



The bite force of the largest fossil rodent (Hystricognathi, Caviomorpha, Dinomyidae)

R. ERNESTO BLANCO, ANDRÉS RINDERKNECHT AND GUSTAVO LECUONA

LETHAIA



Blanco R.E., Rinderknecht, A. & Lecuona, G. 2011: The bite force of the largest fossil rodent (Hystricognathi, Caviomorpha, Dinomyidae). *Lethaia*, DOI: 10.1111/j.1502-3931.2011.00265.x

An exceptionally well-preserved skull of the largest fossil rodent *Josephoartigasia monesi* allows the first analysis of the bite mechanics of this group of South American giant rodents. In this study, we reconstructed the main anatomical features of the skull of this Pliocene rodent, relating them to the bite force at incisors. Bite force was estimated using three different techniques. Two methods suggest that bite forces at incisors of around 1000 N were possible for these mammals. However, the incisors seem to be stronger than expected for this bite force implying that the bite forces may have been greater than 3000 N. We consider three hypotheses: allometric effects, teeth digging or defence against predators, to explain our results. □ *Bite force, Dinomyidae, incisors, largest rodent, Pliocene.*

R. Ernesto Blanco [ernesto@fisica.edu.uy], Facultad de Ciencias, Instituto de Física, Iguá 4225, Montevideo 11400, Uruguay; Andrés Rinderknecht [apaleorinder@yahoo.com] and Gustavo Lecuona [sa_fossil@yahoo.com], Museo Nacional de Historia Natural, CC. 399, 11000, Montevideo, Uruguay; manuscript received on 14/10/2010; manuscript accepted on 04/02/2011.

Dinomyids make up a family of caviomorph rodents that includes the largest rodents ever known (Bondasio 1978 and literature therein). The first undisputed fossil from this family dates back to the middle Miocene (Friasian–Laventan South American Land Mammal Ages), although there are some species from the late Oligocene of Bolivia that may have affinities with this group. Today, the family includes only the ‘pacarana’ (*Dinomys branickii*), a peculiar and poorly studied ‘long headed’ cursorial Amazonian caviomorph (Pocock 1926; Sanborn 1931; Collins & Eisenberg 1972; White & Alberico 1992). The most extreme Dinomyidae is the giant *Josephoartigasia monesi* recovered from Pliocene sediments in Uruguay (Rinderknecht & Blanco 2008).

Although the accuracy of body mass estimations has been debated (Blanco 2008; Millien 2008; Rinderknecht & Blanco 2008) there is agreement that it is the largest fossil rodent so far discovered. Although more than 60 fossil species have been described (Kraglievich 1926, 1930; Mones 1986) our knowledge of anatomy and palaeobiology of these animals is far from satisfactory due to the lack of associated cranial and post-cranial remains. In fact, most specimens are found as isolated teeth and/or small fragments of the skull or mandibles (Mones 1986). The complete skull of *Josephoartigasia monesi* provides a foundation to study the bite mechanics of this species. The bite force is an important aspect of mammal ecology and shed light into the palaeobiology and ecological role of

some species (Christiansen & Wroe 2007; Meers 2002; Therrien 2005a,b; Vizcaíno & De Iuliis 2003; Wroe *et al.* 2005).

In rodents, the well-developed incisors and large bite forces generally have been related to very strenuous functions, such as durophagy, digging burrows and wood processing, among others. Theoretical biomechanical methods have been developed to estimate the maximum bite force of mammals (Thomason 1991; Greaves 1995; Wroe *et al.* 2005; Christiansen 2007) but these methods underestimate maximum bite force. It has been suggested that at the level of cheek teeth the error may exceed a factor of two but at the incisors the error would be a factor between 1.3 and 1.5 (Thomason 1991). More recently, a comparison was made between the estimated bite forces by lever models and *in vivo* measurements in domestic dogs (Ellis *et al.* 2008). The biomechanical lever models generally underestimated bite forces at the canine and at the second molar giving mean values between 39% and 61% of the observed mean. However, it is not always the case that 2-D models underestimate in comparison with 3-D models, as in the case of *Smilodon fatalis* (McHenry *et al.* 2007). Not much empirical data on rodent bite forces are available and many problems preclude obtaining maximum performances in wild animals (see for example Meers 2002). However, the maximum bite force of aware rats was measured as 13 N that yields a bite force per body weight value of 4.33 (Nies & Ro 2004). The allometry of

