

Biting Performance and Skull Biomechanics of a Chisel Tooth Digging Rodent (*Ctenomys tuconax*; Caviomorpha; Octodontoidea)

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ABSTRACT

Biting performance is a key factor in vertebrate groups possessing particular food habits. In subterranean rodents that use the incisors as a digging tool, apart from requirements related to gnawing abrasive diets, the force exerted at the incisors tips must be sufficient to break down soils that are often exceedingly compact. The subterranean genus *Ctenomys* diversified in the southern portion of South America closely associated with the relatively open environments that characterize that region. This genus is considered a "claw and chisel tooth digger," that is, during the excavation of their galleries, the animals break down the soil with both the fore-claws and the incisors. We report here measurements of in vivo bite force in one of the largest species of the genus, *C. tuconax*, which occupies highland grasslands with compacted soils. We document the combined use of claws and incisors observed under field conditions, also providing measurements of soil compaction in the habitat occupied by this species. We report estimates of bite force at the level of the incisors and cheek teeth calculated from the physiological cross-sectional area of jaw muscles. To this aim, anatomical and biomechanical analyses of the mandibular apparatus were performed in preserved specimens. We found that *C. tuconax* bites with a higher force than expected for a mammal of its size. To assess anatomical correlates of biting performance, the morphology of the skull and jaw, and incisor second moment of area were compared with those of other caviomorph rodents with different lifestyle. *J. Exp. Zool.* 319A:74–85, 2013. © 2012 Wiley Periodicals, Inc.

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The structure of the rostral region of the skull and the jaws of vertebrates has diversified mainly in relation to the different trophic behaviors and/or diets, leading to an amazing diversity of morphological adaptations (Schwenk, 2000; Hall, 2005). Other intervening selective pressures are associated with the use of the feeding apparatus during aggressive encounters (territory defense, inter male competition for mates) (Feldhamer et al., 2007). Generally less well known, but of crucial importance in several vertebrate groups, is the use of the skull and jaws during locomotion, for example, for burrowing (Wake, '93). This is the case for some osteichthyan species, some anuran tadpoles,

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gymnophonian amphibians, amphisbaenians (Wake, '93, and references therein), and different fossorial rodents (Lessa et al., 2008; Lin et al., 2010). Within mammals, the feeding apparatus of rodents possesses some of the most specialized features, which has given the group the ability to access hard food items as well as break down compacted soils in those species that dig with the incisors, usually known as “chisel tooth” diggers (Lessa, '90). The overall strengthening of the skull, especially the areas of origin and insertion of mandibular adductor muscles, and procumbent incisors both are typical features of chisel tooth digging rodents (Hildebrand, '85).

Rodents have long, curved, ever-growing incisors for gnawing. These incisors are open rooted, lacking enamel on their lingual side, which allows them to sharpen their tips into chisel-like structures with wear (Ungar, 2010). The other outstanding feature of rodents is the powerful jaw adductor musculature that tends to insert far from the mandible joint, thus providing an increased in-lever arm, which provides a high mechanical advantage in comparison with other mammals. This condition is more pronounced in the suborder Hystricognathi, where the masseter medialis anterior originates in front of the orbit (Woods, '72), a striking condition shared only with certain extinct carnivores (Naples and Martin, 2000). The Caviomorpha (or South American Hystricognathi) includes the most diverse clades of rodents in terms of ecology, body size, and locomotor mode (Mares and Ojeda, '82). Fast running adaptations are present in agoutis (*Dasyprocta*) and maras (*Dolichotis patagonum*); coypus (*Myocastor coypus*) and capybaras (*Hydrochoerus hydrochaeris*) show semi-aquatic life adaptations, whereas porcupines (e.g., *Erethizon*, *Coendou*) show climbing adaptations (Redford and Eisenberg, '92; Galewski et al., 2005).

Among caviomorphs, living and extinct members of the sister families Octodontidae and Ctenomyidae show a progressive development of ever growing hypsodont molars and powerful jaw adductor muscles as adaptations to the drier and more opened biomes of South-Western South America, with a mostly abrasive diet. Behavioral adaptations to this environment include burrowing for both sheltering and improving thermoregulation, which characterize the evolution of both families from the late Miocene-Early Pliocene onward (Verzi, 2001; Lessa et al., 2008). The family Ctenomyidae has evolved a set of morphological adaptations to digging for a period of about 15 million years after its separation from its sister family Octodontidae (Lessa et al., 2008). In particular, the extant genus *Ctenomys* shows a set of morphological, physiological, and behavioral attributes which are convergent with those found in unrelated digging rodents elsewhere in the world (Reig et al., '90; Nevo, '99; Antenucci et al., 2007; Begall et al., 2007). Previous work has focused on some of the functional morphological adaptations of the skull (Verzi, 2002; Hautier et al., 2012) and limbs (Lehman, '63; Morgan and Verzi, 2006; Steiner-Souza et al., 2010). *Ctenomys* is a “claw and chisel tooth digger,” that is, during the excavation of their

galleries, the animals break down the soil with both the fore-claws and the incisors (Lessa et al., 2008). The genus not only shows marked morphological differences with respect to other caviomorph rodents but also its constituting species are to some extent morphologically heterogeneous. For example, it is known that the jaw musculature of a species that uses both the fore-claws as well as the incisors for digging (*C. talarum*) is more developed than that of another species which uses only the fore-claws to break down the substrate (*C. australis*). Furthermore, the former species, which inhabits a relatively compact soil, shows higher incisor procumbency, thus giving a more appropriate angle of attack against the substrate (Vassallo, '98).

Ctenomys tuconax (Thomas, 1925) is one of the largest species within the genus. The procumbency of its incisors, observed in specimens from museum collections (Mora et al., 2003), and the fact that it occupies soils that are compact, allow us to advance the hypothesis that this species uses, in addition to claws, its incisors to break down the soil. Therefore, *C. tuconax* should be able to exert substantial bite forces at the tip of its incisors. This raises another important issue: any incisor, particularly those of rodents, is sufficiently long relative to their basal diameter to be affected significantly by bending stresses (Bacigalupe et al., 2002), which are expected to be especially high in those species possessing major biting performance. Both the shape and the cross sectional area of the incisors are two main factors which determine its robustness, since they affect the second moment of area, a geometrical parameter which estimates the resistance to bending stress (Alexander, '83). Therefore, the incisors of *C. tuconax* are expected to exhibit a relatively higher second moment of area than those of other caviomorph rodents with different mode of life.

