

Another One Bites the Dust: Bite Force and Ecology in Three Caviomorph Rodents (Rodentia, Hystricognathi)



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ABSTRACT

Mammals have developed sophisticated strategies adapting to particular locomotor modes, feeding habits, and social interactions. Many rodent species have acquired a fossorial, semi-fossorial, or even subterranean life-style, converging on morphological, anatomical, and ecological features but diverging in the final arrangement. These ecological variations partially depend on the functional morphology of their digging tools. Muscular and mechanical features (e.g., lever arms relationship) of the bite force were analyzed in three caviomorph rodents with similar body size but different habits and ecological demands of the jaws. *In vivo* forces were measured at incisors' tip using a strain gauge load cell force transducer whereas theoretical maximal performance values, mechanical advantages, and particular contribution of each adductor muscle were estimated from dissections in specimens of *Ctenomys australis* (subterranean, solitary), *Octodon degus* (semi-fossorial, social), and *Chinchilla laniger* (ground-dweller, colonial). Our results showed that *C. australis* bites stronger than expected given its small size and *C. laniger* exhibited the opposite outcome, while *O. degus* is close to the expected value based on mammalian bite force versus body mass regressions; what might be associated to the chisel-tooth digging behavior and social interactions. Our key finding was that no matter how diverse these rodents' skulls were, no difference was found in the mechanical advantage of the main adductor muscles. Therefore, interspecific differences in the bite force might be primarily due to differences in the muscular development and force, as shown for the subterranean, solitary and territorial *C. australis* versus the more gracile, ground-dweller, and colonial *C. laniger*. *J. Exp. Zool.* 321A:220–232, 2014. © 2014 Wiley Periodicals, Inc.

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Mammals exhibit several combinations of musculoskeletal patterns that fit all the particular modes to move through the environment, displaying highly diverse and sophisticated adaptive strategies. Most of them use walking and running as primary locomotor modes, even though they usually show different forms to move depending on the circumstance and the activity (Feldhamer et al., '99). Many species have acquired a fossorial, semi-fossorial, or even subterranean (rarely coming to the surface) life-style, burrowing, compacting, and disaggregating the soil, and dislodging the galleries by means of their limbs, body action (e.g., head rotation and pushing the body forward), their teeth or a combination thereof. As a consequence, they adaptively converged on a particular morphological, anatomical, physiological, and ecological characterization compared with the epigeal counterparts (Hildebrand, '88; Lessa, '90; Wake, '93), such as compact bodies, short and powerful limbs, reinforced and massive skull, low metabolic rates, and high thermal conductance (Hildebrand, '88; Wake, '93; Nevo, '95; Vassallo, '98; Ebensperger and Bozinovic, 2000). Previous studies proposed that a simple evolutionary scenario would establish a more generalized scratch-digging mode, restricted to friable soils, and grades of increasingly specialized semi-fossorial to subterranean taxa, which perform humeral rotation or even chisel-tooth digging under broader ecological opportunities and soil textures (Hildebrand, '88; Lessa and Thaeler, '89; Lessa, '90; Biknevicius, '93; Bacigalupe et al., 2002).

Specifically, Ungar (2010) mentioned that although Rodentia might be the most speciose mammalian order and shows a remarkable versatility, rodents themselves share a pretty similar morphological design; for example, several dental attributes such as one long, robust, curved, open rooted, ever-growing incisor for gnawing in each quadrant, which sharpens into chisel-like structures with wear. These particular attributes have evolved several times among, or even within, families of subterranean rodents (Lessa, '90) and have been fundamental for developing a tooth-digging behavior. It has also been described that rodents search for refuges (e.g., shrub or tree cover, cavities and burrows) looking for protection against extreme climatic conditions and predators (Ebensperger and Blumstein, 2006; Hayes et al., 2007). Even when the South American hystricognath rodents (also known as caviomorph rodents) represent a clade, it is the most diverse rodent clade taking into account their body size, ecology, life-history traits, and locomotor habits (Mares and Ojeda, '82; Woods, '84; Upham and Patterson, 2012). With regards to the ecology and locomotor habits, it has been pointed out that distinctive burrowing techniques have evolved independently in the different families as specializations of a generalized burrowing behavior depending on the environmental conditions (Nevo, '95; Hopkins, 2005; Lessa et al., 2008).

Based on Upham and Patterson's (2012) statement which establish a close phylogenetic relationship between chinchillids–(octodontids–ctenomyids), we focus our study on three species of

those families with highly different ecology and locomotor behaviors:

1. *Chinchilla laniger* Molina 1782 (Rodentia, Chinchillidae; the long-tailed chinchillas) is a ground-dwelling/non-digging rodent native to the rocky or sandy areas of the Andes Mountains in South America, mainly characterized as a half-bounding species that shelter in crevices, holes among or below rocks, or within shrubs (Hildebrand, '88; Nowak, '99; Spotorno et al., 2004). Their colonies involve about 100 individuals, but there have been described colonies up to 450–500 individuals. They are principally herbivorous, consuming herbs, grasses, and sedges, as well as lichens, mosses, and other available vegetation, choosing plants with more fiber and less lignin content (Spotorno et al., 2004; Ungar, 2010).
2. *Octodon degus* Molina 1782 (Rodentia, Octodontidae; the common degus) is a medium size, semi-fossorial caviomorph rodent found in central Chile with low cover of shrubs, which mainly constructs burrows by scratch-digging and, barely, using their slender incisors (Woods and Boraker, '75; Ebensperger, '98; Ebensperger and Bozinovic, 2000). Field studies indicate that they live in social groups consisting of several closely related breeding females and one or more adult males, which share underground complex burrow systems during night-time and emerge from them to forage above ground during the daytime (Ebensperger et al., 2004). As they mainly consume young leaves of herbs and shrubs, digging to obtain food would not be required. Then, most likely multiple ecological variables interact to affect their environmental use; that is, animals probably make trade-offs between predation risk, food availability, and energetics costs of foraging and burrowing to maximize fitness, suggesting that both below- and above-ground components of space use are influenced by variations in vegetative cover (Ebensperger, '98; Ebensperger and Blumstein, 2006; Hayes et al., 2007; Ungar, 2010).
3. *Ctenomys australis* Rusconi 1934 (Rodentia, Ctenomyidae; the sand dune tuco-tucos) is a solitary, territorial, medium size, and subterranean (both scratch- and chisel-tooth digger) rodent that inhabits the coastal sand dunes in the South-eastern Buenos Aires, extending its galleries through soft soils with poor to low primary productivity, cutting off fibrous roots with its incisors, who consumes both subterranean and above-ground plant parts (Vassallo, '98; Cutrera et al., 2010; Ungar, 2010). *C. australis*, just as its congeners, is highly aggressive (with strong and dangerous defensive/offensive bites during fight, for example, in male aggressive encounters; see Zenuto et al., 2002), and has an important medio-lateral component of biting force (i.e., a great contribution on the transverse axis) due to the widening of the mandible and the hypertrophy of the masseter muscles. These modifications allow it to produce the great biting forces needed for both