maximal force was studied by Alexander (1985), who demonstrated that maximal force scales with body mass to the $-1/3$ power. Thus, extrapolating the bite force measured in rats to that of a rodent of around 1000 kg yields a bite force/body weight value of around 0.29. Freeman & Lemen (2008) concludes that body mass and section modulus of the incisors are very good predictors of maximum bite force in living cricetid rodents. This provides a second method for estimating bite force that also can be applied to *J. monesi*.

In this study, we reconstructed the jaw and main jaw adductor muscles of *J. monesi*. From the reconstruction, we estimated the bite force following methods of Thomason (1991). Expected values of bite force were also calculated from body mass and incisors strength estimates. We also discuss the palaeobiological implications of our results.

Materials and methods

A plastic cast was made from the skull of *J. monesi* housed in the Museo Nacional de Historia Natural, Montevideo (MNHN 921, holotype) (Figs 1, 2). To reconstruct the mandibles (not preserved in the holotype), we based our model on a slightly smaller fossil specimen *Isostylomys* (MNHN 2187), which is closely related to *Josephoartigasia*, and the mandible features of the living *Dinomys branickii* (MNHN 3796). To reconstruct the muscles, we dissected the jaw muscles of *Hydrochoerus hydrochaeris* (the largest living rodent), *Myocastor coypus* and *Cavia pamparum* (see Fig. 1). As the myology and biology of *Dinomys* are poorly known, we chose other living hystricognath rodents covering a

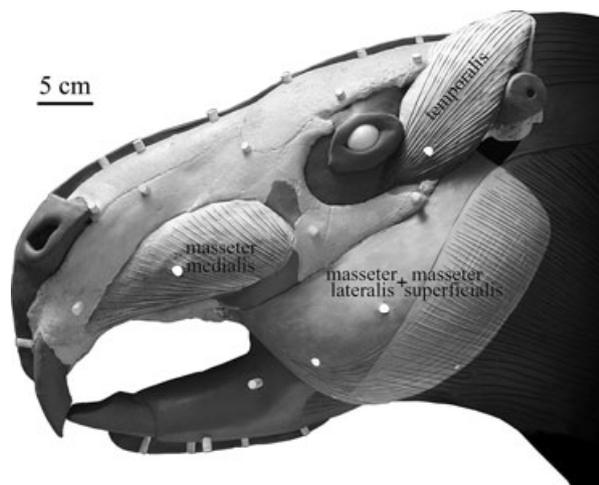


Fig. 1. Anatomical reconstruction of skull, jaw and main jaw adductor muscles of *Josephoartigasia monesi*. Dark areas were not present in the fossil.

broad size range. The main jaw adductor muscles are *musculus masseter* and *m. temporalis*. The effects of pterygoid muscles were considered negligible in comparison with the main adductor muscles.

The reconstruction of *m. temporalis* was relatively easy because the boundaries of the origin area in the skull of Dinomyidae are clearly visible (see Mones 1997). Although in most rodents the *m. temporalis* origin is not clearly bounded, in the Dinomyidae the origin area of this muscle in the deep temporal fossa is very clear (Kraglievich 1926, 1932; Fernández de Álvarez 1958; Rinderknecht & Blanco 2008). This muscle inserts in the coronoid process of the mandible, a structure absent in several dinomyids (Pascual 1967; Mones 1997). Fortunately in the preserved mandibles of many fossil taxa there is a rough region indicating the placement of muscle insertion (see Kraglievich 1926).

The *m. masseter* is divided in several branches (Windle & Parson 1899; Schulman 1906; Edgeworth 1935; Turnbull 1970; Naples 1987; Druzinsky 2010a,b). The main branches considered here are *m. masseter superficialis*, *m. masseter lateralis* and *m. masseter medialis* (=deep masseter or 'ZM', see Druzinsky 2010a). The cross-section of the *m. masseter medialis* can be accurately determined because in caviomorph rodents this branch passes through the infraorbital foramen (Tullberg 1899–1900; Cooper & Schiller 1975; Woods & Hermanson 1985). The cranial origin of *m. masseter medialis* is located in the maxilla-premaxilla masseteric fossa and the mandibular insertion is in a small depression named the masseteric mandible fossa. This fossa lies below p4–m1 in *Dinomys* but in the giant Dinomyidae (subfamily Eumegamyinae) is located between m1 and m2.