This study had three main objectives: (1) To assess whether *C. tuconax* uses the incisors for burrowing (in addition to the claws) and whether they may be better suited to withstand bending stresses caused by chisel-tooth digging. (2) To evaluate biting performance in *C. tuconax*, and its myological and biomechanical correlates. This goal included the functional morphological analysis of the skull and lower jaw, and its comparison with other caviomorph rodents. (3) To evaluate whether *C. tuconax* possess a powerful biting apparatus associated with its specialized mode of life. To this aim our measurements were compared with published values on bite force of other mammalian species.

MATERIALS AND METHODS

Studied specimens of *Ctenomys tuconax* were obtained from natural populations occupying highland grasslands at “El Infiernillo,” near the village of Tafi del Valle, Tucumán Province, Argentina (26°44'S, 65°47'W), during November 2011. Animals were captured using Oneida Victor 0 traps located at burrow entrances. The jaws of the traps were covered with soft rubber (ethylene vinyl acetate). The study was based on 14 specimens of both sexes: 7 males (3 adults and 4 juveniles; body mass range: 200–600 g) and 7 females (6 adults and 1 juvenile; body mass range: 220–430 g). Body external

measurements (head and body length; mandibular width) were taken using a digital caliper (0.01 mm). Upper incisor width (W_i) and depth (D_i) were measured using a digital caliper (0.01 mm) to assess incisor's second moment of area (see below). At the end of the experiments animals were released at their site of capture except four individuals that were sacrificed for anatomical analysis. The use of animals was approved by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) and "Dirección de flora, fauna silvestre y suelos" of Tucumán Province (<http://www.producciontucuman.gov.ar/>).

Behavioral Observations

Digging behaviors of three *C. tuconax* individuals (two males [one adult, one juvenile] and one female) were observed and video recorded with a Sony DCR-SR47 in the field at "El Infiernillo," Tucumán Province, Argentina. For this purpose, plexiglass chambers were constructed and placed underground (following Vassallo, '98) in a grassy area inhabited by the species, characterized by compacted clayey soil. The observations specifically focused on whether claws, incisors, or both structures are used to loosen soil during digging activities. Each individual was observed separately for a period of 20 min. We measured the duration of digging periods, the rate of extension/flexion of forelimbs, and the number of bites performed during digging periods. The data were combined over the three individuals. Soil compaction at sites occupied by *C. tuconax* burrows was measured with a soil penetrometer (probe: 8 mm diameter) (Sigua and Coleman, 2009).

In Vivo Bite Force Measurement

Individual bite force measurements were recorded with a strain gauge load cell force transducer, produced by Necco Technologies (Mar del Plata, Argentina), (0–20,000 g range: 1 g error). For a detailed description of the transducer see Becerra et al. (2011). The separation between the movable bite plates was adjusted so that the gape angle of adults and juveniles was similar ($\sim 10^\circ$). To this aim, articulated skulls and mandibles of adult and juvenile specimens (from skull collections) were positioned on the transducer bite plates with a gape angle $\sim 10^\circ$, and the resulting separation between the bite plates measured. The bite plates were covered with a thin protective coating made of leather for the animals not to damage their incisors. Bite forces were registered during sessions in which animals were induced to bite the transducer plates. They were induced to bite defensively by taking them out of their cages. Each session lasted ~ 1 min and consisted of biting trials that included several bites. Trials ended when the animals refused to bite the transducer, which in some instances occurred after ~ 30 sec of recording. Bite forces were recorded on a PC using the software Terminal (Microsoft, Redmond, USA). 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.

Statistical analyses (see below) only took into consideration these highest bite force values.

Anatomical Analysis and Bite Force Estimation

We studied the mandibular adductor muscles of two adult females and two adult males. Specimens were sacrificed via cervical dislocation shortly after capture (4–6 hr) and stored at -16°C . The muscles were dissected under an Olympus SZ6 stereomicroscope, weighed to the nearest 0.01 g, and finally stored at -16°C for further analysis. The origins and insertions of the muscles were assessed and mapped onto skull photographs based on previous studies such as Woods ('72), De Santis et al. ('98), and Vassallo ('98). Fiber length was measured following the method of Gans et al. ('89). Muscles were submerged in 10% aqueous solution of HNO_3 during 12–24 hr, time depending upon the size of each muscle. Fibers ($n = 12$ –18 per muscle) were selected at random for the calculation of the average fiber length and photographed under the stereomicroscope using an Olympus E620 digital camera. The pinnation angle of the fibers was measured for force calculations. Fiber length and pinnation angle (measured on photographs of the entire muscle) were measured using the software ImageTool 3.0 (<http://compdent.uthscsa.edu/dig/itdesc.html>).

Maximum muscle forces were calculated from the PCSA (physiological cross-sectional area). In pennate muscles it better represents the number of muscle fibers in the muscle. The PCSA of each muscle was estimated following the equation reported in Alexander ('83):

$$\text{PCSA} = \frac{m \cos \sigma}{\rho l}$$

where m is the muscle mass (kg), σ the mean angle of pinnation, ρ the density of mammalian muscle tissue ($1,050 \text{ kg/m}^3$; Méndez and Keys, '60), and l is the mean fiber length (m). The in-force (N) equaled the corresponding PCSA times the maximum isometric stress of striated muscle (250 KPa) (see, for instance, Herzog, '95).