chewing and chisel-tooth digging (Hildebrand, '85). It is important to point out that *C. australis* belongs to the solely and subterranean extant genus *Ctenomys* with more than 60 species which, due to their wide distribution, highly specialized and detailed adaptations, and fruitful cladogenesis, have been largely studied (e.g., Reig and Quintana, '92; Verzi, '94; Vassallo, '98; De Santis and Moreira, 2000; Verzi, 2002; Mora et al., 2003; Castillo et al., 2005; Lessa et al., 2008; Verzi, 2008; Luna et al., 2009; Becerra et al., 2011, 2012b, 2013).

A fundamental aspect to keep in mind is the great differentiation regarding the cranial morphology between these three species specially focusing, for example, on the cranial and diastema's lengths, the mandibular width, the development of the masseteric crest, and the robustness of the zygomatic arch (Vassallo and Verzi, 2001; Álvarez et al., 2011). For example, Becerra et al. (2013) studied 17 species of caviomorph rodents (5 families represented) and found out that representatives of *Ctenomys*, *Octodon*, and *Chinchilla* differentiate their skull and incisors' shapes on the basis of: more robust to more slender incisors, wider to narrower mandible (i.e., larger to smaller masseteric crests), and longer to shorter basilar and rostral length, respectively.

Previous analyses have extensively studied particular morphological features of dental pieces or skull and mandible regions, setting phylogenetic, mechanical, and allometric constraints (Lessa, '90; Vassallo, 2000; Vassallo and Verzi, 2001; Vieytes, 2003; Lessa et al., 2008; Álvarez et al., 2011; Hautier et al., 2011; Becerra et al., 2012b). Working on the deer mice (*Peromyscus maniculatus*), for example, Zelditch et al. (2008) have found that the spatially distributed physical forces produce an overall integrative response with no modularity of the mandible. On the other hand, jaws have been described as a morphologically dual structure associated with both feeding and digging behaviors (Reig and Quintana, '92; Vassallo, '98; Vassallo and Verzi, 2001). Particularly, by the antero-posterior shifting of the mandible, rodents' jaws are divided in two functional regions: one for gnawing (incisors) and other for grinding (cheek-teeth). The former region, used for chisel-tooth digging, requires the capacity to transmit the considerable bite forces (F_o) needed during burrowing at the tip of the incisors. These forces, in turn, depend on the force of the adductor muscles (F_i) and the mechanical advantage (quotient of in- and out-lever arms; Li/Lo) in terms of $F_o = F_i \times Li/Lo$. Then, the increased biting forces of tooth-diggers, should be achieved by greater muscular force (enlarged adductor muscles), greater in-lever arms (muscles with origins and insertions relatively further from the joint), smaller out-lever arms (relatively closer joint and incisors' tip, resulting from the rostral shortening), or a combination thereof (Lessa, '90; Verzi, 2002; Lessa et al., 2008).

The aim of this study was to assess the bite force capacity according to body size and habitat use in three caviomorph rodents *C. laniger* (ground-dwelling, colonial), *O. degus* (semi-

fossorial, social), and *C. australis* (subterranean, solitary). We expected to find a relationship between different ecological usages of the environment (i.e., ecologically different mechanical demands), and the functional morphology of these rodents' mandibular apparatus. Thus, the tuco-tuco, who must break the soil and cut off fibrous roots during burrow digging, should be the strongest biter with the most aggressive behavior (for niche and social reasons, respectively), while the ground-dweller chinchilla should be the weakest and less aggressive biter. Moreover, we expected to find out if differences in biting forces depend mainly on differences in the mechanical advantages, as suggested by previous researchers, or different relative size and force of the adductor muscles instead.

MATERIALS AND METHODS

Live Specimens and Material for Dissections

Sand Dune Tuco-Tucos. *In vivo* measurements were obtained from live individuals of the species *C. australis* ($N = 10$, both sexes included, body mass: 220–410 g), collected from natural populations inhabiting dune habitats close to Necochea, Buenos Aires Province, Argentina (38°37'S, 58°47'W) on November 2009. Animals were captured using Oneida #0 live traps with a thin protective coating made of foamy, located at burrow entrances. On the other hand, musculoskeletal parameters were estimated from specimens ($N = 4$, both sexes included, body mass: 311–470 g) from the same population, yielded at -16°C in the collection of the Laboratorio de Morfología Funcional y Comportamiento, UNMdP. These specimens were collected during previous research projects (field collections in 1992–1993).

Common Degus. Live individuals of the species *O. degus* ($N = 10$, body mass: 172–239 g) were captured on October 2010, using baited Sherman and Tomahawk live traps, from a natural population occupying mountain habitats in Rinconada de Maipú, Santiago de Chile, Chile (33°28.3'S, 70°50'W). Dead animals for dissections ($N = 4$, body mass: 197–298 g) were provided by and dissected using the facilities of the Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Chile.

Long-Tailed Chinchillas. Both live ($N = 10$, body mass: 600–900 g) and dead ($N = 4$, body mass: 456–821 g) individuals of the species *C. laniger* were obtained from the commercial breeding farm Agro Kaykun, Mar del Plata, Buenos Aires Province, Argentina. These animals were fed with a varied and balanced diet composed by herbs and grasses, similar to what they eat in their natural environment.

All procedures followed NIH and ABS/ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching. The use of animals was approved by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) and University of Mar del Plata. At the end of the experiments, all animals not held for

dissection were released at their site of capture in good physical condition, except for *C. laniger* that returned to the breeding farm.