The reconstruction of the other two branches of the *m. masseter* is more uncertain because the insertions and origins are not as well-defined (see Saban 1968). The *m. masseter lateralis* inserts in the angular process of the mandible and in the skull the origin is marked by a jugal fossa. In our specimens, the insertions and origins can be roughly determined but the different branches cannot be distinguished. The *m. masseter superficialis* also inserts in the angular process of mandible (superficial to *lateralis*) forming the *pars reflexa* (Saban 1968; Cooper & Schiller 1975). The anterior limit of the origin of this muscle is located in the zygomatic apophysis of maxilla between P4 and M1. As the muscles fibres in both branches are aligned similarly, we represented *m. masseter lateralis* and *m. masseter superficialis* as a single cross-section. The origins of these muscles are along the zygomatic arch, thus it is difficult to determine the muscle force direction. These errors were considered in our sensitivity analysis.

The dissections of *Myocastor coypus* show that the relative muscle mass of the *m. masseter superficialis* and *m. masseter lateralis* (considered together) varies significantly among individuals. Our sensitivity analysis, described below, takes into account this effect.

Muscle cross-sectional areas were measured from sliced samples of the reconstructed muscles. Lever arms were measured from the skull with reconstructed mandible with a digital vernier caliper (Figs 1, 2). All data appear in Table 1. The maximum bite force was estimated from a quasistatic model of biting assuming that all the main muscles act together during maximum isometric force production:

$$F = (AM \cdot s_m + ADM \cdot s_{dm} + AT \cdot s_t) \times \frac{300\text{kPa}}{s_F}$$

where *AM* (*m. masseter superficialis* and *m. masseter lateralis* together), *ADM* (*m. masseter medialis* also known as deep masseter) and *AT* (*m. temporalis*) are the cross-section areas of main adductor muscles; s_m , s_{dm} and s_t are the lever arms of the forces M, DM and T of the three muscle groups (Fig. 2), s_F is the lever arm of the bite force; 300 kPa is a typical value of the maximum stress developed by skeletal muscles (Fig. 2).

We employed a sensitivity analysis to estimate the changes in bite force when the values for each reconstructed parameter varied by 20%. We calculated bite force in these rodents from two predictors: body mass and incisor strength, using equations obtained from data collected from extant rodents (Freeman & Lemen 2008):

$$\log_{10}(\text{bite force}) = 0.430 \times \log_{10}(\text{body mass}) + 0.416$$

$$\log_{10}(\text{bite force}) = 0.566 \times \log_{10}(Z) + 1.432$$

where bite force is in newtons, body mass is in grams and *Z* is the section modulus of incisors at alveolar level with all dimensions measured in mm.

As estimates of the body mass of *J. monesi* vary widely (Blanco 2008), we used two ranges of body mass: 350–1534 kg obtained by Millien (2008) and

Table 1. Data used in the biomechanical model.

	Measured value
<i>Masseter superficialis</i> + <i>lateralis</i> cross section	50 cm ²
<i>Masseter superficialis</i> + <i>lateralis</i> lever arm	133.5 mm
<i>Masseter medialis</i> cross section	25 cm ²
<i>Masseter medialis</i> lever arm	133.9 mm
<i>Temporalis</i> cross section	20.5 cm ²
<i>Temporalis</i> lever arm	38.59 mm
Biting force lever arm	338.2 mm

468–2686 kg obtained by Rinderknecht & Blanco (2008).

Results

The mean bite force obtained from the reconstructed model was 959 N with the variation in bite force obtained from the sensitivity analysis of 799–1199 N (Table 2). Bite force values varied widely in the sensitivity analysis with changes in bite force lever arm but, fortunately, this measurement was fairly certain. The *masseter superficialis* + *lateralis* cross-section and lever arm were also important parameters for this analysis. Fortunately, bite force was not very sensitive to variations in these parameters (a 20% variation in these parameters was associated with a 13% variation in bite force). Other parameters were not important in the sensitivity analysis; the effect of varying these parameters for the *temporalis* muscle was almost negligible (a 20% variation was associated with a less than 2% variation in bite force).

