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Patterns of variation in the tympanic bulla of tuco-tucos (Rodentia, Ctenomyidae, Ctenomys)

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Abstract As subterranean rodents live in burrows and are constrained by the physics of their environment to vocalize, mainly in low frequencies, their expanded middle ear cavities are associated with enhanced lower-frequency hearing. Previous literature has widely acknowledged inflated tympanic bulla as a character to be found in the majority of the *Ctenomys* species. To explore the morphology of *Ctenomys* tympanic bulla, we studied a sample of 669 skulls, obtained from 21 species, for tympanic bulla size, volume, and internal structure. The study determined that bullar inflation does not seem to be the rule in *Ctenomys* and that the relationship between bullar size (volume) and skull size do not correspond to the phylogeny based on cytochrome b sequences thus probably being a species-specific adaptive characteristic. We also found that the internal bullar structure differs between taxa, depending on the relative contributions of cancellous (alveolar) and septate patterns to the partitioning of the bulla.

Keywords Tympanic bulla size · Comparative analysis · Middle ear internal structure · Subterranean rodents

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Introduction

Subterranean rodents are particular organisms, which have an almost worldwide distribution. Being adapted to underground life, even not closely related taxa, share many convergent characteristics and slightly different solutions to similar problems posed by the subterranean niche, which makes these animals popular research subjects for behavioral and evolutionary comparative studies.

In many species of subterranean or desert rodents, tympanic bullae size, volume, and internal structure are important parameters related to low-frequency hearing improvement and were the subject of many previous studies (Simkin 1965; Lay 1972; Webster and Webster 1975; Gardner and Emmons 1984; Lombard and Hetherington 1993; Francescoli 1999; Schleich and Vassallo 2003). Gerbillidae and Heteromyidae show inflated bullae probably adapted to detect low-frequency sounds emitted by their predators (Webster and Webster 1971; Randall 1994) or low-frequency sounds and/or seismic signals produced by footdrumming (Randall 1993, 1994). Many subterranean species have inflated tympanic bullae (Stein 2000), but some lack this characteristic and achieve enhanced low-frequency hearing through modifications at the inner ear level, as in *Spalax ehrenbergi* or *Heterocephalus glaber* (Heffner and Heffner 1992, 1993; Francescoli 2000).

Tuco-tucos (*Ctenomys*) are a group of subterranean rodents endemic to the southern part of South America (Peru, Bolivia, southern Brazil, Argentina, Paraguay, Uruguay, and part of Chile). The genus includes some 60 species thought to have appeared mostly after a process of explosive speciation during the Pleistocene. They are adapted to subterranean life in similar ways as other subterraneans, but they are unique in the fact that they forage aboveground during short excursions outside their tunnels, and probably, this fact has constrained the retention of fully functional eyes used in combination with hearing to prevent predation (Reig et al. 1990). They are mainly solitary animals, but at least up to three species are

known to be social: *Ctenomys sociabilis*, *Ctenomys peruanus*, and *Ctenomys opimus* (Pearson 1959; Pearson and Christie 1985; Lacey et al. 1997; E. Lacey, personal communication).

Many authors have noticed that subterranean rodents, in general, and tuco-tucos, in particular, have inflated tympanic bullae, probably related with the reception of low-frequency emissions from conspecifics (Francescoli 1999, 2000; Schleich and Vassallo 2003; Schleich and Busch 2004). Francescoli (2000) has underlined this characteristic for some *Ctenomys* species known to emit low-frequency vocalizations.

Schleich and Vassallo (2003) have analyzed skulls from 13 *Ctenomys* species (48 individuals, one to seven individuals per species), mostly from Argentine populations, and compared their cranial features and bullar volumes (BVs) with four specimens of the fossil ctenomyid *Actenomys*, and 11 species of surface dwelling caviomorphs (35 individuals, 1–10 per species). Their study concluded that bullae were larger in *Ctenomys* than in surface caviomorphs, and in *Actenomys*, they were intermediate (Schleich and Vassallo 2003). The authors suggested that larger bullae may reflect good low-frequency hearing and could be an adaptation for subterranean vocal communication. If this generalization is true, it should be expected that all *Ctenomys* species, or at least those known to vocalize in low frequencies, have

inflated bullae. Nevertheless, close examination of more species suggested to one of us (G.F.) that the enlarged bullae may not be a general feature of all *Ctenomys* species.

The main objectives of this study are: (1) determining if bullar inflation is a general character of tuco-tucos, using a larger sample than that used by Schleich and Vassallo (2003) both in number of individuals per species and in number of species, trying to cover all the distribution area of the genus; (2) determining if bullar inflation is a character constrained by the phylogeny of the genus, or its presence in many species could be interpreted as an adaptation to some environmental factor.

Materials and methods

Specimens

Skulls obtained from 21 *Ctenomys* species (669) were studied for BV and internal structure. All studied skulls were from adult animals, as established in the collections data. A detailed list of the sampled species with the number of skulls measured is presented in Table 1, and the localities and accession numbers of all specimens used are presented in Appendix 1.