Cleaned skulls of specimens and their articulated mandibles were photographed in lateral, dorsal, ventral, and frontal views. As indicated above, the gape angle was set at 10° . The line of action of each muscle was assessed from these digital photographs taking into account the origin and insertion for each muscle based on previous dissections. The coordinates of place of origin and insertion of muscles, and the lower jaw joint were determined using the software ImageTool 3.0, trigonometrically integrating them into 3D coordinates from the different skull views. The length of the in-lever arm of each adductor muscle (i.e., the perpendicular distance extending from the line of action to the jaw joint) was trigonometrically determined based upon the three-dimensional coordinates. Out-lever arms (i.e., the distance extending from the biting point to the jaw joint) were determined taking into account the different biting points (incisor, premolar, molar 3; Fig. 1). Finally, the moment across the jaw joint for each

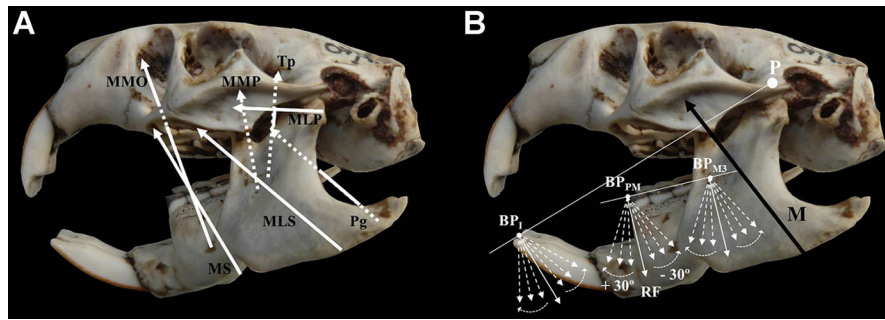


Figure 1. Skull and jaw of "robust" tuco-tuco (*Ctenomys tuconax*). (A) Jaw adductors line of action. MS: m. masseter superficialis, MLS, m. masseter lateralis; MMO, m. masseter medialis anterior; MMP, m. masseter medialis posterior; MLP, m. masseter lateralis posterior; Pg, m. pterygoideus; Tp, m. temporalis. (B) Skull and jaw showing the biomechanical model used for bite force estimation based on the computation of the static force equilibrium. M, adductor muscles force; P, pivot (mandibular condyle); BP, biting point (I, incisor; PM, premolar; M3, molar 3). RF, food or soil reaction force.

adductor muscle was calculated. Bite force estimation was based on the computation of the static force equilibrium, in which muscles' moment across the jaw joint equals the food or soil reaction force moment (Hildebrand and Goslow, 2001; Herrel et al., 2008). All muscle moments were summed for both sides of the jaw, and from this quantity the bite moment and the bite force were derived. Bite forces were estimated for the aforementioned 10° gape angle and three bite points: at the incisor, premolar, and molar 3. Bite forces were calculated for different orientations of the food or soil reaction forces with respect to the lower jaw, as the actual orientation of the reaction force is often unpredictable and may depend upon the texture of the soil or food item, as well as on the position of the jaw (Herrel et al., '98). The angle of the food reaction forces (AFRF) was set to vary between -30° and +30° from the right angle formed by the occlusal plane and the vertical food reaction force (Fig. 1).

Bite Force in Comparison With Other Mammals

We compiled published results on bite force from other mammalian orders (including taxa from Chiroptera, Carnivora, Rodentia, and Didelphimorpha) to analyze the allometric relationship between these forces and body mass. The data were taken from Van Daele et al. (2009), Freeman and Lemen (2008; Fig. 3), Calderón et al. (2006), Christiansen (2007), and Becerra et al. (2011). The bite forces compared were measured at similar jaw position (anterior teeth). All of these data were analyzed together with our own measurements of in vivo bite force from *C. tuconax*.

Museum Specimens Studied

To assess skull and mandible morphology in *C. tuconax* a comparative analysis with other caviomorph species with different modes of life was performed. In 77 adult specimens belonging to 17 species of caviomorph rodents the following skull measurements (Mora et al., 2003) were taken using a digital caliper

(0.01 mm): rostral length (the length of the tooth-bearing portion of the skull); basilar length; diastema length; condyle–tip of the incisor length (a measure of the out-lever arm of the mandible adductor muscles, Verzi et al., 2010a); incisor width; zygomatic width; mandibular width. The studied species were: Family Caviidae: *Cavia aperea*, *Kerodon rupestris*, *Galea spixii*, *Microcavia australis*, *Dolichotis patagonum*. Family Chinchillidae: *Lagostomus maximus*, *Lagidium viscaccia*, *Chinchilla laniger*. Family Myocastoridae: *Myocastor coypus*. Family Octodontidae: *Octodontomys gliroides*, *Spalacopus cyanus*, *Octomys mimax*, *Tympanoctomys barrerae*. Family Ctenomyidae: *Ctenomys talarum*. Family Echimyidae: *Proechimys dimidiatus*, *P. albispinus*. The skull and mandible variables were log₁₀-transformed. A principal component analysis (PCA) of the correlation matrix was used to investigate interspecific size and shape variation (Bookstein et al., '85).

Incisor Resistance to Bending Stress

Procumbent incisors, like those of *C. tuconax*, are assumed to be an adaptation to chisel-tooth digging in subterranean rodents (Lessa, '90). Mechanical resistance to bending was estimated using the second moment of area (*I*), a geometrical parameter that indicates how resistant a particular structure is to bending stress (Alexander, '83). In the calculation of (*I*) we used external measurements because the incisor part that is under bending stress is solid. The 2nd moment of area of the incisors about the sagittal (anterior–posterior) axis was calculated as:

$$I = \frac{\pi}{4[(W_i/2)(D_i/2)^3]$$

considering incisor cross section as an ellipse with major axis (*W_i*) represented by the transverse diameter of the incisor, and minor axis (*D_i*) represented by its antero-posterior diameter (Verzi

et al., 2010a; Becerra et al., 2012b). These variables were taken at the incisor's tip just behind the chisel.

Statistical Analyses

ANOVA and ANCOVA on bite force and body mass were performed to test for differences between sexes. Analyses were performed using STATISTICA 10.0 (StatSoft, Tulsa, USA). Intra- and interspecific allometric analyses of bite force vs. body mass, as well as interspecific allometric analyses of incisor 2nd moment of area versus body mass were based on Model II (reduced major axis regression) because neither variable is considered independent (i. e., there was error associated with the measurements of both x and y [Sokal and Rohlf, '95]) and it is the structural relationship between the two variables that is required. Measurements were \log_{10} -transformed prior to analysis. Analyses were performed using a software developed by Andrew Bohonak, San Diego State University (available from <http://www.bio.sdsu.edu/pub/andy/RMA.html>). A regression performed on phylogenetically independent contrasts (Felsenstein, '85) using the PDAP (Midford et al., 2003) package module in the program MESQUITE (Maddison and Maddison, 2006) yielded similar results.