In Vivo Bite Force Measurement

Individual bite force measurements at incisors' tip were taken with a strain gauge load cell force transducer (Fig. 1; A.I. Vassallo-Necco Technologies, Mar del Plata, Argentina), 0–20,000 g (range), error 1 g, recording four values per second, and then data were transformed into Newton (for a more detailed description, see Becerra et al., 2011). Bite forces were registered during sessions in which animals were induced to bite the transducer plates. The bite plates were separated to set a similar gape angle ($\sim 10^\circ$), and covered with a thin protective coating made of leather, so animals did not damage their incisors. 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 often occurred after 30–40 sec of recording. Bite forces were recorded on a PC using the Terminal software for Windows (Microsoft, Redmond, WA, USA). Each session was repeated four to six times per individual. Animals were induced to bite defensively by taking them out of their cages or traps, accompanied by air being suddenly blown at them behind their ears by the operator with the mouth if needed. The strongest bite from all sessions was assumed to represent maximal bite performance for each individual, following Becerra et al. (2011). For statistical procedures, from a larger sample ($N_{\text{tucos-tucos}}: 55$; $N_{\text{degus}}: 26$; $N_{\text{chinchillas}}: 14$), we focused only on the ten adult above-mentioned specimens with the greatest bite performance, that is, those with the highest residual values of the regression between bite force and body mass, for each species (both sexes equally included).

Anatomical Analyses, Muscle Forces, and Theoretical Estimation of the Bite Force at Incisors Tips

Cleuren et al. ('95) established that using different sections of a muscle complex allows an extensive modulation of bite force and

slight morphometric differences may determine shifts in feeding ecology of closely related species, consequently a rigorous determination of the orientation of the muscle force vectors appear to be of crucial importance. So, following Woods ('72), we studied all mandibular adductor muscles [*m. masseter superficialis* (*MS*); *m. masseter lateralis, pars superficial* (*MLS*); *m. masseter lateralis, pars posterior* (*MLP*); *m. masseter medialis, pars anterior* (*MMO*); *m. masseter medialis, pars posterior* (*MMP*); *m. temporalis* (*Tp*); *m. pterygoideus* (*Pg*)] in four adult specimens of each species (*C. laniger* and *C. australis*: $N_{\text{males}} = 2$; $N_{\text{females}} = 2$; *O. degus*: $N_{\text{males}} = 1$; $N_{\text{females}} = 3$). The physiological cross sectional area (a strength indicator, *PCSA*) of each muscle was calculated following Alexander ('83): $PCSA = m \cdot \cos(\alpha) / \rho \cdot l$; where *m* is the muscle mass (kg), α is the mean angle of pinnation, ρ is the density of muscle tissue (1,050 kg/m; Méndez and Keys, '60), and *l* is the mean fiber length (m). For that purpose, muscles were photographed, carefully dissected under a trinocular stereomicroscope (Olympus SZ61, Olympus, Tokyo, Japan), individually weighed and finally stored at -16°C . Then, they were submerged in 10% aqueous solution of HNO_3 for 24 hr, for collagen tissue digestion and fiber isolation. This last procedure involved a subsequent sectioning of the muscles in approximately equal halves, following muscle fiber direction. Afterwards, we carefully separated the fibers and randomly isolated a single fiber from one of the two exposed edge surfaces. This process was carried out until muscle sections became too small to be manipulated. Selected fibers ($N = 10\text{--}12$ per muscle) were separated and photographed under trinocular stereomicroscope using an Olympus E620 digital camera. Meanwhile, from previous muscles' photographs, the angle of pinnation was estimated. Since the pennate muscles (*MS* and *Tp*) are fan-like shaped ("convergent muscles" sensu Martini, 2006), their fibers' orientation continuously vary from the muscle's line of action to a maximal value at the fan's edges. Then, the angle of pinnation was set as the mean angle in that angle range, both sides averaged; and, therefore, it was calculated as a quarter of the angle formed between those

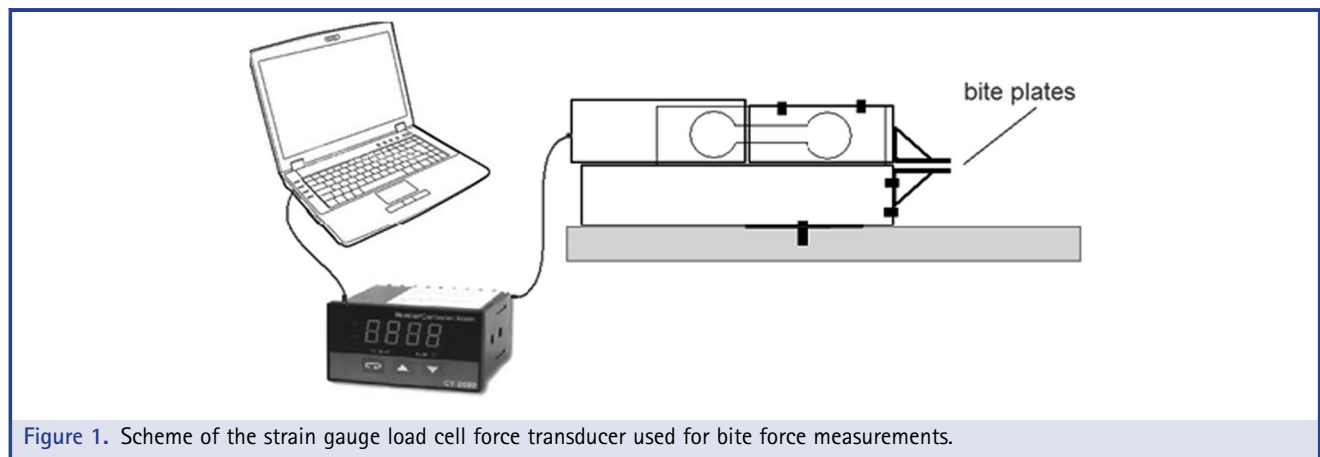


Figure 1. Scheme of the strain gauge load cell force transducer used for bite force measurements.

edges. Fiber length and angles of pinnation were measured using the software ImageTool 3.0 for Windows. Estimations of maximal force developed by each muscle were achieved by multiplying that *PCSA* and the maximum isometric stress of 250 kPa (Herzog, '95; Herrel et al., 2008), the most commonly used value for mammalian striated muscle in the literature.

Cleaned skulls and articulated mandibles were photographed in lateral, dorsal, ventral, and frontal views, setting the gape angle at 10°, that is, similar to the gape angle used at *in vivo* measurements. Based on previous dissections, we assessed the line of action of each muscle from these digital photographs taking into account the centroid of the origin and insertion areas, that is, the mean point of the outermost limits of those areas, according to three-dimensional axes. Since *MS* and *Tp* are not straightforwardly orientated for jaw adduction, we took into account their tendons' line of action. The centroids coordinates, as well as those of the temporo-mandibular joint (*TMJ*), 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 *TMJ*; *Li*) was trigonometrically determined based upon the three-dimensional coordinates (see Davis et al., 2010 for improvements by 3D lever modeling; Becerra et al., 2013). Then, a 3D in-lever arm can be calculated by means of the following equation: $Li^2 = X^2 + Y^2 + Z^2$; where *X*, *Y*, and *Z* represent the in-lever components in the three dimensional axes (i.e., antero-posterior, dorso-ventral, and medio-lateral axes). Then, out-lever arms (i.e., the distance extending from the biting point to the *TMJ*; *Lo*) were determined, and every mechanical advantage (*Li/Lo*) was calculated.

