



Sexual selection in a polygynous rodent (*Ctenomys talarum*): an analysis of fighting capacity

Federico Becerra^a, Alejandra I. Echeverría^a, Alejandra Marcos^a, Adrià Casinos^b, Aldo I. Vassallo^{a,*}

^a Departamento de Biología, Instituto de Investigaciones Marinas y Costeras, CONICET - Universidad Nacional de Mar del Plata, Casilla de Correo 1245, 7600 Mar del Plata, Argentina

^b Departament de Biologia Animal (Vertebrats), Universitat de Barcelona, Ave. Diagonal 645, 08028 Barcelona, Spain

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ABSTRACT

The South American subterranean rodent genus *Ctenomys* (Caviomorpha: Octodontoidea), which uses both claws and teeth to dig, shows striking morphological adaptations to its specialized mode of life. Among other traits, the genus has evolved a powerful jaw musculature and procumbent incisors that are used for dento-excavation. Behavioral observations indicate that these traits are also used during male aggressive encounters, which characterize the polygynous mating system of one of the species of the genus, *Ctenomys talarum*. A question emerges about sexual selection: could it have induced further changes in traits primarily evolved as adaptations for digging? To address this issue, we studied functional and morphological attributes of the jaw and incisors in specimens of *C. talarum*. Incisor bite forces were measured on wild females and males from a local population (Mar de Cobo; Buenos Aires Province) by means of a strain gauge load cell force transducer. Museum specimens coming from the same population were studied to assess anatomical attributes of both sexes. Since this species exhibits dimorphism in body size, the possible effect of body mass on the studied traits was analyzed. Males and females showed significant differences in biting performance and mandibular width, but when size was taken into account these differences disappeared. However, other dimorphic traits can vary with a certain independence with respect to size, particularly the 2nd moment of area of the incisors and, to a lesser extent, incisor procumbency. The former geometrical parameter, which is proportional to the bending strength, was highly dimorphic. This fact suggests that, during aggressive encounters between males, biting would place large bending loads on the incisors.

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1. Introduction

Within mammals, male reproductive success is strongly correlated with competitive ability, and this has resulted in the evolution of large body size and weaponry (Andersson, 1994). As a consequence, polygynous mating systems in mammals are usually characterized by sexual size dimorphism, males generally being larger than females (Fairbairn, 1997). Inter-male aggressive encounters can be more or less ritualized; on these occasions the result of this type of encounter is not the opponent's death, nor severe physical damage, but the retreat of the subordinate individual. The structures utilized in this type of encounters clearly possess the potential to produce lethal injuries (e.g., deer antlers; sheep horns; babirusa tusks), though these seldom occur (Feldhamer et al., 1999). Nonetheless, in some cases the aggression among males is less ritualized, and the weapons involved may cause the opponent's death in some instances. For example,

species of subterranean rodents are generally very territorial and aggressive, being able to exert strong and dangerous forces at their incisors' tip (Nevo, 1999; Van Daele et al., 2009). In *Ctenomys talarum*, even though females possess exclusive territories that are defended actively just like those of males (Cutrer et al., 2006), in general, they show lower levels of aggression (Vassallo and Busch, 1992). The hazardous nature of a bite to conspecifics is directly related to the absolute measure of bite force. Yet the allometric scaling between body mass and bite force is responsible for the fact that small mammals, in general, can exert bite forces proportionately greater than larger species (see, however, Wroe et al., 2005; Van Daele et al., 2009). Obviously, the aggressiveness is another important determinant of the outcome of intraspecific encounters.

South American subterranean rodents of the genus *Ctenomys* (Caviomorpha: Octodontoidea), called tuco-tucos, exemplify an explosive cladogenesis occurring within the limits of a genus (Reig et al., 1990; Lessa and Cook, 1998). In a wide distribution from Perú to Tierra del Fuego, the genus *Ctenomys* exhibits a broad range of body sizes, with body masses from 100 g (*C. pundti*) to more than 1000 g (*C. conoveri*) (Redford and Eisenberg, 1992). The genus *Ctenomys*, which uses both claws and teeth for digging, shows

* Corresponding author.