RESULTS

Observations on Digging Behavior

The animals (two males [one adult, one juvenile] and one female) began to excavate galleries within minutes of being placed in the glass chamber. Because digging behavior was studied in glass chambers assembled in the field, roots, rocks and more compacted fragments were also present. Digging behaviors alternated with both exploratory behaviors and latency periods. Digging periods (mean duration = 16.7 sec; range 6–65 sec; $N = 29$) included both the use of the forelimbs and the incisors in a coordinated and effective manner. During fore claw digging, successive extension and flexion of the forelimbs (mean rate = 5.3 times per second; $N = 32$) loosened the soil. Tooth digging events were interspersed among relatively longer claw digging periods. Each tooth digging event consisted of 2–6 consecutive bites. When animals used the claws for digging, the soil was broken down into powder or small

fragments. By contrast, when using the incisors, the soil was broken down into $\sim 1.5 \text{ cm}^3$ clods. Therefore, it seems that *C. tuconax* combines both “scratch” and “chisel-tooth” digging modes to break down the soil. Average soil compaction at areas ($N = 10$) occupied by burrows of *C. tuconax* was 324 N/cm^2 (range 276–383).

Bite Forces Recorded From Live Specimens

In vivo absolute bite forces recorded in the subterranean rodent *C. tuconax* were significantly higher in adult males than in adult females (mean bite force 74.9 N vs. 53.8 N, respectively; $F_{[1,7]} = 5.32$, $P = 0.02$; Table 1). The highest value, 97.9 N, nearly 17 times its weight was registered in a 600 g male individual. Based on the geometric similarity hypothesis, it is expected that cross-sectional areas of muscles, and hence bite force, scale against body mass with an exponent of $2/3$ (0.66). Therefore, a significant positive allometric relationship between body mass and bite force was found (slope = 1.11 [95% CI: 0.90–1.32]; $R^2 = 0.91$; Fig. 2A). No significant differences were observed either in the slope or elevations between both sex scaling equations (parallelism $F_{[1,12]} = 0.26$, $P = 0.62$; ANCOVA: $F_{[1,12]} = 0.001$, $P = 0.97$). Considering that any length must scale to body mass with an exponent of $1/3$, the scaling prediction of bite force to any length measurement, as mandibular width, is 2. Therefore, an isometric relationship between mandibular width and bite force was found (slope = 2.05 [95% CI: 1.58–2.53]; $R^2 = 0.86$; Fig. 2B).

Bite Forces Calculated From Muscles

The mandibular adductor musculature of *C. tuconax* is composed of the masseter (three heads), the pterygoideus, and the temporalis muscles (Fig. 3). As other ctenomyids, *C. tuconax* possesses a massive masticatory apparatus in comparison with other related caviomorph rodents [see Woods ('72), De Santis et al. ('98), and Vassallo ('98) for a detailed description of *Ctenomys* jaw adductor muscles]. Muscles differ markedly in their masses: m. masseter superficialis and lateralis contribute most to the overall mass of mandibular adductors (Table 2; Fig. 3). The muscles masseter superficialis, masseter lateralis, and temporalis are able to produce higher in-forces compared with the other mandibular adductor

Table 1. In vivo bite force and body measurements (mean \pm SD) in the subterranean rodent robust tuco-tuco (*Ctenomys tuconax*).

	Bite force (N)	Body mass (g)	Body length (mm)	Head length (mm)	Head height (mm)	Mandibular width (mm)
Males						
Adults ($N = 3$)	74.9 \pm 24.3	520 \pm 100.7	229.0 \pm 20.9	59.7 \pm 1.9	38.3 \pm 2.0	53.3 \pm 4.1
Juveniles ($N = 4$)	30.0 \pm 5.9	225 \pm 33.2	180.0 \pm 12.2	46.8 \pm 1.8	28.5 \pm 2.9	33.9 \pm 2.7
Females						
Adults ($N = 6$)	53.8 \pm 5.8	395 \pm 19.6	202.01 \pm 14.4	59.5 \pm 3.7	37.3 \pm 2.8	44.9 \pm 2.2
Juveniles ($N = 1$)	33.8	220	168.7	48.5	31.2	33.3

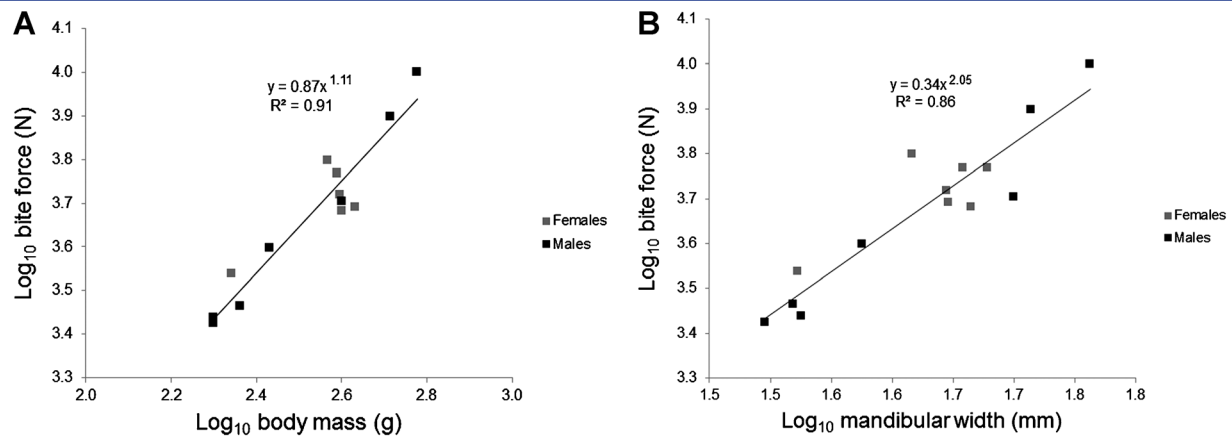


Figure 2. In vivo bite force against body mass (A) and mandibular width (B) in *Ctenomys tuconax*.

muscles, especially in males (Table 2). Nonetheless, the relatively small anterior part of the m. masseter medialis and the m. masseter superficialis have the greatest mechanical advantage of all adductor muscles; hence, their contribution to bite force should be very important. The overall bite force at the level of the incisors calculated for all adductor muscles was about 133.9 N for adult males and 82.3 N for adult females (Table 2).