Since medio-lateral components of every pair of opposite muscles cancel each other (Cleuren et al., '95; Olivares et al., 2004), dorso-ventral, antero-posterior, and medio-lateral components of the muscle force were calculated and decoupled to estimate what Hildebrand and Goslow (2001) named as *effective muscle force* (*Fi*) by means of the only sagittal components. According to this, bite force estimation (*Fo*) was based on the computation of the static

moment equilibrium, in which the sum of muscles' moments across the *TMJ* equals the food or soil reaction force moment, that is, $Fo \cdot Lo = \sum(Fi \cdot Li)$ (see Hildebrand and Goslow, 2001; Herrel et al., 2008; Becerra et al., 2011, 2013). Since 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), we calculated bite forces using different orientations of the food or soil reaction forces with respect to the lower jaw. The angle of the food/soil reaction forces (*AFRF*) was considered to vary up to 30° away from the right angle formed by incisors' tip-*TMJ* out-lever arm (named as 60–120°; Fig. 2). At last, the contribution of each muscle to the bite force was calculated as the relation between the effective muscle force and the theoretical estimation of the bite force (*Fi/Fo*), at the angle of food/soil reaction force equal to 90°.

Statistical Analyses

Normality was assessed; variables were \log_{10} transformed when necessary (*Fo*: both *in vivo* and theoretical; *PCSA*: *MLP*, *MMP*, *Tp*, and *Pg*; *Fi*: *MLP*, *MMP*, and *Pg*) to perform parametric tests.

First of all, *in vivo* bite forces of the three studied species (maximum values averaged by species) were tested with results on bite force from other mammalian taxa (e.g., Chiroptera, Carnivora, Rodentia, Didelphimorpha), at similar jaw position (anterior teeth), published by Calderón et al. (2006), Christiansen (2007), Van Daele et al. (2009), and Becerra et al. (2011, 2013). Thus, we carried on a scaling analysis to see if the bite force presents an allometric (either positive or negative) or isometric relationship to the body mass using the Reduced Major Axis software, assuming a type-II regression model (Sokal and Rohlf, '95). This model was used because there was error associated to the measurement of both *X* and *Y* variables and it is the structural relationship between the two variables that is required (Warton et al., 2006; Smith, 2009). A scaling analysis tests the similarity (isometry) or dissimilarity (allometry) of proportions settled by two variables throughout a sample, being usually the body size one of them (Schmidt-Nielsen, '91). Thus, as a force is proportional to its physiological

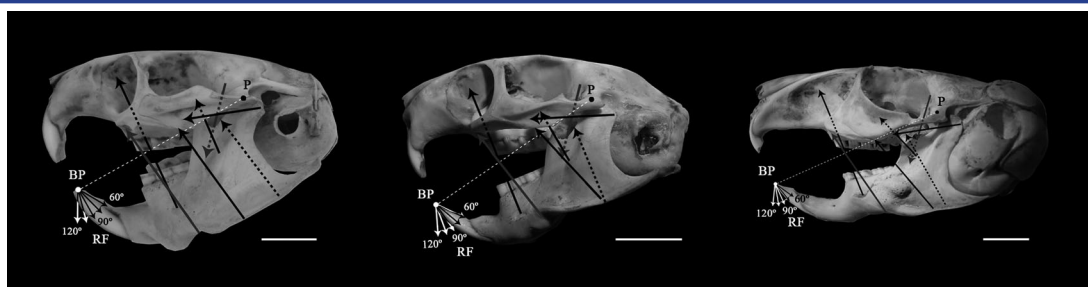


Figure 2. Biomechanical models for bite force estimation based on the computation of the static force equilibrium. Skull and jaw of *Ctenomys australis* (left), *Octodon degus* (middle), and *Chinchilla laniger* (right). P, pivot (mandibular condyle); BP, biting point; RF, food or soil reaction force. Scale: 1 cm.

cross sectional area and the body mass is to its volume, the expected ratio for isometry would be established by: force \propto area \propto volume^{2/3}. Then, any significant departure from the predicted exponent of 0.667, studied by means of a *t*-test, would imply that small animals bite stronger, and big animals bite weaker, than their expected performances according to body sizes (i.e., negative allometry; lower exponent), or vice versa (i.e., positive allometry; higher exponent). Meanwhile, residual values in a regression test allow the particular interpretations of specific deviations from the overall scaling pattern, beyond the body size effect. Finally, we assessed the relationship between bite force and the main morphological variables for skull shape: mandibular width, zygomatic width, and diastema length (Fig. 3; see Becerra et al., 2013; and references therein). For this purpose, individual bite force was regressed to the respective animal's body mass, while each morphological variable was separately regressed to the respective basilar length (i.e., the best body size indicator in the head; Patton and Brylski, '87) on available skulls and mandibles from dissections and previous samples housed in Laboratorio de Morfología Funcional y Comportamiento, UNMDP, Argentina. Then, relative values of morphological variables were regressed against relative values of bite force (i.e., morphological residual values vs. biting residual values).

Since both the mechanical advantage (*Li/Lo*) and contribution to the biting force of every single muscle (*Fi/Fo*) are non-dimensional indices, and then independent to body size, they were assessed by ANOVAs, as well as the differences between the *in vivo* and estimated bite forces and those calculated at several angles of food/soil reaction force, for the three species. Parallelism and ANCOVA on *PCSA* and *Fi* were performed for every single muscle considering body size (by means of the body mass) as continuous predictor and the species as categorical factor to assess the interspecific variation. Differences in theoretical and *in vivo* bite forces, between species, were analyzed by parallelism tests and ANCOVA as well. Finally, the mechanical advantage of *MLS* and the muscular force of *Tp* were evaluated by Kruskal–Wallis tests

due to the lack of normality of these variables, even after log₁₀ transformations.