Table 1 Species included in this study with their contributed number of skulls, mean skull length (\pm SD), and mean bullar volume (\pm SD)

Species	No. of skulls	Mean skull length \pm SD (mm)	Mean bullar volume \pm SD (mm ³)
<i>Ctenomys boliviensis</i>	52	45.39 \pm 6.75	464.25 \pm 150.00
<i>Ctenomys colburni</i>	37	34.55 \pm 3.29	328.87 \pm 62.85
<i>Ctenomys dorsalis</i>	12	35.37 \pm 3.58	284.95 \pm 46.99
<i>Ctenomys frater</i>	17	38.17 \pm 2.25	286.94 \pm 46.23
<i>Ctenomys fulvus</i>	12	39.95 \pm 2.80	556.21 \pm 118.19
<i>Ctenomys haigi</i>	59	35.79 \pm 3.67	341.68 \pm 78.26
<i>Ctenomys lewisi</i>	28	41.48 \pm 5.58	319.20 \pm 67.95
<i>Ctenomys magellanicus</i>	24	43.59 \pm 6.02	508.84 \pm 119.33
<i>Ctenomys maulinus</i>	36	40.53 \pm 4.17	308.27 \pm 61.40
<i>Ctenomys mendocinus</i>	48	35.21 \pm 3.80	342.24 \pm 82.53
<i>Ctenomys opimus</i>	96	44.03 \pm 4.05	625.62 \pm 108.00
<i>Ctenomys pearsoni</i> (kar. ^a Canelones)	11	44.84 \pm 1.70	261.36 \pm 20.96
<i>C. pearsoni</i> (kar. Solis)	31	44.56 \pm 2.49	294.83 \pm 48.92
<i>C. pearsoni</i> (Uruguay)	4	41.66 \pm 3.33	331.83 \pm 50.34
<i>Ctenomys pearsoni</i> ^b	35	42.66 \pm 1.76	252.05 \pm 33.02
<i>Ctenomys peruanus</i>	15	43.73 \pm 8.91	613.73 \pm 222.06
<i>Ctenomys rionegrensis</i>	37	38.57 \pm 2.20	296.06 \pm 38.15
<i>Ctenomys sociabilis</i>	16	39.18 \pm 4.28	284.75 \pm 56.13
<i>Ctenomys</i> sp.	27	40.39 \pm 3.68	378.71 \pm 71.99
<i>Ctenomys steinbachi</i>	15	44.87 \pm 6.86	467.67 \pm 125.76
<i>Ctenomys torquatus</i>	57	39.01 \pm 2.38	311.09 \pm 49.56

^a Karyomorph, populations of the same species but with karyological differences

^b The authors doubt that the species determination is correct based on the locality

The following measurements were obtained for each skull: (i) basal skull length (SL, from the anterior inferior border of the *foramen magnum* to the anterior part of the premaxillary bones); (ii) zygomatic breadth (ZB, greatest distance across zygomatic arches); (iii) bullar length (BL, length of straight line connecting the anterior point of insertion of the bulla into the basilar region and the posterior point of the bulla); (iv) bullar width (BW, straight-line distance approximately perpendicular to bullar length line, measured at the auditory meatus position); (v) bullar height (BH, straight-line perpendicular to the plane defined by bullar length and width, measured at the auditory meatus position; Fig. 1). All measures were taken using a digital caliper (Mitutoyo Digimatic CD-8" C) with a precision of 0.01 mm. All bullar measures were taken from the left bulla, unless it was not preserved.

Morphological variables

BV estimations were achieved, to allow comparisons, through the formula of an elliptical cone previously used by Schleich and Vassallo (2003), where $BV = [\pi ((1/2BL)(1/2BW))BH]/3$. Bullar internal structure was determined by visual inspection trans-illuminating the intact translucent bulla. As our study was based on a noninvasive technique we could not measure

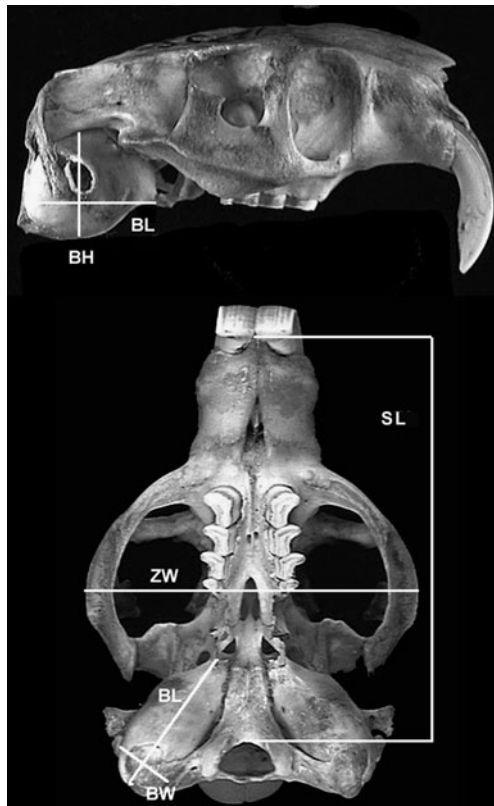


Fig. 1 Photographs of a *Ctenomys* skull illustrating the measurements taken. Above: BH bullar height, BL bullar length; below: SL basal skull length, ZW zygomatic width, BL bullar length, BW bullar width

the thickness of the cancellous bone of the bulla and, as a consequence, we used an estimation of the whole BV obtained from the external measurements of the bulla. We classified bullae into three patterns: (i) alveolar (A), when 70% or more of their cells (compartments on the internal bullar surface) are roughly rounded and small; (ii) septal (S), when 70% or more of their cells are clearly elongated and bigger than those of the alveolar type; and (iii) combined (C), when roughly 50% of each type of cells are present (Fig. 2).