Effect of Bite Point, and the Angle of the Food-Reaction Force

C. tuconax bites harder at the occlusal surface of the molariforms, where forces are 60–80% higher compared with those of the incisors. Minimum bite force was generated at different angles of the food reaction force for incisors and molariforms. Minimum bite force at incisors was generated under rather perpendicular AFRF, whereas for the molariforms this angle is about 65° (Figs. 1B and 4). Non-substantial differences were observed between bite forces generated at the anterior part of the molariform teeth (premolar) and its posterior part (molar 3; Fig. 4).

Bite Force in Comparison With Other Mammals

When bite force from *C. tuconax* and other mammalian species were regressed against body mass, the data showed an overall negative allometry (slope = 0.58 [95% CI: 0.55–0.61]; $R^2 = 0.90$; see Fig. 5), that is, an exponent significantly different from that predicted under the geometric similarity hypothesis (0.66) was obtained. In Figure 5, it can be seen that bite force in *C. tuconax* was higher than expected for a mammal of its size. Nonetheless, the plot of residuals against body mass (Fig. 6) indicated that other mammalian species seem to be able to exert even comparatively higher bite forces.

Skull and Lower Jaw Morphology

To assess anatomical correlates of biting performance of *C. tuconax*, a PCA was employed to detect skull morphological variation beyond size differences among caviomorph rodent species. The first axis of the PCA on seven skull and jaw variables provided a measure of overall size variation, because all variables

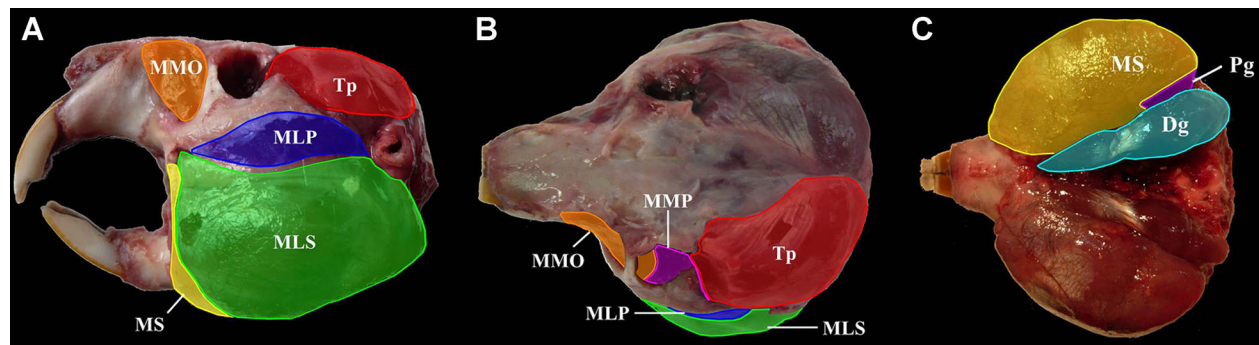


Figure 3. (A) Lateral; (B) dorsal; and (C) ventral views of the masticatory apparatus of *Ctenomys tuconax*. Muscle references as in Figure 1A. Dg, m digastricus (jaw abductor).

Table 2. Muscle parameters and forces exerted by jaw adductor muscles of the subterranean rodent robust tuco-tuco (*Ctenomys tuconax*). Values are means for two adult males and females. PA, pinnation angle; PCSA, physiological cross-sectional area; AFRF, angle of food/soil reaction force. (Overall bite force at the level of the incisors.)

	Mass (g)	PCSA (mm ²)	Fiber length (mm)	Force (N)	Mechanical advantage	Contribution (%)
Males						
m. masseter superficialis (PA: 20°)	3.135	207.33	14.26	58.59	0.51	37.31
m. masseter lateralis	3.205	231.51	13.06	69.45	0.33	29.18
m. masseter lateralis posterior	0.465	63.26	6.935	18.98	0.14	3.50
m. masseter medialis anterior	0.735	79.06	8.77	23.72	0.49	14.46
m. masseter med. Posterior	0.465	63.06	5.68	18.92	0.26	6.31
m. pterygoideus	0.41	60.11	6.43	18.03	0.20	4.62
m. temporalis (PA: 30°)	1.57	135.14	10.96	34.97	0.10	4.62
Overall bite force AFRF 90°				133.9		
Females						
m. masseter superficialis (PA: 19°)	1.655	121.79	12.82	34.50	0.52	36.15
m. masseter lateralis	1.415	124.58	10.71	37.37	0.31	23.61
m. masseter lateralis posterior	0.17	21.94	7.31	6.58	0.10	1.38
m. masseter medialis anterior	0.485	65.55	6.98	19.66	0.49	19.53
m. masseter medialis posterior	0.17	58.88	7.13	17.66	0.23	8.65
m. pterygoideus	0.315	49.69	5.98	14.91	0.21	6.54
m. temporalis (PA: 34°)	0.695	72.17	9.08	17.98	0.11	4.15
Overall bite force AFRF 90°				82.3		

correlated highly and positively with this axis. Skull and jaw variable loadings ranged from 0.746 to 0.991 on the “size” axis, which explains 87.6% of total variance (Table 3). As expected, this axis separated larger caviomorph species (e.g., *Lagostomus maximus*) from smaller ones (e.g., *Octodontomys gliroides*) (Fig. 7).