E-mail address: avassall@mdp.edu.ar (A.I. Vassallo).

striking morphological adaptations to life underground. Among other traits, *Ctenomys* has evolved a powerful jaw musculature and procumbent incisors that are used as “digging tools” for dento-excavation (Vassallo, 1998; Lessa et al., 2008; Becerra et al., 2011). Behavioral observations indicate that these traits are also used during male aggressive encounters, which characterize the polygynous mating system of the species studied here, *C. talarum*. A question emerges about sexual selection: could it have induced further changes in traits primarily evolved as adaptations for digging?

In *C. talarum* (body mass range 100–200 g) aggressive interactions can lead to the establishment of a hierarchical relationship among males (Zenuto et al., 1999a,b). Previous studies (Zenuto et al., 2001, 2002) have shown that agonistic encounters are very aggressive, scarcely ritualized, and that incisors are used, injuring the opponent. The local population of *C. talarum* at Mar de Cobo (Buenos Aires Province) has a female-biased sex ratio and it is common to find adult males showing scars on their bodies (Busch et al., 1989). This female-biased sex ratio most likely results from differential predation upon sex (Kittlein et al., 2001), and may, at least in part, also result from significant male mortality due to the strong and potentially dangerous bites inflicted in their aggressive encounters (Busch et al., 2000).

In herbivorous subterranean rodents such as *Ctenomys*, the energy cost associated with displacement through the soil is assumed to be high. Vleck (1979, 1981) estimated that, depending on soil type, the energy expenditure associated with burrowing may be more than 300 times higher than the energy required for similar transportation above ground. Although the genus *Ctenomys* is not restricted to burrowing for foraging and other activities (Antinuchi et al., 2007), the body size that a particular species can attain depends on environmental energy and primary productivity (Medina et al., 2007). In other words, body size variation of the different species of *Ctenomys* strongly depends on local environmental conditions. Despite strong selection for energy efficiency, sexual size dimorphism occurs in all *Ctenomys* species, although size differences between males and females are highly variable (Medina et al., 2007). Zenuto et al. (1999b) reported a 1.3 ratio for body mass dimorphism in the local population of *C. talarum* (Mar de Cobo, Buenos Aires Province, Argentina). We also analyzed the degree of sexual dimorphism in other attributes of the fighting apparatus that are linked to male dominance in *C. talarum*. We hypothesized that males are able to exert relatively stronger bite forces at their incisors' tip than females and possess a broader mandible for the insertion of a powerful adductor musculature. In addition, in order to improve their robustness and fighting capacity, males' incisors must be able to withstand greater bending stress and have an appropriate angle for attacking the opponent. Procumbent incisors, projected forward from the skull, increase the likelihood of injuring the opponent during encounters. Hence, we hypothesized that males' incisors are characterized by both an increased 2nd moment of area (a geometrical parameter proportional to the bending strength) and a broader procumbency angle than female ones.

2. Materials and methods

2.1. Live specimens

For this study, individuals of the species *C. talarum* were obtained from natural populations occupying grasslands and dune habitats near the coastal village of Mar de Cobo, Buenos Aires Province, Argentina (37°45'S, 57°56'W), from August to November 2008. Animals were captured using tubular mesh live traps located at burrow entrances. The study was based on 31 adult specimens of both sexes, 15 males and 16 females. The animals were

held in captivity 3–6 days before taking bite force measurements. Animals were maintained under a 12 h light: 12 h dark photoperiod (lights turned on at 0700). Relative ambient humidity ranged from 50% to 70% and temperature was automatically controlled ($24 \pm 1^\circ\text{C}$). Specimens were housed individually in plastic cages (42 cm $\times$ 34 cm $\times$ 26 cm) with wood shavings as bedding. All animals were fed ad libitum with a diet composed of a variety of vegetables (see Zenuto et al., 2001). Animals were weighed just prior to taking bite force measurements (see Section 2.2) on an electronic scale (0.01 g). Mean body mass was 146.7 g (males) and 129.8 g (females).