Morphological statistical analyses

We used permutation test to examine the effect of bullar internal structure (S, A, C) on BV by sex. To this end, we calculated mean differences between two samples (S vs. A, S vs. C, A vs. C) and contrasted it against a probability density function generated from mean differences of 10,000 re-samples. We used permutation test to examine the effect of sex on BV for each species (male vs. female). The assumptions of normality and homogeneity of variance were tested using the Kolmogorov–Smirnov and Levene's tests, respectively. All statistical tests were two-tailed. We present data as mean \pm SD. Analyses were conducted using the program R 2.4.1 (R Development Core Team 2006). Graphic correlation of SL versus BV, and Kendall Tau correlation were done using Statistica 5.5 (StatSoft 1999). Mann–Whitney *U*-test was performed in PAST 2.09 (Hammer et al. 2001). We assumed a significant difference at $p < 0.05$.

Phylogenetic analyses

To control for possible phylogenetic nonindependence of BV and skull length, we used the phylogenetic independent contrasts (IC) method for continuous variables (Felsenstein 1985). We regressed the standardized contrasts of BV against skull length.

Cytochrome b sequences for 14 species of tuco-tucos were compiled from GenBank (Appendix 2). Seven non-ctenomyid species of rodents (see Fig. 3) were chosen as outgroups

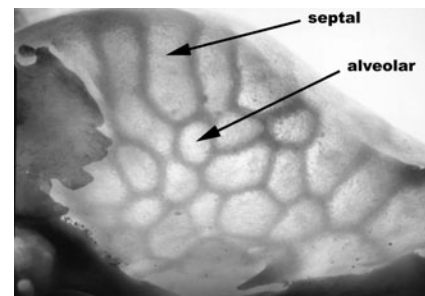


Fig. 2 Photograph of a *Ctenomys* tympanic bulla showing, by transparency, the internal structure. The two basic cell types contributing to the internal bullar patterns (septal, combined, and alveolar) are shown

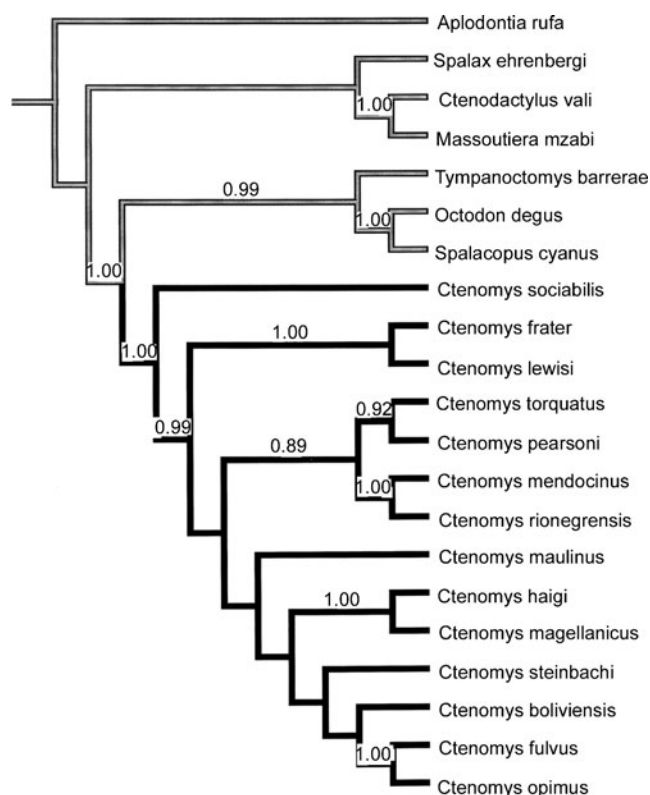


Fig. 3 Majority rule consensus tree of the Bayesian analyses for *Ctenomys*. Numbers at nodes represent the posterior probability values

based on Huchon and Douzery (2001), Mascheretti et al. (2000), and Wilson and Reeder (2005). Sequences were aligned using ClustalX 1.83 (Thompson et al. 1997) via Mesquite (Maddison and Maddison 2008). The preferred model for the Bayesian analyses was selected with Modeltest (Posada and Crandall 1998, 2001) using the Akaike Information Criterion (AIC; Akaike 1974). The best fitting model was GTR+ γ +I (Rodríguez et al. 1990; Yang 1994). Bayesian analyses were carried out using MrBayes V3.12 (Huelsenbeck and Ronquist 2001) with the settings as specified in Agnarsson and May-Collado (2008) and May-Collado and Agnarsson (2006). The Markov chain Monte Carlo (MCMC) search was ran with 10,000,000 generations sampling the Markov chain every 1,000 generations, and the sample points of the first 7,000,000 generations were “burn-in.” The PDAP module in Mesquite (Midford et al. 2008) was used to estimate IC (Felsenstein 1985).

Here, we used a novel primary-data based phylogeny with branch length estimates. The phylogeny generally agrees well with recent rodent phylogenies (e.g., Montgelard et al. 2008) and thus represents a reasonable hypothesis for studying the evolution of characters (Pagel and Harvey 1988). We preferred MCMC phylogenetic tree sampling to composite phylogenies. Composite phylogenies often reflect taxonomy, not necessarily phylogeny, and typically lack accurate branch length estimates, two aspects that reduce the efficiency of

comparative analysis. Probably the use of composite phylogenies lacking resolution and accurate estimates of branch lengths may have obscured the underlying patterns (e.g., Malia Jr. et al. 2003). In addition, previous hypotheses about *Ctenomys* phylogeny, as those presented in Slamovits et al. (2001) or Castillo et al. (2005), were not used because they included fewer species than in our sample.

Results

Mean values of skull length and BV for the species included in the sample are presented in Table 1.