The expected bite force calculated from estimated values of body mass ranged from 630 to 1515 N, with a value of 991 N for a body mass of 1000 kg (see Table 3). The expected bite force calculated from the section modulus of the incisors was 3214 N, a value much larger than all the other estimations.

Discussion

The bite force estimate from the biomechanical model and the anatomical reconstruction (799–1199 N) is consistent with the expected value for a rodent with a body mass in the range estimated for *J. monesi* (630–1515 kg). However, the incisors seem to be much stronger than the expected for such bite forces (the estimate of bite force calculated from incisor strength was 3214 N). These results represent a much greater extrapolation beyond the data used to produce the predictive equation of Freeman & Lemen (2008). Therefore, a first explanation is that the equation itself does not reliably predict bite force in such a large rodent. However, the same argument can be applied to the equation of Thomason (1991) insofar as Thomason's correction factors and the work of Ellis *et al.* (2008) are based on much smaller taxa than *J. monesi*. The discrepancies in bite force estimates could also be due *J. monesi* having a larger safety factor in comparison with that of other rodents. Safety factors can be larger in situations, where the loads in the structure are more unpredictable or if the cost of a failure is too large (Alexander 1981). The former implies that rodents' incisors were used for tasks with less

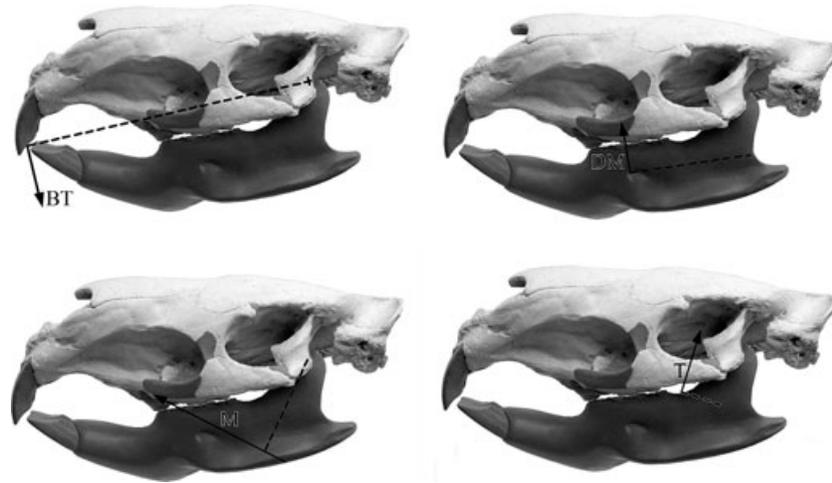


Fig. 2. Anatomical reconstruction of skull of *Josephaartigasia monesi* showing estimated bite force directions and lever arms (dotted lines). Abbreviation: BT, bite force; DM, *masseter medialis*; M, *masseter lateralis* + *masseter superficialis*; T, *temporalis*.

Table 2. Results of the mechanical model and sensitivity analysis.

Studied case	Maximum bite force (N)
Reconstructed anatomy case	959
+20% <i>masseter superficialis</i> + <i>lateralis</i> area (or +20% <i>masseter superficialis</i> + <i>lateralis</i> lever arm)	1080
-20% <i>masseter superficialis</i> + <i>lateralis</i> area (or -20% <i>masseter superficialis</i> + <i>lateralis</i> lever arm)	840
+20% <i>masseter medialis</i> area (or +20% <i>masseter</i> <i>medialis</i> lever arm)	1019
-20% <i>masseter medialis</i> area (or -20% <i>masseter</i> <i>medialis</i> lever arm)	899
+20% <i>temporalis</i> area (or +20% <i>temporalis</i> lever arm)	974
-20% <i>temporalis</i> area (or -20% <i>temporalis</i> lever arm)	943
+20% biting force lever arm	799
-20% biting force lever arm	1199

Table 3. Results of the predictive indicators of bite force, body mass and section modulus of incisors.