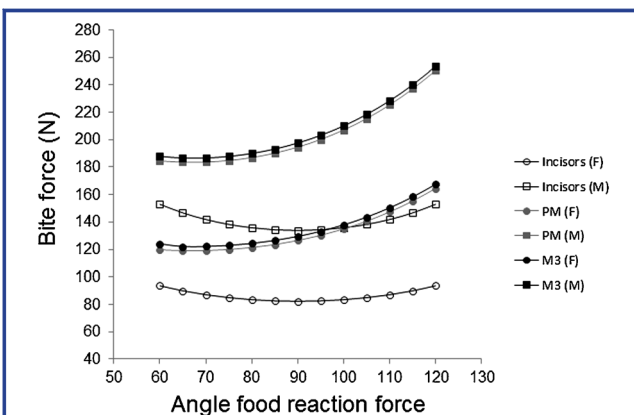


Figure 4. Bite force at incisor and molars for a given range of angles of the food reaction force (based on the computation of the static force equilibrium, Fig. 1B). M, Males; F, females. PM, premolar; M3, molar 3.

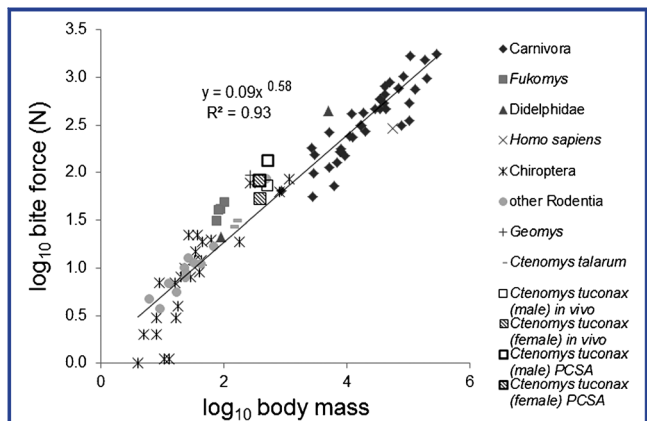


Figure 5. Bite force plotted against body mass in different species of subterranean rodents from tuco-tucos (genus *Ctenomys*), African mole-rats (genus *Fukomys*), and pocket gophers (genus *Geomys*), and other mammals (data from Calderón et al., 2006; Christiansen, 2007; Freeman and Lemen, 2008; Van Daele et al., 2009; Becerra et al., 2011). Other Rodentia includes: *Peromyscus leucopus*, *Onychomys leucogaster*, *Reithrodontomys megalotis*, *Zapus hudsonius*, *Perognathus flavescens*, *Dipodomys ordii*.

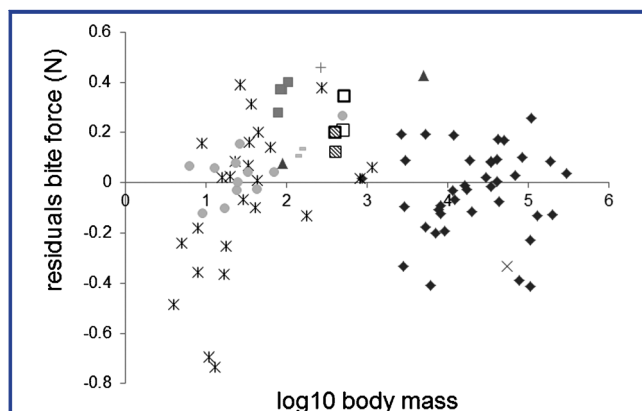


Figure 6. Residuals of the regression between bite force and body mass for subterranean rodent species and other mammals. References as in Figure 5.

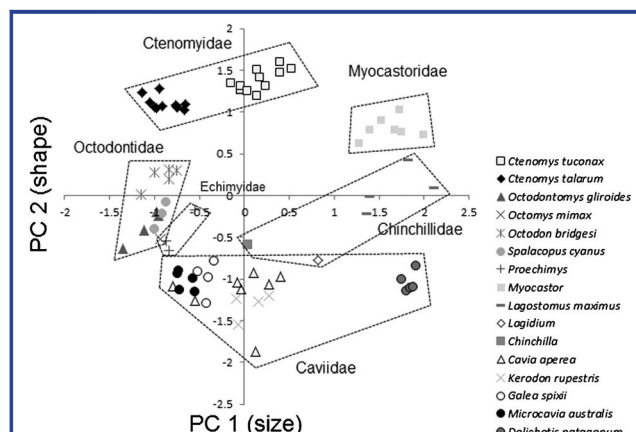


Figure 7. Plot of scores on PC 1 (size) and PC 2 (shape) axes from a PCA of skull variables measured in *Ctenomys tuconax* and other caviomorph rodents. Polygons enclose caviomorph rodent families.

The second axis explained 11% of total variance. This axis produced a contrast between the variables incisor width and mandible width (a measure of jaw adductor muscle development) which have positive loadings, and skull size variables, such as basilar and rostral length, which have negative loadings (Table 3). This loading pattern denotes interspecific differences in both incisor's robustness and jaw adductor muscle development, supporting the general statement that this represents a "shape" axis. Caviomorph species scores were clearly discernible on the shape axes (Fig. 7). The big sized *C. tuconax*, and the relatively small *C. talarum* were separated from gracile forms having slender incisors and relatively less developed jaw muscles, such as *Kerodon rupestris* and *Octodon bridgesi* (Fig. 7). The contrast between the variables diastema length and mandibular width on

this second axis (negative and positive loadings, respectively; Table 3) indicated that the enlargement of jaw adductor muscles may be associated with a reduction of the diastema length, a condition that may influence the out-lever arm of those muscles.

Incisor Resistance to Bending Stress

Incisor second moment of area and body masses were compiled for 30 species of caviomorph rodents, with different habits and ecology, from Becerra et al. (2012b), and compared with the values of *C. tuconax* obtained in the present study. As mentioned above, the 2nd moment of area is a geometrical parameter that indicates how resistant a particular structure is to bending stress. Considering all species together, the incisors' second moment of area isometrically scaled against body mass with a slope of 1.26 (CI 1.06–1.51; $R^2 = 0.90$) (under the geometric similarity hypothesis, the scaling prediction of incisors' 2nd moment of area to body mass is 1.33). The values for *C. tuconax* were located above the regression line, that is, they have incisors with higher second moment of area than expected for a caviomorph rodent of similar size (Figs. 8 and 9). A regression performed on phylogenetically independent contrasts yielded similar results [slope 1.46 (CI 1.21–1.55); $R^2 = 0.91$].