Significant sexual differences in BV were detected in *Ctenomys magellanicus* and *Ctenomys rionegrensis*, out of 20 species surveyed for this character. *C. magellanicus* males ($853.29 \pm 240.56 \text{ mm}^3$, $n=10$) have larger volumes than females ($742.24 \pm 209.9 \text{ mm}^3$, $n=12$; Permutation test, $p=0.04$). This is also the case of *C. rionegrensis* males ($561.69 \pm 49.17 \text{ mm}^3$, $n=17$) having larger volumes than females ($470.28 \pm 55.12 \text{ mm}^3$, $n=21$; Permutation test, $p<0.001$). For both species, SL and ZB were compared between males and females (Mann–Whitney *U*-test, all comparisons nonsignificant), tendencies were for males to have higher values than females, except for SL in *C. rionegrensis*, in which mean values were very similar. For subsequent analyses, we pooled together males and females. In the case of *C. magellanicus* and *C. rionegrensis*, we used a similar sample size of males and females and pooled it together.

We found support for the monophyly of the family Ctenomyidae (Fig. 3). IC revealed no significant associations between SL and BV ($n=14$, $p>0.05$, $R^2=0.25$, Fig. 4).

BV variation in all tuco-tuco skulls sampled totalized a coefficient of variation (CV) of 37.9%, with species' CVs spreading across all the range. Seven tuco-tuco species presented CVs higher than 20% (*Ctenomys peruanus*, *Ctenomys boliviensis*, *Ctenomys steinbachi*, *Ctenomys mendocinus*, *Ctenomys magellanicus*, *Ctenomys haigi*, and

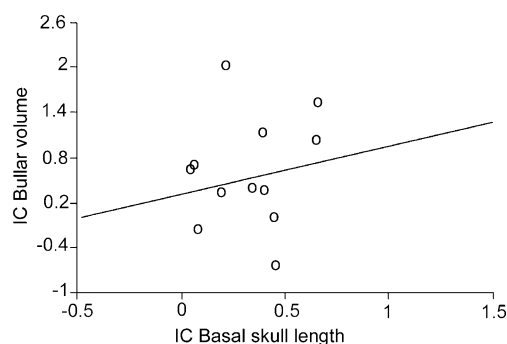


Fig. 4 Regression analysis between independent contrasts (IC) for basal skull length and bullar volume. $R^2=0.25$

Ctenomys fulvus, in a decreasing order), and only two species showed CVs under 10% (*Ctenomys pearsoni* and the Solís karyomorph of the *C. pearsoni* complex, in a decreasing order). Variation in BV appears related to the variation in skull size. As shown in the graphic correlation (Fig. 5), most species seem to present this relationship, but some escape from it and have bigger or smaller bullae than expected. Kendall Tau correlation showed no significant relationship between both measurements ($n=21$, Kendall Tau=0.171, $z=1.087$, $p=0.277$).

Mean volumes for each bullar structural pattern were: $476.513 \pm 187.38 \text{ mm}^3$ ($n=218$) for S type, $360.263 \pm 112.06 \text{ mm}^3$ ($n=325$) for C type, and $346.002 \pm 91.42 \text{ mm}^3$ ($n=114$) for A type. Tympanic bulla structural patterns for each sampled species are shown in Table 2.

All species known to be social lack type A structure or have a very low number of bullae in the category, but there are other species lacking A-type bullae with a yet unknown social status. There were no significant differences in mean BV for males between S-type ($n=10$, $728.80 \pm 326.01 \text{ mm}^3$) and C-type ($n=11$, $596.64 \pm 181.54 \text{ mm}^3$) bullae (permutation test, $p=0.25$), between S- and A-type ($n=6$, $541.33 \pm 112.73 \text{ mm}^3$) bullae ($p=0.198$), or between A- and C-type bullae ($p=0.53$). The same pattern was found when comparing females.

Discussion

The fact that subterranean rodents have enlarged bullae has been argued many times in the specialized literature (Agrawal 1967; Burda et al. 1990; Francescoli 1999, 2000; Hooper 1968; Schleich and Vassallo 2003; Stein

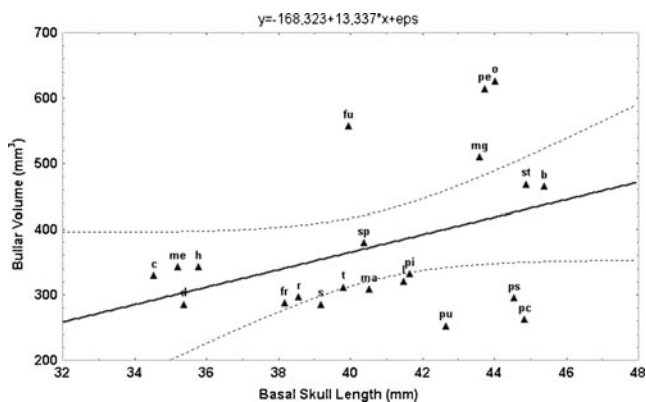


Fig. 5 Graphic showing the distribution of species bullar volume mean values in relation to mean basal skull length. Linear equation is shown. Code: b: *C. boliviensis*, c: *C. colburni*, d: *C. dorsalis*, fr: *C. frater*, fu: *C. fulvus*, h: *C. haigi*, l: *C. lewisi*, mg: *C. magellanicus*, ma: *C. maulinus*, me: *C. mendocinus*, o: *C. opimus*, pc: *C. pearsoni* (karyomorph Canelones), ps: *C. pearsoni* (Uruguay), pi: *C. pearsoni?*, pe: *C. peruanus*, r: *C. rionegrensis*, s: *C. sociabilis*, sp: *C. sp.*, st: *C. steinbachi*, t: *C. torquatus*

2000). However, within the genus *Ctenomys*, this character seems to be variable (Francescoli 1999).