All procedures followed ABS/ASAB Guidelines for the Treatment of Animals in Behavioral Research and Teaching. The use of animals was approved by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) and the University of Mar del Plata. At the end of the experiments the animals were released at their site of capture in good physical condition.

2.2. In vivo bite force measurement

Individual bite force measurements were taken with a strain gauge load cell force transducer (Fig. 1), produced by Necco Technologies (Mar del Plata, Argentina), 0–20,000 g (range), error 1 g (for a more detailed description, see Becerra et al., 2011). Bite force measurements were recorded on a PC using the software HyperTerminal (Windows XP, Microsoft). Bite forces were registered during experimental sessions in which animals were induced to bite the transducer plates. The bite plates were covered with a thin protective coating made of leather, so the animals did not damage their incisors. The temporal sequence of the experiments was: (i) animals were induced to bite defensively by taking them out of their cages. (ii) Each session lasted ~ 1 min and consisted of biting trials that included several bites. (iii) Trials ended when the animals refused to bite the transducer, which in some instances occurred after 30–40 s of recording. (iv) Each session was repeated 4–6 times per individual. The strongest bite from all sessions was assumed to represent maximal bite performance for each individual, following Becerra et al. (2011).

2.3. Museum specimens

This analysis was based on 36 adult specimens of both sexes (18 males and 18 females), coming from the Mar de Cobo local population. The specimens are housed at the collections of the Museo Municipal de Ciencias Naturales “Lorenzo Scaglia”, Mar del Plata, Argentina. The following linear measurements were taken using a digital caliper (to the nearest 0.01 mm): maximum mandibular width across the masseteric crests (Mw); upper incisor width (Iw) and thickness (Id) (Fig. 2). Maximum mandibular width was used as an estimator of the development of adductor jaw musculature (Olivares et al., 2004; Vassallo and Mora, 2007). Mandibular width is a good predictor of muscle development, and thus of bite force (Becerra et al., 2011), because the mandibular angle, the site of insertion of masseter muscles, contributes largely to this variable (see for example Verzi, 2002). Mechanical resistance of incisors was estimated considering incisor cross-section as an ellipse with the major axis (Iw) represented by the transverse diameter of the incisor, and the minor axis (Id) represented by its anteroposterior diameter (Biknevicius et al., 1996; Verzi et al., 2010). The 2nd moment of area of the incisors (Io) about the sagittal (anterior-posterior) axis, calculated as $I_o = \pi/4[(Iw/2)(Id/2)^3]$, was used to estimate resistance to bending stress (Irgens, 2008). To measure upper-incisor procumbency, the angle formed between the chord of the exposed incisor and a line parallel to the occlusal plane of the upper molariforms (Thomas' angle; Fig. 2) was measured on camera lucida drawings using a protractor (Reig et al., 1965) and later

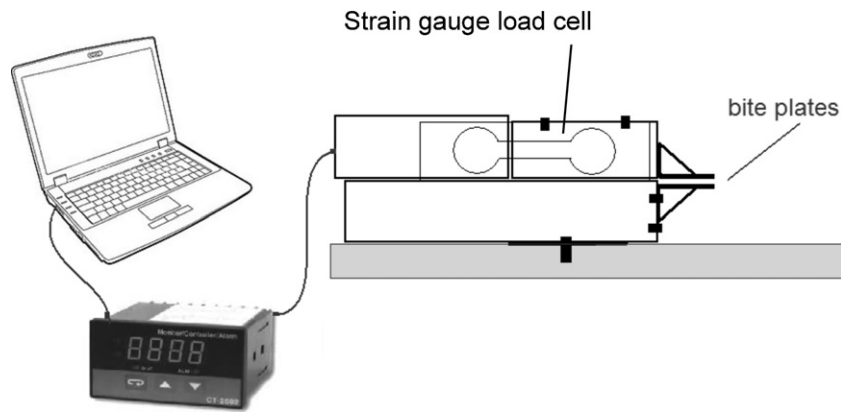


Fig. 1. Force transducer setup used for bite force measurements in *Ctenomys talarum*.

transformed into radians for regression analyses. Procumbency was assessed using a Nikon SMZ645 stereomicroscope (Nikon Corp., Tokyo, Japan).

