epicondyle, and right humerus without head. †*Ctenomys* sp. 2 (Costa Bonita, Buenos Aires Province, Argentina; middle Pleistocene): MLP 91.IV.25.96, right humerus. †*Ctenomys* sp. 3 (Punta Hermengo, Buenos Aires Province, Argentina; Pleistocene): MLP 91-IV-30-39, right and left humeri from different specimens. †*Ctenomys* sp. 4 (El Pescado Creek, Buenos Aires Province, Argentina; Pleistocene): MLP 55-V-30-2, right humerus without deltoid process. †*C. chapalmalensis* (Chapadmalal area, Buenos Aires Province, Argentina; San Andrés Formation, late Pliocene): MACN 19249, right humerus without head; MMP 358-S, left humerus with deltoid process damaged. †*Actenomys priscus* (Chapadmalal area, Buenos Aires Province, Argentina; Chapadmalal Formation, Pliocene): MMP provisional no. 4-1-90 (3 specimens: 2 right humeri, 1 with damaged head, and 1 left humerus); MMP 395-S, left humerus without head; MMP 397-S, left humerus with damaged head; MMP 367-S, left humerus; MMP 586-S, right humerus with damaged head; MMP provisional no. 77d, right humerus; MMP 1566-M, damaged left humerus; MLP 91-IV-5-255, left humerus.