DISCUSSION

Our results show that *C. tuconax* has a robust excavatory/masticatory apparatus and it is capable of exerting large bite forces at the level of its incisors. Compared to other mammalian species, this rodent exerts bite forces higher than expected for a mammal of comparable body mass. Nonetheless, it was clear that other mammalian species seem to be able to exert even comparatively higher bite forces, for example the North American pocket gopher (*Geomys bursarius*; Rodentia, Geomyidae) and the

Table 3. Skull variable loadings on principal components of skull variables measured in *Ctenomys tuconax* and other caviomorph rodents.

Variable	Variable loadings		
	PC1	PC2	PC3
Basilar length	0.970	−0.217	0.068
Rostral length	0.972	−0.228	0.003
Diastema length	0.959	−0.267	0.044
Incisor width	0.746	0.653	0.126
Mandibular width	0.902	0.400	−0.151
Bi-zygomatic width	0.989	−0.073	−0.082
Condyle-incisive length	0.991	−0.089	0.012
Variance explained (%)	87.6	11	0.7

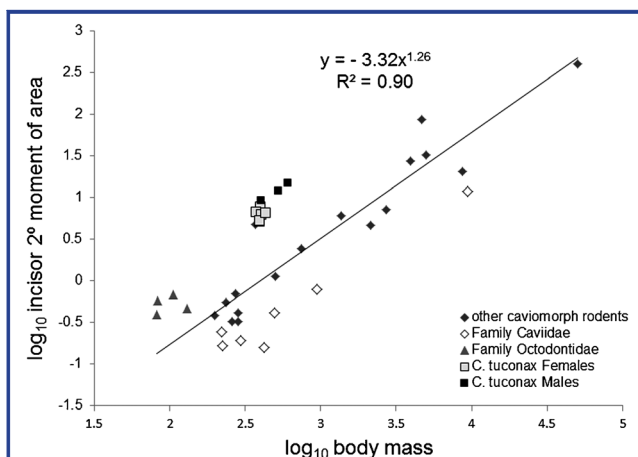


Figure 8. Incisor second moment of area plotted against body mass in *Ctenomys tuconax* and other caviomorph rodents.

teeth-digging African mole-rats (genus *Fukomys*; Rodentia, Bathyergidae). We observed that *C. tuconax*, in addition to the forelimbs, uses its incisors to dig. We also documented that this species lives in very compact soils, since the average soil hardness is 324 N/cm², a value that exceeds at least twice those values measured in other species of *Ctenomys* (Cutrera et al., 2006, 2010).

Bite force was significantly higher in adult males than in adult females. Most species of *Ctenomys* probably have a polygynous

mating system, in which aggressive interactions lead to the establishment of a hierarchical relationship among males (Zenuto et al., '99). Behavioral observations suggest that agonistic encounters between males are very aggressive, scarcely ritualized, and that incisors are used to injure the opponent (Zenuto et al., 2001). Since scaling equations were similar for both sexes considering either the exponents or the elevations, the higher bite force observed in males of *C. tuconax* is assumed to be the result of sexual selection acting upon overall body size rather than specifically on the mandibular apparatus, as observed in another species of the genus (Becerra et al., 2012a). The positive allometric relationship between bite force and body mass may reflect jaw muscles hypertrophy during the species' normal development. On the contrary, the isometric relationship between bite force and mandibular width would be due to the fact that the latter character is associated, in caviomorph rodents, to the degree of development of the jaw muscles (Vassallo and Verzi, 2001).

When performing estimations of bite force based on muscle PCSA, inertial forces of the structures involved and bone strain were ignored, but they still may affect out-forces exerted by the incisors. These factors may explain differences between in vivo measurements and PCSA based estimates of bite force. Another point to consider here is that when measuring bite force or other behavioral/physiological parameters, the question still exists how much effort the tested individual expended, that is, whether the individual exerted the maximum force it could.