ANOVA and ANCOVA analyses were performed using Statistica 6.0 and Microsoft Excel. Bivariate allometric equations of $\log_{10}$ data were calculated as reduced major axis (Model II) regressions because neither variable was considered independent (i.e., there was error associated with the measurements of both x and y) and the structural relationship between the two variables is the one that is required (Legendre and Legendre, 1998; see also Sokal and Rohlf, 1981). The slope, the intercept, and their respective confidence intervals were calculated using a program for running Model

II regressions developed by A. Bohonak (San Diego State University, www.bio.sdsu.edu/pub/andy/RMA.html).

3. Results

Bite forces recorded in the subterranean rodent *C. talarum* were significantly higher in adult males than in adult females (mean bite force 31.68 N and 27.44 N, respectively; $F_{[1,29]} = 5.28$, $P = 0.029$). Bite forces were marginally correlated with body mass in adult males ($F_{[1,14]} = 4.23$, $P = 0.06$) while a non-significant correlation was found in adult females ($F_{[1,15]} = 0.34$, $P = 0.57$; Table 1 and Fig. 3A). Notwithstanding, a considerable dispersion of the data around the regression line and a low coefficient of determination were observed in males (Table 1; Fig. 3A). Maximum mandibular width (an estimator of the development of masseter muscles) was significantly higher in adult males than in adult females (mean mandibular width 31.27 mm and 28.41 mm, respectively; $F_{[1,32]} = 28.15$, $P < 0.001$). No significant differences were observed either in the slope or the y -intercept between both sex scaling equations (ANCOVA: $F_{[1,32]} = 0.02$, $P = 0.90$; Table 1; Fig. 3B). After controlling for body size, no significant differences between sexes were observed either for bite force ($F_{[1,29]} = 0.05$, $P = 0.82$) or mandibular width ($F_{[1,32]} = 3.09$, $P = 0.09$).

The 2nd moment of area of the incisors in adult males was significantly higher than in adult females (mean 2nd moment of area 1.44 mm and 0.79 mm⁴, respectively; $F_{[1,29]} = 39.12$, $P < 0.001$). This trait was significantly correlated with body mass in adult males ($F_{[1,13]} = 13.14$, $P = 0.003$) but not in adult females ($F_{[1,16]} = 3.25$, $P = 0.09$; Table 1 and Fig. 3C). After controlling for body size, sex differences persisted in the incisors' 2nd moment of area ($F_{[1,29]} = 30.03$, $P < 0.001$).

The incisors' procumbency was significantly higher in adult males than in adult females (mean incisors' procumbency 1.80 rad (102.7°) and 1.73 rad (99.1°), respectively; $F_{[1,33]} = 4.48$, $P = 0.04$). This trait was not significantly correlated with body mass in either sex ($F_{[1,16]} = 1.60$, $P = 0.22$; $F_{[1,17]} = 0.88$, $P = 0.36$, for males and females, respectively, Table 1 and Fig. 3D).

4. Discussion

We found that, in addition to the previously reported body size dimorphism in the subterranean rodent *C. talarum* (Zenuto et al., 1999b), sexual dimorphism also exists in some traits which constitute the fighting apparatus of the species. Whereas little to no dimorphism between sexes was observed either for bite force or mandibular width when body size was taken into account, males showed relatively sturdier and more procumbent incisors than females, even after controlling for body size. This dimorphism