RESULTS

In Vivo Bite Force

The *in vivo* bite forces of the studied species followed the negative allometric relationship against body mass present in mammals ($R^2 = 0.923$; $P < 0.001$; Fig. Fig. 4A), with an allometric coefficient significantly lower than the expected value of 0.667 (coefficient: 0.558; CI: 0.524–0.592; *t*-test $P = 0.031$). *C. australis* appeared to be much stronger biter than what it should be according to its body mass (mean value: 68.703 N; residual value: +0.271), while *C. laniger* presented the opposite performance (mean value: 23.491 N; residual value: –0.396) and *O. degus* fell near to the regression line (mean value: 21.879 N; residual value: –0.058). Particularly, these bite forces showed notable differences, being *C. australis* the strongest and *C. laniger* the weakest of the three studied species (ANCOVA: $F = 96.763$, $P < 0.001$; see post hoc tests' results and deviations in Fig. Fig. 4B). Considering the skull and mandible morphology of these species, the *in vivo* bite force turns to be mainly predicted by the mandibular width at the level of masseteric crests ($R^2: 0.888$, $P < 0.01$), barely by the zygomatic width ($R^2: 0.354$, $P = 0.02$), but no significant relation was found to diastema length ($R^2: 0.141$, $P = 0.17$).

Anatomical Analyses, Muscle Forces, and Theoretical Estimation of the Force at Incisors Tips

The mandibular adductor musculature of *C. australis*, *C. laniger*, and *O. degus* is composed of the *Mm. masseter* (three heads), *pterygoideus*, et *temporalis* (Fig. 5). Specially, the largest and most contributive muscles turned to be the *MS*, *MLS*, and *MMO* (this last being a result of the hystricomorph condition, in which part of the *M. masseter medialis* is moved forward through the infraorbital foramen; Woods, '72), in different proportions depending on the

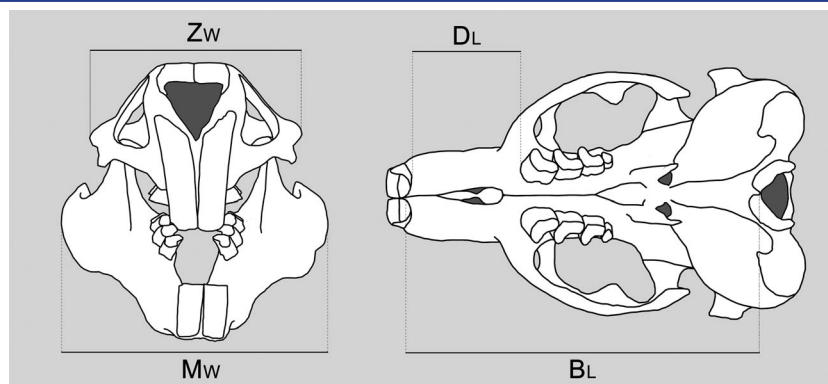
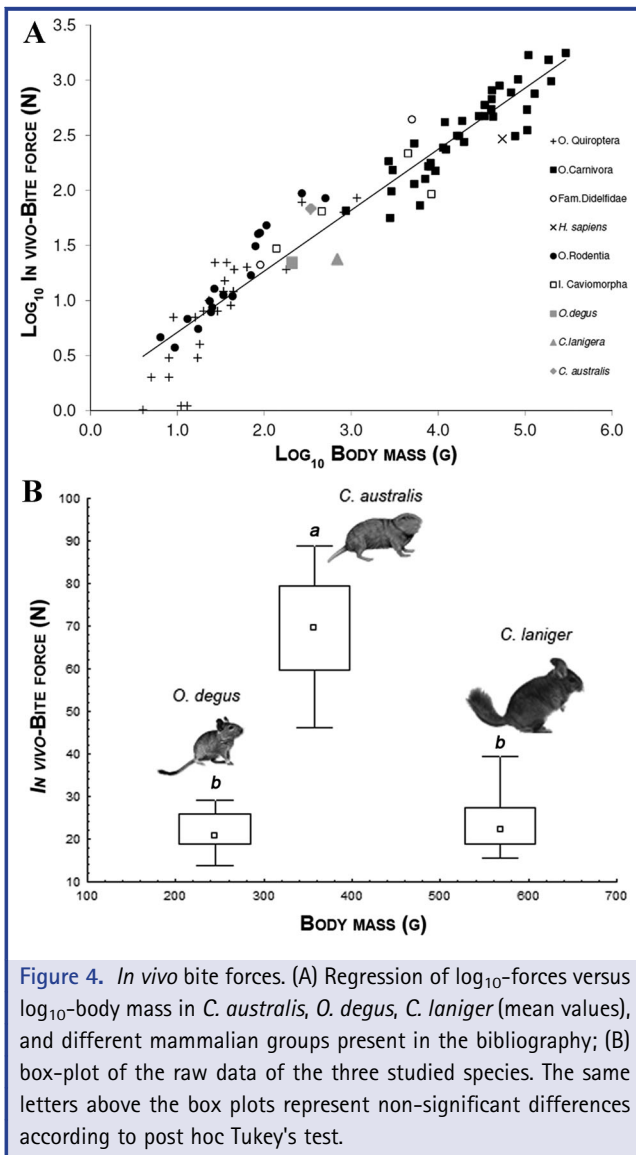


Figure 3. Frontal (left) and palatal (right) view of a caviomorph rodent's skull and mandible, with the main parameters that shape the head. Zw, zygomatic width; Mw, mandibular width; DL, diastema length; Bl, basilar length (body size indicator).



species (Table 1; Fig. 6). The only interspecific significant differences were found in the mechanical advantages of the *MMP*, *Tp*, and *Pg*, three of the less contributive muscles to the overall biting force, where *C. laniger* got separated below to the other two species (see overall and post hoc results in Fig. 6A).

On the other hand, it was notable that every muscle (except for the *MMO*) presented statistical differences for both *PCSA* and *Fi*, where *C. australis* showed a much stronger adductor musculature than the other species, except for the *Pg* where *C. laniger* took the lead (since *PCSA* and *Fi* results behaved according to the same pattern, the latter's plot was omitted; see overall and post hoc results in Fig. 6B).