In this study, we quantitatively assessed the variation of ctenomyid tympanic bullae, both in their size and internal partitioning. The fact that *Ctenomys* has partitioned bullar cavities has been mentioned by previous authors (Tullberg 1899; Gardner and Emmons 1984; Mason 2004) with a descriptive goal or together with some interpretations of the probable functionality of this character. Descriptions mentioned the bullae as filled with cancellous bone or as being partitioned in sub-cavities separated by large septa. The functional interpretations involved a support function for the septae or a low-frequency hearing enhancement due to partitioning.

Our results show that there is no phylogenetic effect in the relationship between the SL and BV, suggesting that the differences in bullar size are not due to inherited characters. We detected both interspecific and intraspecific variability in internal bullar structure. These results support the possibility that bullae bigger or smaller than expected could derive from species-specific adaptive processes.

In other mammal groups like in some other rodents (Heteromyidae and Gerbillidae: Lay 1972; Momtazi et al. 2008; Pavlinov and Rogovin 2000; Randall 1993, 1994; Ravicz et al. 1992; Sheets 1989; Webster and Webster 1975; Echimyidae: Gardner and Emmons 1984; Gliridae: Potapova 2001), in Xenarthra (Squarcia et al. 2007), or in Lagomorpha (Liao et al. 2007), enlarged or inflated bullae are supposed to be related with adaptations to different levels of environmental aridity/humidity, to different altitudinal levels or to different hearing needs in relation with their own sounds or those produced by predators.

In *Ctenomys*, bullar inflation has been often related to improved hearing in the low-frequency band, mostly because of the tuco-tuco vocalizations having a strong low-frequency component, as in other subterranean rodents (Francescoli 2000).

Analyzing some of the claimed relations between bullar size and other environmental, morphological, or behavioral factors, we could see that: first, the proposed relation among environmental aridity/humidity levels and bullar inflation is not very clear as an explanation of the differences in bullar morphology, because there are several species of tuco-tucos that inhabit grasslands with good humidity levels and have medium-sized bullae (as expected from their skull size) like in *Ctenomys torquatus* or species like *C. sociabilis* and *C. haigi* that live in the same habitat (arid steppe grassland punctuated at irregular intervals by wet meadows; Lacey and Wiczorek 2003) and have smaller bullae than expected (the former) and bigger bullae than expected (the latter).

Second, the proposed relation among bullar size and altitude is also not very clear. Liao et al. (2007) proposed this relation for pikas (*Ochotona daurica*) to explain their finding that animals of this species have smaller bullae the

Table 2 Occurrence of types of internal bullar structure in *Ctenomys* species (657 bullae examined)

Species	No. of skulls	Bullar types (%)		
		Septal	Combined	Alveolar
<i>Ctenomys boliviensis</i>	52	31	63	6
<i>Ctenomys colburni</i>	37	11	86	3
<i>Ctenomys dorsalis</i>	11	18	82	–
<i>Ctenomys frater</i>	16	69	6	25
<i>Ctenomys fulvus</i>	12	58	17	25
<i>Ctenomys haigi</i>	59	7	24	69
<i>Ctenomys lewisi</i>	27	63	37	–
<i>Ctenomys magellanicus</i>	24	4	75	21
<i>Ctenomys maulinus</i>	35	29	51	20
<i>Ctenomys mendocinus</i>	46	–	39	61
<i>Ctenomys opimus</i>	96	81	17	2
<i>Ctenomys pearsoni</i> (kar. Canelones)	11	46	27	27
<i>C. pearsoni</i> (kar. Solís)	30	30	43	27
<i>C. pearsoni</i> (Uruguay)	4	–	100	–
<i>C. pearsoni</i> *	35	–	91	9
<i>Ctenomys peruanus</i>	15	100	–	–
<i>C. rionegrensis</i>	37	3	89	8
<i>Ctenomys sociabilis</i>	16	94	6	–
<i>Ctenomys</i> sp.	27	44	48	8
<i>C. steinbachi</i>	11	82	9	9
<i>Ctenomys torquatus</i>	56	–	96	4

*The authors doubt that the species determination is correct based on the locality

higher the altitude they live in. For tuco-tucos, this does not seem to be true, because some animals of *C. peruanus* and *C. opimus* in our sample, having bigger bullae than expected, were captured near the cities of Puno (Perú) and Potosí (Bolivia), both cities being higher than 3,500 m of altitude. If the bullae in tuco-tucos were to follow the alleged correlation between altitude and bullar size, *C. peruanus* and *C. opimus* should have smaller bullae than expected, and not the contrary tendency they really exhibit.

Third, with respect to the relation among enhanced low-frequency hearing and bullar size suggested by [Schleich and Vassallo \(2003\)](#), some literature on subterranean and non-subterranean rodents seem to support this view as a way to improve communication in low-frequency bands or as a way to detect predators ([Francescoli 1999, 2000](#); [Lay 1972](#); [Lombard and Hetherington 1993](#); [Pavlinov and Rogovin 2000](#); [Randall 1993, 1994](#); [Schleich and Busch 2004](#); [Stein 2000](#); [Webster and Webster 1975](#)).