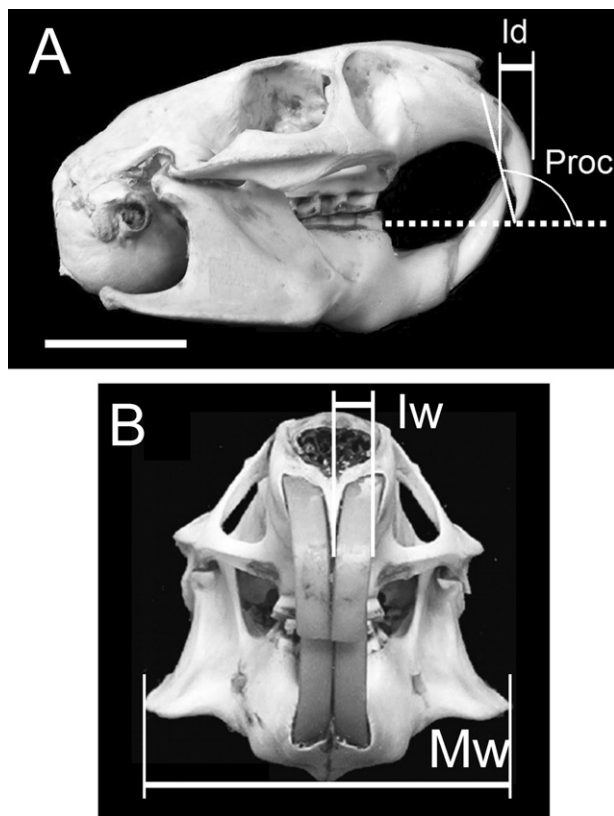


Fig. 2. Variables measured on skulls of *Ctenomys talarum*. (A) Lateral and (B) frontal view of an adult male skull. Scale bar = 1 cm. Abbreviations: Id, upper incisor thickness; Iw, upper incisor width; Mw, maximum mandibular width across the masseteric crests; Proc, upper incisor procumbency.

Table 1
Allometric equations ($y = ax^b$) of bite force and skull variables against body mass in adult males and females of *Ctenomys talarum*.

	Equation	<i>P</i>	<i>R</i> ²	95% confidence interval	
				<i>b</i>	<i>A</i>
<i>Bite force</i>					
Males	$y = -1.48x^{1.38}$	0.06	0.24	0.63–2.12	–3.1 to 0.13
Females	$y = -1.2x^{1.25}$	n.s.	0.02	0.54–1.95	–2.69 to 0.29
<i>Mandibular width</i>					
Males	$y = 0.76x^{0.34}$	0.01	0.37	0.19–0.48	0.43 to 1.08
Females	$y = 0.86x^{0.28}$	0.01	0.47	0.17–0.39	0.63 to 1.1
<i>Incisor's 2nd moment of area</i>					
Males	$y = -4.39x^{2.08}$	0.003	0.53	1.18–2.97	–6.34 to (–2.44)
Females	$y = -2.39x^{1.09}$	n.s.	0.17	0.54–1.63	–3.53 to (–1.24)
<i>Incisors' procumbency</i>					
Males	$y = -0.27x^{0.25}$	n.s.	0.09	0.12–0.38	–0.55 to 0.00
Females	$y = -0.36x^{0.29}$	n.s.	0.05	0.14–0.44	–0.66 to (–0.05)

P, significance of regression; n.s., non-significant.

is assumed to be associated with the polygynous mating system of the genus *Ctenomys* (Zenuto et al., 1999a). In the population under study (Mar de Cobo, Buenos Aires Province), this mating system operates through the establishment of dominance hierarchies among males, which are very aggressive and territorial (Vassallo and Busch, 1992; Zenuto et al., 2001, 2002). We found that jaw and incisor measurements, as well as bite performance, were more or less correlated with body mass, in some instances depending on the sex. The fact that some of the studied traits were significantly correlated with body mass in males suggests that, at least partly, sexual selection acting on male body size may account for the dimorphism in jaw and incisor traits in *C. talarum*. Nonetheless, it was clear that when regressed to body mass, the studied traits showed a considerable dispersion around the fitted line (Fig. 3). For example, whereas bite force was significantly higher in adult males than in adult females, bite force and body mass were only