Finally, after calculating all muscles' effective force and relating them to their corresponding lever arms, the theoretical bite force

(*F_o*) for each species was estimated. Whereas estimations based upon musculoskeletal features yielded greater values than *in vivo* measurements, the statistical analyses still exhibit differences in the theoretical bite force between the three species and their body sizes, being *C. australis* the strongest biter while *O. degus* and *C. laniger* did not showed differences to each other (Parallelism: $F = 11.790$, $P = 0.008$; *C. australis* bit at 83.80%, *O. degus* at 55.20% and *C. laniger* at 35.19% of their theoretical bite forces). Particularly the *MS*, *Tp*, *MMO*, and *Pg* differentiate their contribution to the bite force, having *C. australis* the greatest contribution for the former two muscles while *C. laniger* took the lead on the latter two muscles (see overall and post hoc results in Fig. 6C). Even though the different food/soil reaction forces varied depending on the angle, being forces at 90° the minimum and those at 60° and 120° the maximum, non-significant differences were found in the theoretical bite force for any species (ANOVA: $F_{12,39} = 0.199$, $P = 0.998$; $F_{12,39} = 1.296$, $P = 0.260$; $F_{12,39} = 1.081$, $P = 0.402$; for *C. australis*, *O. degus*, and *C. laniger*, respectively).

DISCUSSION

Vertebrates show a huge diversification of their mandibular apparatus due to their evolutionary traits and particular adaptations. Nonetheless, it has been proposed that some overall patterns remained solid between different taxa, such as the optimization of the musculoskeletal system functioning, by modifying their mechanical advantages (Hildebrand, '88; Liem et al., 2001). For example, the execution of greater biting forces is usually associated to the shortening of the rostrum, as mentioned in the introduction section, in felids with respect to canids (Van Valkenburgh and Ruff, '87; Christiansen and Adolfssen, 2005), in granivorous finches' beaks with respect to birds with other feeding habits (Zusi, '93; Van der Meij and Bout, 2004; Herrel et al., 2005), and in durophagous reptiles (Rieppel, '93; see however Herrel et al., 2002). Even though rodents present a homogeneous masticatory apparatus, caviomorph species developed several particular adaptations that modified their skull in ways that might affect its performance. Then, we focused our study on the differences in a major feature of digging behavior (i.e., bite force performance) as a consequence of changes in the biomechanics and/or differential development of the adductor muscles, according to body size and habitat use. We found that the subterranean, solitary, and territorial *C. australis* is a stronger biter than it was expected given its relatively small size and *C. laniger* exhibited the opposite outcome, while the semi-fossorial *O. degus* is close to the expected value based on mammalian bite force versus body mass regressions. On the other hand, despite the previous proposal of mandibular performance optimization by skull shortening (i.e., enhancing the mechanical advantage, *Li/Lo*) in ctenomyids and other subterranean rodents (e.g., Hildebrand, '88; Vassallo and Verzi, 2001; Verzi, 2002), our results strikingly showed no differentiation on the mechanical advantage of the main adductor muscles. Then, differences in biting

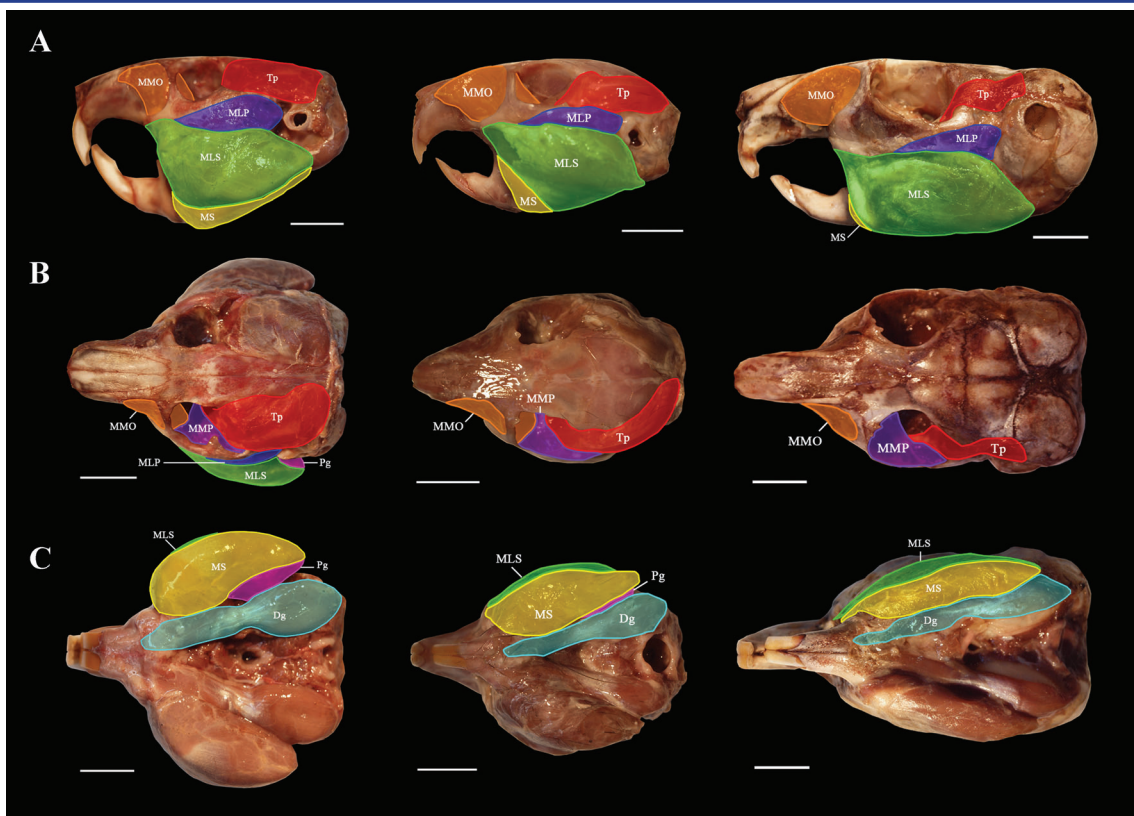


Figure 5. Lateral (A), dorsal (B), and ventral (C) views of the jaw adductor musculature in *C. australis* (left), *O. degus* (middle), and *C. laniger* (right). MS, *M. masseter superficialis*; MLS, *M. masseter lateralis-pars superficialis*; MLP, *M. masseter lateralis-pars posterior*; MMO, *M. masseter medialis-pars anterior*; MMP, *M. masseter medialis-pars posterior*; Tp, *M. temporalis*; Pg, *M. pterygoideus*; Dg, *M. digastricus* (jaw abductor). Scale: 1 cm.

Table 1. Muscle parameters and forces exerted by jaw adductor muscles for four adult individuals of *C. australis*, *O. degus*, and *C. laniger*.