Fourth, [Verzi and Olivares \(2006\)](#) proposed possible mechanical constraints on bullar inflation in *Ctenomys*. The presence of an articular postglenoid region and the position of the bones to functionally use teeth and jaws for digging should prevent bullar inflation in some species of tuco-tucos. The interpretation of these results from [Verzi and Olivares \(2006\)](#) under the light of our data is difficult because of some reasons: (i) only six species out of 15 studied by [Verzi and](#)

[Olivares \(2006\)](#) are included in our study; (ii) these authors don't use any measure of volume; the only measure related to the bullae is the "anterior depth of the auditory bullae" (see [Table 1](#) in [Verzi and Olivares 2006](#)), and this creates difficulty in comparing their measures (a 1D measure) with our measures of BV as a whole (a 3D measure); (iii) some of the species that these authors include in their different morphotypes have been observed as digging in other ways under different conditions (i.e. *C. pearsoni* has been observed using its incisors to dig only in extremely hard soils but usually digs with its forepaws as reported by [Altuna et al 1993](#)), and for many of the species included, there is no behavioral information about their usual ways of digging; and (iv) the number of individuals for each species in [Verzi and Olivares' \(2006\)](#) sample is low in comparison to our samples and this feature makes difficult a generalized comparison.

Even if there are no significant differences between the volumes of the three different types of internal bullar structure, our results suggest that bigger bullae tend to have S or C internal structure (mainly S) and smaller bullae tend to have mainly A internal structure. Our data also show intraspecific variability in the internal bullar structure.

This tendency could be an indication of some kind of enhanced reception of certain sound frequencies because, as some authors have suggested before ([Gardner and Emmons 1984](#); [Hooper 1968](#); [Mason 2006](#); [Rosowski 1994](#); [Simkin](#)

1965; Webster and Webster 1975), heavily partitioned bullae tend to enhance low-frequency hearing, as inflated non-partitioned bullae do. Increased bullar size (and volume) provide animals with the possibility of “damping” the vibrations going into the middle ear, thus reducing middle ear impedance, lowering middle ear stiffness, and increasing low-frequency sound transduction (Ravicz et al 1992; Rosowski 1994). In fact, Ravicz et al (1992) found that a change in the relation between the impedance of the middle ear air space and the impedance of the chain “tympanic membrane–ossicles–cochlea” due to an increase in middle ear volume can lead to a reduction in middle ear stiffness by a factor of four.

Many Ctenomyidae species sensibly differ in BV from the expected values based on their skull size, presenting smaller bullae than expected as in *C. pearsoni* complex Solís or Canelones karyomorphs or bigger bullae than expected as in *C. opimus* (Fig. 5). Assuming that the observed variation in bullar size is related to the stated theoretical relationship among bullar size and improved low-frequency hearing, leading to the conclusion that different bullar sizes could be related to different hearing needs (Francescoli 2000; Mason 2004), and accepting the argument that inflated bullae increase low-frequency hearing, we can reasonably expect smaller bullae to be associated with the use of higher frequencies.

Bullar partitioning is also important in the transduction of airborne signals because partitioned middle ear cavities seem to operate as a frequency-dependent “volume selector” (Rosowski 1994), as an amplifier or dampener of certain sounds, and/or as a filter of undesirable background noise (Simkin 1965; Hooper 1968).

Our data show that there are intraspecific and interspecific differences in internal bullar structure and that bigger bullae tend to have S or C internal structure (mainly S), while smaller bullae tend to have mainly A internal structure. Obviously, in this connection, the size of the animals is important, because Ravicz et al (1992) have shown that, in larger animals, skull size is larger enough to allow fairly large middle ear volumes so that, theoretically, larger animals can have medium-sized bullae with a type S partitioning and still have a decrease in middle ear stiffness sufficient to allow an improvement in low-frequency hearing.

Hooper (1968) and Gardner and Emmons (1984) suggested that bigger bullae and their increased partitioning favor improvement in low-frequency hearing and frequency filtering. Thus, if middle ear volume can be constrained by environmental limitations acting on the animal’s head size or structure (Ravicz et al 1992; Verzi and Olivares 2006), bullar partitioning is not necessarily limited by the same constraints and could act as a sort of compensating mechanism to BV, depending on the species’ hearing needs. Nevertheless, there are other data that relativize this

view (see Rosowski et al. 2006 for a discussion on the effect of middle ear partitioning in *Chinchilla lanigera*).

On the other hand, Argyle and Mason (2008) find septa dividing the middle ear of *Octodon degus* and consider them as similar to the ones appearing in *C. lanigera* providing mechanical support for the bullae and tympanic annulus in this species, but they also stress that in *Octodon*, *Spalacopus*, and *Ctenomys*, in which septa are more prominent, they might have a more significant effect on sound transmission. Argyle and Mason (2008) consider that caviomorph middle ear morphology is very similar regardless of habitat, and that this issue indicates that low-frequency hearing sensitivity is plesiomorphic for this group. This opinion has not been supported by these authors performing a phylogenetic comparative study. In this paper, on the other hand, we have compared the effect of the phylogeny on the relation among BV (usually related to enhanced low-frequency hearing) and skull length, and results indicate that species-specific adaptive processes could be more important than the ancestor-descendant relationship in this case.

We did not find sexual differences in BV, except for two species: *C. magellanicus* and *C. rionegrensis*. Sexual differences would not be expected if some of the environmental adaptations mentioned above were involved in the shaping of the BV and internal structure, because both sexes live under the same environmental conditions. On the other hand, the revealed sexual dimorphism in these species could reflect some sex-specific adaptations (i.e. different needs for communication with pups in females, or differences in long-distance signal hearing in males).

In summary, our comparative study indicates that correlation between SL and BV does not correspond to the phylogeny based on the Bayesian inferences of the cytochrome b sequences, and that some species-specific adaptations related to hearing and mechanical constraints imposed by digging-related cranial structures could be linked to the shaping of bullar morphology in *Ctenomys*.

More information is needed on the biology of all ctenomyid species and, possibly, their different populations inhabiting different environments for understanding the factors underlying the observed variation in the tympanic bullae of tuco-tucos.