marginally correlated in males. Bite force ultimately depends on the development of the jaw adductor muscles, which in the present study was estimated measuring the maximum mandibular width of studied museum specimens (Verzi, 2002; Vassallo and Mora, 2007). The correlation of this trait with size was poor (Table 1 and Fig. 3B). Our results suggest that the possibility exists that sexual selection may not just act on male overall body size, but specifically on some traits of the male fighting apparatus. For example, we found a dramatic dimorphism in the 2nd moment of area of the incisors that was higher in males even after the body size effect was removed. This parameter, which is proportional to the bending strength (Biknevicius et al., 1996; Verzi et al., 2010) is probably of importance during male encounters. Large bending stresses occur most likely during struggling while their incisors are locked up biting the opponent (Vassallo and Busch, 1992; Zenuto et al., 2001, 2002). Observations of agonistic encounters showed that bites were

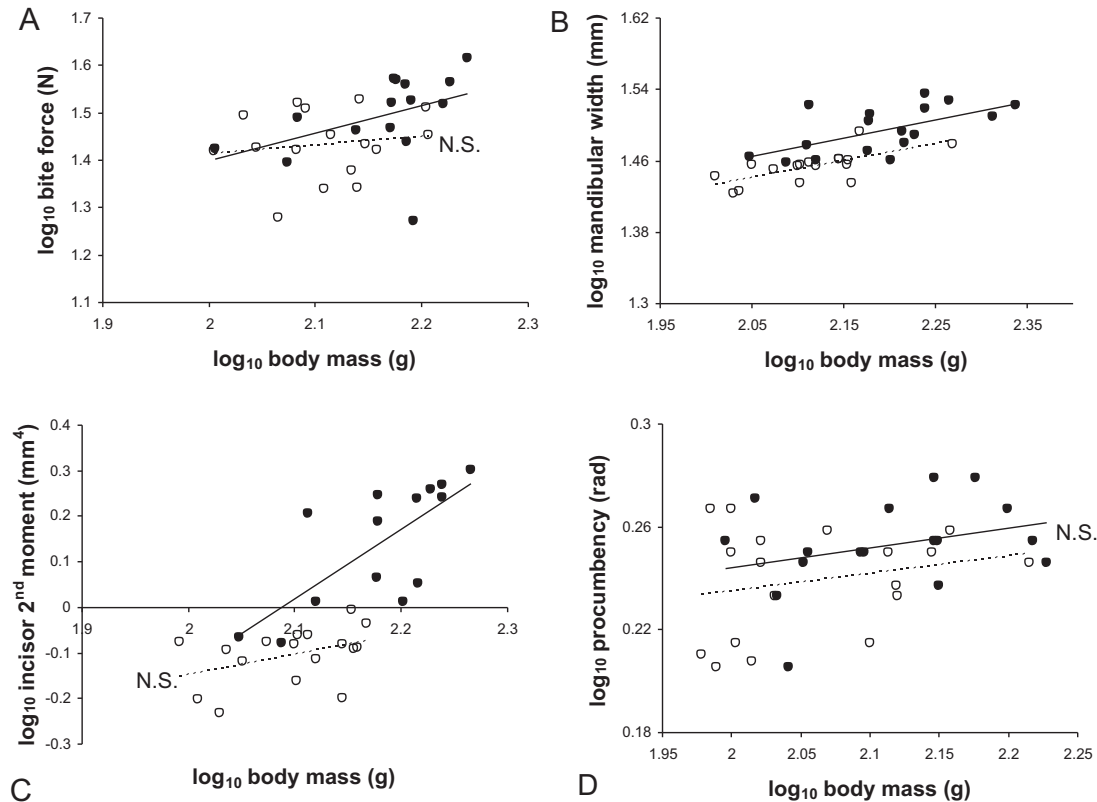


Fig. 3. Regressions of (A) bite force and (B–D) skull variables against body mass in adult specimens of *Ctenomys talarum*. Solid circles: males; open circles: females.