	<i>Ctenomys australis</i> (N = 4)				<i>Octodon degus</i> (N = 4)				<i>Chinchilla laniger</i> (N = 4)			
	Muscle mass (g)	Fiber length (mm)	PCSA (mm ²)	Fi (N)	Muscle mass (g)	Fiber length (mm)	PCSA (mm ²)	Fi (N)	Muscle mass (g)	Fiber length (mm)	PCSA (mm ²)	Fi (N)
MS	1.520	12.540	109.212	26.917	0.495	12.326	35.217	9.184	0.750	9.004	70.536	17.435
MLS	1.236	9.786	123.356	29.801	0.734	10.151	67.798	16.464	0.964	9.268	96.870	24.209
MLP	0.204	7.025	29.105	7.160	0.070	6.819	9.630	2.230	0.123	7.811	15.640	3.737
MMO	0.576	10.636	45.521	11.380	0.355	11.220	30.270	8.232	0.594	8.593	59.996	14.995
MMP	0.454	8.297	52.893	12.797	0.229	8.684	25.094	5.973	0.313	7.686	41.320	9.673
Tp	0.689	7.778	73.546	18.227	0.261	8.121	29.280	6.988	0.172	6.180	25.321	6.321
Pg	0.243	8.897	25.677	4.997	0.173	8.166	19.915	4.710	0.450	6.152	74.757	17.316
Overall eBF (N) [AFRF = 90°]				81.979				39.630				68.197

PCSA, physiological cross-sectional area; Fi, proportion of the muscle force that is transmitted to the incisors and cheek-teeth; eBF, estimated bite force; AFRF, angle of food/soil reaction force.

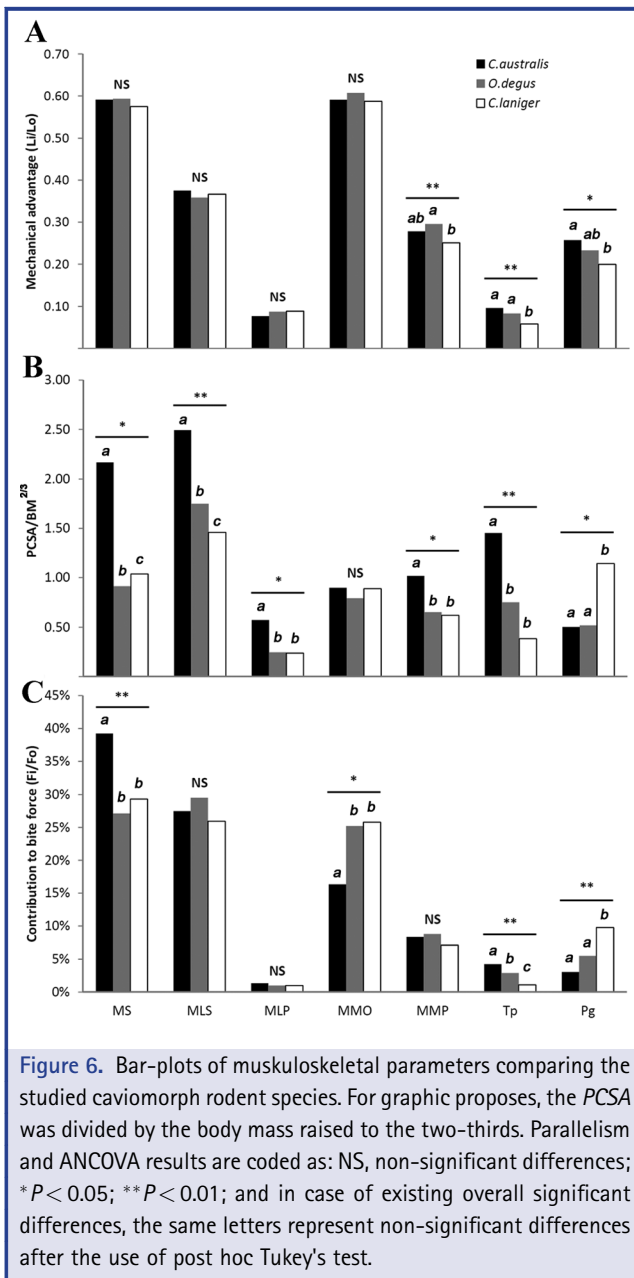


Figure 6. Bar-plots of musculoskeletal parameters comparing the studied caviomorph rodent species. For graphic proposes, the PCSA was divided by the body mass raised to the two-thirds. Parallelism and ANCOVA results are coded as: NS, non-significant differences; * $P < 0.05$; ** $P < 0.01$; and in case of existing overall significant differences, the same letters represent non-significant differences after the use of post hoc Tukey's test.

performances, between species with diverse ecological behavior, would mainly depend on the muscle size rather than its mechanical advantages.

Several authors have analyzed the variation of the skull and mandible morphologies and their potential implications (e.g., Lessa, '90; Vassallo, '98; Vassallo and Verzi, 2001; Mora et al., 2003; Lessa et al., 2008; Álvarez et al., 2011; Hautier et al., 2011). An improvement of the bite force would be possible through an increased muscular force (+Fi; Lessa, '90); a distancing of the line of action of this force from the condyle producing a larger moment

arm [+Li; see Greaves ('82) for limitations; Vassallo (2000)]; or the shortening of the out-lever arm by the approximation of the condyle to the incisors (-Lo) but this would be limited by the need of procumbent incisors in chisel-tooth digging species (Lessa, '90; Verzi, 2002). Some researchers have even proposed that the shortening of the rostral region of the skull in subterranean species, for example, by means of a short diastema and a further forward coronoid apophysis, could increase the mechanical advantage by reducing the out-lever arm (Verzi, 1994, 2002; Vassallo, '98). However, it has been noticed that the forward insertion of the muscles, such as the MMO moving through the enlarged infraorbital foramen, is accompanied by a reduction in the third molar and the shortening of the zygomatic arch (Verzi, 2002), what might keep the lever arm relationships as it was also found for these animals by Vassallo (2000). Moreover, our findings showed that, despite all the differences in the skull morphology between *C. australis*, *O. degus*, and *C. laniger*, no significant changes can be observed in the mechanical advantages of the most important muscles, which might mean that the skull shortening seen in *C. australis* could be reducing not only the out-lever arm (TMJ incisors), but also the in-lever arms (TMJ-muscles action lines).