C. tuconax bites harder at the occlusal surface of the molariforms, where forces are higher compared with those

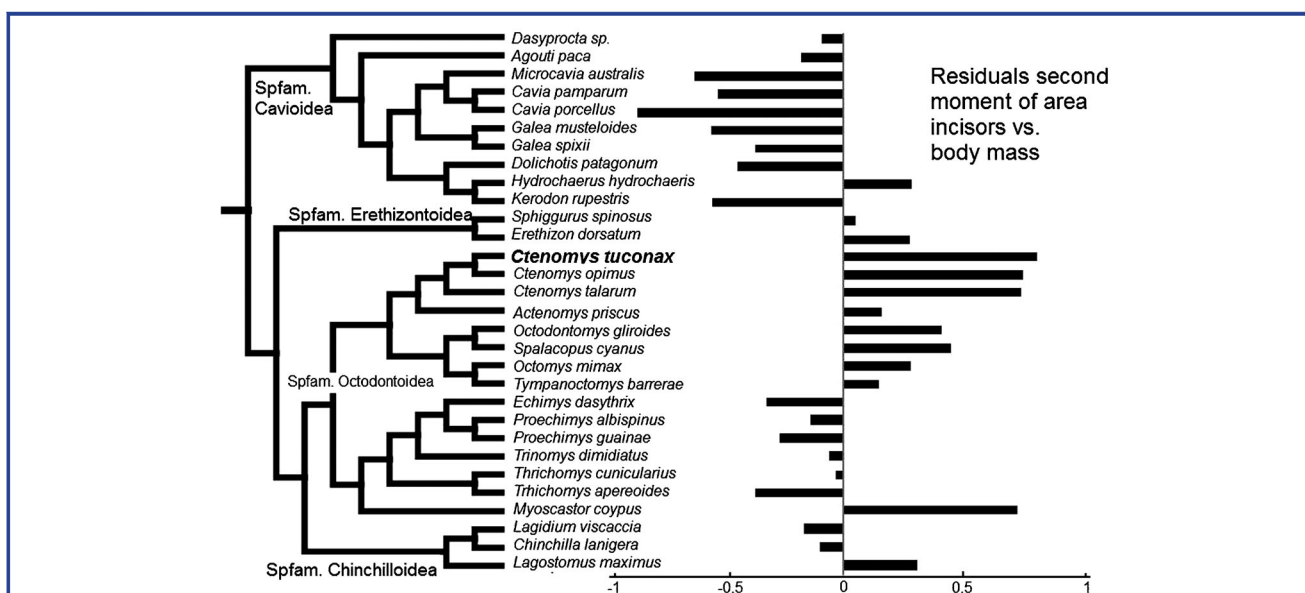


Figure 9. Residuals of the regression between incisor second moment of area and body mass in *Ctenomys tuconax* and other caviomorph rodents. Phylogeny based on different sources: Opazo (2005), Patterson and Velazco (2006), Spotorno et al. (2004).

exerted at the incisors (Fig. 4). Thus, bite point influences bite-force generation in this rodent, as has been demonstrated for other mammals (Van Daele et al., 2009 and references therein). However, non-substantial differences were observed between bite forces generated at the anterior molariform teeth (premolar) and last molar (M 3). This fact might be due to the general shortening of the rostral skull and molariform series existing in the genus *Ctenomys* (Verzi, 2002, 2008), which most likely leads to little difference between muscles' moment arm at first and last molar. The exertion of high bite forces at the molariform teeth, and the progressive development of overgrowing molars (Verzi, 2001) are probably key features which allow the consumption of the relatively less nutritious and more abrasive vegetation in the southern portion of South America (Becerra et al., 2012b).

Ctenomys is the only living genus of the family Ctenomyidae whose living and extinct representatives are all more or less adapted to burrowing (Casinos et al., '93; Fernández et al., 2000). This genus diversified in the relatively drier and opened biomes of South-Western South America, where a mostly abrasive diet probably fostered the development of a robust mandibular apparatus and incisors (Verzi et al., 2010b). This scenario also promoted the development of burrowing for sheltering and pup nursing, and even the acquisition of subterranean habits in species belonging to different caviomorph rodent families (Lessa et al., 2008). In these rodents, the generalized way of digging seems to be by means of the fore-claws, while the use of incisors (chisel tooth digging) only evolved in very specialized subterranean forms, such as *Spalacopus cyanus* (the Chilean coruro), the extinct genus *Eucelophorus*, and some species within *Ctenomys* (reviewed by Lessa et al., 2008; Verzi, 2008). The latter has been characterized in most previous works as a "claw and chisel tooth digger." However, few studies have documented the use of the incisors by the different species. We observed the effective use of the fore-claws and the incisors for breaking down the soil in *C. tuconax*. Compared with the sister family Octodontidae, whose representatives show variable commitments to burrowing, the skull and jaw of *C. tuconax* show a general strengthening. In particular, the angular process of the lower jaw is strongly developed, and hence lateralized with respect to the tooth row. This condition is associated with the development of a major masseteric musculature which inserts upon the angular process (Vassallo and Verzi, 2001, see also Hautier et al., 2011). Even more interesting is the fact that in *C. tuconax* this condition is associated with a shortening of the diastema (Fig. 7; Table 3), the portion of the rostrum that in rodents lies between the incisors and the cheek teeth. The shortening of the diastema produces the reduction of the out-lever arm of jaw adductor muscles, and hence an increase of the mechanical advantage of these muscles. Another feature that differentiates *C. tuconax* from other caviomorph rodents is the high incisors' resistance to bending stress, as shown by the second moment of area. In taxa with incisors largely procumbent, like *C.*

tuconax, these teeth are most projected forward (Mora et al., 2003). For this reason, they do not work at right angles only; they must therefore resist bending stresses particularly when the animals are engaged in chisel tooth digging.

C. tuconax (mean body size 550 g), an inhabitant of the heights of Tucumán Province (3,000 m), is one of the largest species within the genus. The present study shows that this species has the ability to use the incisors to break soils that are much harder than those occupied by other species (Cutrera et al., 2006, 2010). In subterranean rodents that use the forelimbs and incisors as digging tools, as is the case of *Ctenomys*, it is commonly found that the incisors are used when the animal faces hard soils or fibrous roots (Camín et al., '95; Vassallo, '98). This change in "digging tool" is explained by the fact that the mechanical advantage of the jaw adductor muscles in the order Rodentia, and hence the out force exerted at the level of incisors, is higher compared with other lever systems of the skeleton, including the forearm (Hildebrand, '85). Clearly, the use of the incisors by the big sized *C. tuconax* is an important factor that allows this species to excavate its burrows in compact soils. Nonetheless, the negative allometric relationship between bite force and body size (Fig. 5; see also Van Daele et al., 2009) suggests that larger subterranean rodent species might have some restrictions to exert sufficient force at the level of incisors to break down compacted soils. Considering soil compaction of the habitat occupied by the small sized *C. talarum* (mean body size 170 g), and taking into account incisors' cross-section, it was assessed in a previous study that the pressure exerted by jaw adductor muscles at the level of incisors is three times higher than that required for soil penetration (Becerra et al., 2011). The same analysis can be performed using data obtained from *C. tuconax*. Taking into account our bite force measured at the level of incisors, which can reach 64 N (both sexes averaged), the pressure exerted by the incisors of *C. tuconax* (incisor cross section $\approx 0.15 \text{ cm}^2$) is calculated as $64 \text{ N} / 0.15 \text{ cm}^2 = 427 \text{ N/cm}^2$. This value is approximately 1.3 times higher than that required for penetrating the soil of its habitat (note that the average soil compaction at *C. tuconax* habitats is 324 N/cm^2). This oversized bite force has been found in other systems such as reptiles (Pfaller et al., 2011) and fishes (Huber et al., 2008). It may be concluded that, despite the compacted soil of its typical habitat, and the observed negative allometry of bite force against body mass, chisel tooth digging is an effective digging mechanism in this caviomorph rodent.

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