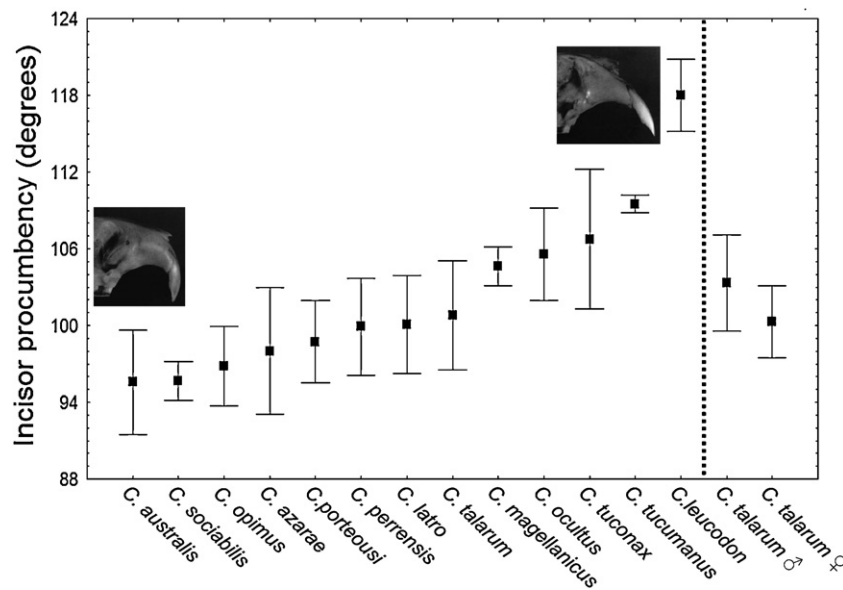


Fig. 4. Interspecific variation in incisors' procumbency within the genus *Ctenomys* and sexual dimorphism within the species *C. talarum*. Procumbency (mean and standard deviation) shown in degrees (from Mora et al., 2003).

focused in two locations of the body: head and tail. Males suffered important injuries during the establishment of a hierarchy of dominance (Zenuto et al., 2001). When biting an opponent, not only masticatory muscles but probably their trunk and limb muscles are also involved; this would place large bending loads on the incisors. We can assume that selection for digging with the incisors has resulted in a jaw musculature that is plenty strong enough to damage a conspecific. However, the substantially more robust incisors of males suggest that there is a greater risk of breaking an incisor during fighting than during digging.

Males showed statistically significant higher incisor procumbency angles than females, though the ranges of males and females clearly overlap. Both sexes showed a lack of correlation of this variable with body mass. The higher incisor procumbency angle observed in males in the present study provides a more effective angle for attacking the opponent. Selection pressures associated with different soil conditions, and different commitments to dento-excitation, may have resulted in considerable interspecific variation on the incisors' procumbency (Fig. 4; see also Lessa, 1990; Lessa et al., 2008; Fernández et al., 2000). The particular arrangement of the incisor root in *Ctenomys* facilitates changes in the arc described by the entire incisor which, ultimately, generate changes in procumbency (see, for example, Landry, 1957; Lessa, 1990). This structural configuration of the skull and the incisors has resulted in changes in the angle of procumbency, which is to some extent decoupled from the body size effect of species of *Ctenomys* (Mora et al., 2003). As mentioned above, body size variation in *Ctenomys* and other subterranean rodent species is severely constrained due to the digging energetic costs associated with each particular habitat (Vleck, 1979, 1981; Luna and Antinuchi, 2007). The variability in incisors' procumbency in the subterranean genus *Ctenomys* was therefore viewed as an adaptation to dento-excitation (Mora et al., 2003). We suggest that the particular arrangement of the incisor root probably also underlies the emergence of sexual dimorphism in procumbency, as observed in the present study.

The frequent use of incisors during inter-male aggressive encounters (Zenuto et al., 2002), coupled with field evidence demonstrating a skewed sex ratio favoring females and a high incidence of scars in males (Busch et al., 1989) both indicate that bite force and incisor robustness may be decisive in terms of the outcome of aggressive encounters. We conclude that sexual selection

acting on male body size resulted mainly in dimorphism in the fighting capacity of *C. talarum*, but also influenced the incisors' robustness and, to a lesser extent, the incisors' procumbency, these traits being relatively independent of body size.

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