The higher strength of all *Mm. masseter* (except for the MMO) *et temporalis* seen in *C. australis* might be related to the great bite forces exerted at the incisors' tip during chisel-tooth digging and the aggressive behavior during the territorial encounters mentioned above. These results agreed with Samuels' (2009) descriptions for herbivorous rodents and conclusions of Lessa et al. (2008), who settled that the observed trend toward more massive skulls and greatly expanded muscles is the best way for satisfying the higher functional demands, after considering the structural constraints. Besides, Hautier et al. (2011) have mentioned that, even when the hystricognathous condition of the mandible would not be as useful as it was thought for systematical classifications because of evolutionary parallelism, greater expansions of the mandible (i.e., masseteric crests) might allow the insertion of larger muscles as it was found in *C. australis* versus the more gracile in *C. laniger*. In fact, our results showed that bite force is mainly predicted by the masseteric crests expansion (i.e., mandibular width) but it is not by the rostral shortening (i.e., diastema length). Moreover, it is remarkable that the *Mm. masseter superficialis et lateralis-pars superficialis*, which are responsible for about 60% of the total bite force, present high differences in their size and theoretical force in favor to *C. australis* (Table 1). Particularly, a special consideration could be taken to the *M. pterygoideus* seen in *C. laniger*, which overwhelmed the theoretical force of *C. australis* and *O. degus*, but no deeper comprehension was sought because of its notably low contribution to the bite force.

The fact that *C. australis* was the strongest biter when compared to *O. degus* and *C. laniger* (the weakest one of the three studied species) suggests that this pattern could not only be influenced by

the food or habitat characteristics (e.g., soil and vegetation hardness), but by higher functional demands of the mandibular apparatus by means of a more frequent chisel-tooth digging and aggressive interactions (e.g., defensive/offensive bites). Within the caviomorph rodents, the superfamilies Octodontoidea and Chinchilloidea mainly evolved throughout the relatively arid Andean-Patagonian regions, developing special adaptations for a fossorial or even subterranean life, such as wider mandibular crests, more robust zygomatic arches, and masseter muscles (Vucetich and Verzi, '95; Vucetich et al., '99; Olivares et al., 2004; Verzi et al., 2010; Becerra et al., 2012b). Particularly, *C. australis* has been described as a solitary and subterranean/scratch- and chisel-tooth digging species that involves its mandibular apparatus in feeding, intermale aggressive, and locomotor behaviors (Vassallo, '98; Mora et al., 2003; Becerra et al., 2011, 2012a, 2013). Oppositely, *C. laniger* is a colonial animal with non-procumbent incisors and non-digging, cursorial, and half-bounding habits that shelters in crevices and holes among the rocks (Hildebrand, '85; Jiménez, 1995, '96; Nowak, '99; Becerra et al., 2012b). Meanwhile, *O. degus* is a social and semi-fossorial rodent (Soto-Gamboa, 2004; Soto-Gamboa et al., 2005) described primarily as scratch-diggers barely using their non-procumbent incisors in the construction of the burrows (Redford and Eisenberg, '92; Ebersperger and Bozinovic, 2000; Lessa et al., 2008). Becerra et al. (2012b), by studying some mechanical properties of dental pieces in caviomorph rodents, have observed that the cross-sectional area as well as the second and polar moments of inertia (indicators of bending and torsion resistance) seem to be rather linked to locomotor habits, showing that animals with more mechanically demanded and greater use of their teeth during locomotor activities, such as *C. australis*, present stiffer incisors than the more slender ones of *C. laniger*. Additionally, they have seen that food properties might rather be related to molar features. Thus, the sum of the morphological and ecological characteristics of the studied species suggests that, for *C. australis*, a greater development of the adductor musculature might enhance its biting performance, which in turn might result in a more effective and/or more efficient exploitation of the subterranean niche.

When *in vivo* performances or physiological parameters are under study, there is always a motivational factor that might affect the observations. Even though it has been mentioned that it cannot be ensured how much effort tested animal expended (Davis et al., 2010), differences between *in vivo* and estimated forces might also be due to some ignored parameters of the static biting model, such as the inertial forces of the structure involved and bone/joint strain. Moreover, the orientation of the real food/soil reaction force, the uncertainties of patterns of muscles' activation, muscle coordination, or the muscular recruitment level might add some differentiation between those two data sets (Cleuren et al., '95; Herring, 2007). On the other hand, variations on the gape angle directly influence in the muscular mechanical advantage, with an overall trend toward decreased bite force

with increasing gape angle (Dumont and Herrel, 2003). Thus, for *C. australis*, the only studied species that widely opens its jaws during digging behavior (up to 45°; Becerra et al., unpublished data), theoretical bite force was found to decrease from 81.979 N to 61.448 N when gape angle increased from 10° to 45°. Then, further investigations will deeper investigate the effect of other aspects of biting modulation that influence the bite performance, such as the biting behavior (i.e., which dental pieces are involved during bites; Santana and Dumont, 2009) and the variation of gape angle (Dumont and Herrel, 2003; Williams et al., 2009).

Finally, as it was previously mentioned, the caviomorph rodents have evolved up to one of the most diverse clades taking into account their body size, ecology, life-history traits, and locomotor habits (Mares and Ojeda, '82; Woods, '84; Upham and Patterson, 2012). This huge diversification, especially on morphological traits and their ecological implications (e.g., locomotor capabilities) have been largely studied on the postcranium of this clade (see, e.g., Elissamburu and Vizcano, 2004; Rocha-Barbosa et al., 2005; Morgan, 2009). On the other hand, the mandibular apparatus of these rodents has been able to promote an equivalent evolutionary diversification as well. Many published analyzes on Caviomorpha support our findings, especially, by describing the morphological diversification of cranial, mandibular, and dental traits (e.g., angular process' size, zygomatic width, dental procumbency, molariforms' microstructure), and linking them to their different ecological niches, diets, social and locomotor skills, and functional potentialities, for example, for the subterranean lifestyle (see, e.g., Vassallo, '98; Fernández et al., 2000; Bacigalupe et al., 2002; Verzi, 2002; Mora et al., 2003; Mardegan Issa et al., 2007; Vieytes et al., 2007; Lessa et al., 2008; Álvarez et al., 2011). So, changes in the performance of biting force would allow the mandibular apparatus to be involved in some other behaviors (e.g., digging) beyond the strictly trophic one, which in the case of *Ctenomys* is closely linked to the occupation of a distinctive ecological niche.

Summarizing, probably due to a subterranean and/or fossorial lifestyles and mainly to their social skills, these small caviomorph rodents have developed huge differences not in their lever arm relationships but in their muscles' features themselves. Then, while on one side *C. australis* (a subterranean, solitary and highly territorial rodent) is found to be a strong biter; on the opposite side *C. laniger* (a colonial and epigeal rodent) is a weak biter; and *O. degus* (a semi-fossorial and social rodent) is left in between.

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