Predictor	Bite force (N)
Body mass (350 kg)	630
Body mass (468 kg)	714
Body mass (1000 kg)	991
Body mass (1534 kg)	1191
Body mass (2686 kg)	1515
Section modulus of incisors	3214

predictable forces, such as biting heterogeneous materials with variable compositions. Another possibility is that biting is done not only by jaw closing but also with skull movements and this second factor produces

more variable forces. A large cost of failure could be explained by a stronger dependency on the incisors to maintain a high fitness as for example by depending on the incisors for obtaining food or some other valuable resource. However, as the rodent's incisors grow continuously, it seems unlikely that the cost of failure could be extraordinary large.

The large incisors strength could instead be a consequence of some structural difference between *J. monesi* and the living rodents from which the predictive equation was constructed (Freeman & Lemen 2008). This would imply that *J. monesi* encountered larger stresses in incisors for the same amount of bite force. In a series of works on living fossorial rodents, incisor procumbency has been shown to be strongly related to two factors: body mass and tooth-digging behaviour (Lessa & Patton 1989; Lessa & Stein 1993). A study on scaling has shown that if there is strong positive allometry on rostral length, as is the general tendency in mammals, incisor procumbency must be increased with body size (Lessa & Patton 1989). Millien (2008) has recently proposed that in *J. monesi*, positive allometry on rostral length is even stronger than the general tendency for other mammals. The procumbency of the incisors of *J. monesi* can be only estimated because the incisors are broken at the alveolar level. However, it is clear from the rostral geometry and the curvature of the incisors roots that *J. monesi* incisors are extremely procumbent. Lessa & Patton (1989) considered the allometry of procumbency and predicted the extreme procumbency that is observed in giant rodents. As greater procumbency implies a larger angle between the incisor and the bite force, the moment of force is also larger. That produces larger bending stresses than for same bite force in a smaller rodent. We expect that extreme procumbency

produces an overestimation of bite force from incisor strength indicators. Procumbency is also associated with fossorial habitats (Lessa & Patton 1989, 1989; Lessa & Stein 1993). Although we must consider several possibilities, we think that procumbency is the most likely explanation of the discrepancies in bite force between the incisor strength and other two methods of estimation.

We estimated the cross-sectional areas of muscles assuming that they are all muscles had parallel fibres, rather than pinnate structure. This possibility could explain some of the discrepancies between different methods. But this effect cannot explain all of the difference because our sensitivity analysis did not produce such a large change in bite force when cross-sectional area was increased by 20% (see Table 2).

The absolute bite force of *J. monesi* seems to be close to the predicted value obtained from body size. This estimate of bite force is very large. For example, it is much larger than the bite force of almost all carnivores with bite force estimated by similar methods to the biomechanical model applied here (Wroe *et al.* 2005; Christiansen 2007). For large bodied herbivores bite aperture seems to be a more relevant value for fitness than bite force (Shiple *et al.* 1999). The *masseter medialis* seems to be a peculiar adaptation related to increasing incisal bite force in caviomorph rodents. Druzinsky (2010b) compared the bite force of two groups of rodents: *Aplodontia rufa* that has primitive adductor muscles morphology and sciuriform rodents that have an anterior lateral masseter morphology that suggests that this muscle is the functional analogue of *masseter medialis* in caviomorphs. Sciuriform rodents have a larger incisal bite force than *Aplodontia rufa* and the anterior lateral masseter of sciuriforms is responsible for 40% of the bite force whilst the same muscle in *Aplodontia rufa* provides only 1–4% of the bite force. These features suggest that the cross-sectional areas and lever arms of muscles such as the anterior lateral masseter of sciuriforms and the medial masseter of caviomorphs are adaptations for producing large incisal forces. Our sensitivity analysis shows that varying the cross-sectional area or lever arm length of the *masseter medialis* produces variations in bite force slightly smaller than the variations produced by changing these parameters for the complex of the *masseter superficialis* and *lateralis*, whereas changing these parameters for the *temporalis* muscle produced little change in bite force (see Table 2). These kinds of adaptations to increase incisal bite force are a peculiarity of rodents that seems to be important in *J. monesi*.