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Appendices

Appendix 1 List of examined skulls of *Ctenomys* (species identifications and localities are taken from the museum labels)

Species	Locality	Museum	Numbers
<i>Ctenomys boliviensis</i>	Chuquisaca, Bolivia	AMNH	262290, 262292
<i>C. boliviensis</i>	Sta. Cruz, Bolivia	AMNH	256008, 260801–05, 260807–11, 260814–15, 260817–18, 260820–22, 260824–34, 262288–89, 263920, 264521–37, 264539
<i>Ctenomys colburni</i>	Aisen, Chile	FMNH	134270–71, 134274, 134276–77, 134295
<i>C. colburni</i>	Sta.Cruz, Argentina	AMNH	5675, 25670–73, 25676
<i>C. colburni</i>	StaCruz, Argentina	FMNH	124513–14, 124516–28, 124530–33, 124535–36, 124538–41
<i>Ctenomys dorsalis</i>	Chaco, Paraguay	FMNH	54346–48, 54390–92, 54396–98, 63868, 63870
<i>C. dorsalis</i>	Paraguay	FMNH	134278
<i>Ctenomys frater</i>	Jujuy, Argentina	FMNH	23241–42, 29051–52
<i>C. frater</i>	Salta, Argentina	FMNH	23235–37, 29048–49, 35232, 41275–76
<i>C. frater</i>	Tarija, Bolivia	AMNH	263011–14
<i>C. frater</i>	Tarija, Bolivia	FMNH	29065
<i>Ctenomys fulvus</i>	Antofagasta, Chile	FMNH	23218, 23220, 23222, 23225, 23792, 34916
<i>C. fulvus</i>	Antofagasta, Chile	MVZ	116797–116800
<i>C. fulvus</i>	Laguna Blanca, Argentina	FMNH	46137–38
<i>Ctenomys haigi</i>	Neuquén, Argentina	MVZ	151036, 158478, 159438–39, 163820, 183291, 193693
<i>C. haigi</i>	RíoNegro, Argentina	MVZ	151037, 152172, 154625, 158440–41, 159440–41, 164038–41, 164043, 165860, 166421–24, 171168–70, 175151–55, 175802–04, 183292–96, 184880–86, 184892–93, 184895, 184897–184903, 185053, 191024
<i>Ctenomys lewisi</i>	Cochabamba, Bolivia	AMNH	264557–58, 264560
<i>C. lewisi</i>	Sta.Cruz, Bolivia	AMNH	264548–51, 264553–56
<i>C. lewisi</i>	Tarija, Bolivia	AMNH	263015–21, 263023–24, 263026, 264541–47
<i>Ctenomys magellanicus</i>	Magallanes, Chile	FMNH	50735
<i>C. magellanicus</i>	Patagonia, Argentina	AMNH	14286–87
<i>C. magellanicus</i>	RíoNireguao, Chile	FMNH	23232–34
<i>C. magellanicus</i>	Sta.Cruz, Argentina	AMNH	17444
<i>C. magellanicus</i>	Tierra del Fuego, Argentina	FMNH	50737–51
<i>C. magellanicus</i>	Tierra del Fuego, Argentina	MVZ	164145
<i>C. magellanicus</i>	Valle del Lago, Argentina	FMNH	18191
<i>Ctenomys maulinus</i>	Chile	AMNH	91657
<i>C. maulinus</i>	Cautín, Chile	AMNH	91658
<i>C. maulinus</i>	Lonquimay, Chile	MVZ	154131–34
<i>C. maulinus</i>	Malleco, Chile	FMNH	23214, 23216–17
<i>C. maulinus</i>	Mendoza, Argentina	MVZ	162933–35
<i>C. maulinus</i>	Neuquén, Argentina	MVZ	163426, 163462, 164044, 171171–72, 171174–75, 183298–99, 183305–08, 183310, 183312, 185055
<i>C. maulinus</i>	Nuble, Chile	AMNH	254498
<i>C. maulinus</i>	Río Maule, Chile	FMNH	50731–33
<i>C. maulinus</i>	Talca, Chile	MVZ	154135–38
<i>Ctenomys mendocinus</i>	La Pampa, Argentina	MVZ	173719
<i>C. mendocinus</i>	Mendoza, Argentina	MVZ	16643, 151038, 162936–37, 166417–20, 166426, 166429–30, 181572–73
<i>C. mendocinus</i>	Metan, Argentina	FMNH	46130–31
<i>C. mendocinus</i>	Neuquén, Argentina	FMNH	29046–47, 29063, 46135
<i>C. mendocinus</i>	Neuquén, Argentina	MVZ	134269, 181574–76
<i>C. mendocinus</i>	RíoNegro, Argentina	MVZ	162283–85, 163424–25, 163823, 181571
<i>C. mendocinus</i>	San Luis, Argentina	MVZ	169022–28, 169030–32, 169034–36

Appendix 1 (continued)

Species	Locality	Museum	Numbers
<i>C. mendocinus</i>	Stgo.Estero, Argentina	FMNH	46132–33
<i>C. mendocinus</i>	Tucumán, Argentina	FMNH	41267–68
<i>Ctenomys opimus</i>	Esperanza, Bolivia	FMNH	53630, 53632–37, 53639–41, 53643
<i>C. opimus</i>	Jujuy, Argentina	FMNH	29050, 41287
<i>C. opimus</i>	Moquegua, Perú	MVZ	115957–59, 115962–63, 115965–68
<i>C. opimus</i>	Mte.Sajama, Bolivia	FMNH	53644
<i>C. opimus</i>	Oruro, Bolivia	AMNH	244654–55, 246960–61, 260837, 260839–42, 260844–50, 260898, 263030–31, 263033–48
<i>C. opimus</i>	Oruro, Bolivia	MVZ	120237
<i>C. opimus</i>	Potosí, Bolivia	AMNH	263049–53
<i>C. opimus</i>	Puno, Perú	MVZ	115969–77, 115979–82, 139608–10
<i>C. opimus</i>	Tacna, Perú	MVZ	114765, 115983–89, 115991–93, 115995, 141622–25
<i>Ctenomys pearsoni</i> (kar. Solís)	Balneario Solís, Uruguay	CA	191–2, 197–8, 201–2, 226–7, 230–1, 242–3, 245, 247, 263–5, 267–8, 270, 279, 305, 347, 361, 365, 367. 712, 714
<i>C. pearsoni</i> (kar. Solís)	Las Flores, Uruguay	CA	302, 309
<i>C. pearsoni</i> (kar. Solís)	Bella Vista, Uruguay	CA	312
<i>C. pearsoni</i>	El Relincho, Uruguay	CA	341
<i>C. pearsoni?</i>	Lavalleja, Uruguay	AMNH	206512–23, 206525–27, 206529–32, 206534–37, 206539–47
<i>C. pearsoni?</i>	Maldonado, Uruguay	FMNH	29264, 29302, 44813
<i>C. pearsoni</i>	Penino, Uruguay	CA	318, 353
<i>C. pearsoni</i>	Playa Pascual, Uruguay	CA	352
<i>C. pearsoni</i> (kar. Canelones)	Roosevelt, Uruguay	CA	258, 336–7, 342–5, 351, 356, 359
<i>C. pearsoni</i> (kar. Canelones)	Shangrilá, Uruguay	CA	716
<i>Ctenomys peruanus</i>	Puno, Perú	FMNH	52465–66
<i>Ctenomys peruanus</i>	Puno, Perú	MVZ	114766, 114768, 115996–116005, 139611
<i>Ctenomys rionegrensis</i>	El Abrojal, Uruguay	CA	772, 1030, 1037–8, 1046–7, 1052–3, 1058–9, 1062, 1064–5
<i>C. rionegrensis</i>	Portones, Uruguay	CA	787, 789–790, 794–5, 798–803, 843–4, 846–8, 850, 901, 912, 933, 953, 971
<i>C. rionegrensis</i>	RíoNegro, Uruguay	AMNH	232219
<i>C. rionegrensis</i>	RíoNegro, Uruguay	FMNH	29067
<i>Ctenomys sociabilis</i>	Neuquén, Argentina	MVZ	165852, 166425, 169014, 171176, 183315, 184868, 184870, 184874–77, 185051, 185054, 185214, 192236–7
<i>Ctenomys</i> sp.	Chquisaca, Bolivia	AMNH	263922, 263925–7, 263929–30, 263943–4, 263946–53
<i>Ctenomys</i> sp.	Sta.Cruz, Bolivia	AMNH	263931–41
<i>Ctenomys steinbachi</i>	Sta.Cruz, Bolivia	FMNH	75339–40, 260851–53, 260855–57, 262293–97, 51894–5
<i>Ctenomys torquatus</i>	Cerro Largo, Uruguay	AMNH	206462–3, 206465, 206467–8, 206470–5, 206478–86, 206489–206506, 206509–11, 206548–9
<i>C. torquatus</i>	Río Grande do Sul, Brasil	AMNH	235986, 238010–16
<i>C. torquatus</i>	Tacuarembó, Uruguay	AMNH	206550–55

kar. karyomorph. ? the authors doubt that the species determination is correct based on the locality, *AMNH* American Museum of Natural History (New York), *FMNH* Field Museum of Natural History (Chicago), *MVZ* Museum of Vertebrate Zoology (Berkeley), *CA* Sección Etología, Facultad de Ciencias (Montevideo)

Appendix 2 GenBank accession numbers of cytochrome b sequences for the rodent species included in phylogenetic analysis, and natural logarithms of basal skull length (SL) and bullar volume (BV) for *Ctenomys*

Species	LnSL	LnBV	GenBank accession #
Order Rodentia			
Outgroups			
<i>Ctenodactylus vali</i>	–	–	AJ389532
<i>Massoutiera mzabi</i>	–	–	AJ389533
<i>Aplodontia rufa</i>	–	–	AJ389528
<i>Nannospalax ehrenbergi</i>	–	–	AJ389537
<i>Octodon degus</i>	–	–	AM407929
<i>Spalacopus cyanus</i>	–	–	AF007061
<i>Tympanoctomys barrerae</i>	–	–	AF007060
Family Ctenomyidae			
<i>Ctenomys boliviensis</i>	3.82	6.42	AF007040
<i>Ctenomys frater</i>	3.64	6.00	AF007046
<i>Ctenomys fulvus</i>	3.69	6.67	AF370688
<i>Ctenomys haigi</i>	3.58	6.23	AF422920
<i>Ctenomys lewisi</i>	3.73	6.10	AF007049
<i>Ctenomys magellanicus</i>	3.77	6.67	DQ333327
<i>Ctenomys maulinus</i>	3.70	6.09	AF370703
<i>Ctenomys mendocinus</i>	3.56	6.23	AF007062
<i>Ctenomys opimus</i>	3.78	6.81	AF370701
<i>Ctenomys pearsoni</i>	3.73	6.13	AF119108
<i>Ctenomys rionegrensis</i>	3.65	6.23	AF538375
<i>Ctenomys steinbachi</i>	3.80	6.55	AF007044
<i>Ctenomys sociabilis</i>	3.67	5.96	EU035177
<i>Ctenomys torquatus</i>	3.68	6.05	AF119111

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