Josephoartigasia monesi skull has a very long diastema; large diastemas are associated with long rostral lengths. The toothless diastema enables rodents to

gnaw without ingesting unwanted material, as the lips can be drawn into the space behind the incisors, to close off the rear part of the mouth. A squirrel can gnaw through the shell of a nut but ingest nothing until it reaches the kernel, a beaver can fell a tree without filling its mouth with wood shavings, and a tooth-digging rodent can create a burrow without filling its mouth with sediments. The diastema also enables grazing mammals to eat long lengths of grass. When a rabbit, for instance, eats long grass it bites it off near the ground allowing the long ends to protrude from the side of the mouth through the diastema. These ends are drawn into the mouth by the tongue as chewing proceeds. (Alexander 1990 and references therein). However, the relatively small size of the tooth row of *J. monesi* in comparison with other skull measurements was considered previously (Blanco 2008) to suggest that this animal was not a good grazer and that it probably fed primarily on soft plants. Therefore, it is possible that *J. monesi* used its diastema to process non-alimentary items like tooth-digging rodents and nut eating squirrels do.

We think that the large absolute bite force of *J. monesi* yields additional palaeobiological clues. Freeman & Lemen (2008) discussed possible reasons for animals to have very large bite forces, and the only possibilities that seem consistent with their statistical results are fossoriality and durophagy. Both of these habits could have been used by *J. monesi* as the long diastema also suggests. Fossoriality may be disputed because this animal was so large. Nevertheless, there is fossil evidence in South America of burrows that were probably made by megamammals with body masses greater than 1 tonne (Zárate *et al.* 1998; Bargo *et al.* 2000; Vizcaíno *et al.* 2001). However, some of these burrows are from the Pleistocene, an age without fossil records of giant dinomids (but see Paula Couto 1951). *J. monesi* could have used digging not only for fossoriality, but also for feeding roots. The incisors may also have been a defensive weapon against terror birds (Phorusrhacidae) and carnivorous marsupials (Borhyaenidae). The incisors were probably the main defensive weapon against predators, if we consider that rodents are generally not well-suited for fast running and do not have natural weapons as the horns or antlers of other herbivores. Many living rodents use their small size to avoid predators by hiding from them, but large rodents such as *J. monesi* probably needed some other defensive strategy and a powerful incisor bite force, such as the one estimated here, is a very likely possibility. Despite the large lever arm of the bite force of *J. monesi* due to the long rostrum, the bite force is similar to the large canine bite force of some carnivores that depend on powerful bites to kill large

mammals. For example, Wroe *et al.* (2005) estimated the canine bite force for very powerful predators, such as *Panthera pardus* and *Ursus arctos* to be 467 and 751 N respectively. Both values are smaller than our estimate of 959 N for *J. monesi*. The only animals with comparable bite forces in the study by Wroe *et al.* (2005) were the extinct *Smilodon fatalis* (976 N), that probably preyed in very large mammals, and *Panthera onca* (1014 N), that is able to pierce the skulls of medium size mammals (Turner & Antón 1996 and references therein). However, we must be cautious with these comparisons.

If we accept an intermediate body mass estimate of ca. 1000 kg then *J. monesi* does not have a high bite force for its size; thus, although the estimated bite force of the giant rodent is close to that predicted for *S. fatalis*, the sabre-toothed cat was approximately one-third its body size. It also seems likely that *S. fatalis* produced a weak bite force for its size relative to other cats (McHenry *et al.* 2007). *P. onca* can penetrate the skull of medium sized prey with a similar bite force, but its teeth are in very different shape than those of rodent incisors. But in any case, it is clear that the estimated incisor bite force of *J. monesi* was enough to produce heavy damage if used as a defensive weapon, even against large terror birds or marsupial carnivores. If the incisors were used against charging predators, the safety factor of the incisors may have been large due to extremely unpredictable loads, and the large bite force would be useful to increase the damage. The long rostrum would have kept the eyes and other delicate parts of the head and neck far from the predator's weapons as the defensive bite was applied.

Procumbency due to large body size, tooth-digging behaviour and defence against predators are three hypotheses consistent with the strange association of large absolute bite force, excessive strength of the incisors and a long diastema in *J. monesi*.

Acknowledgements. – We are grateful to Jessamyn Markley and Enrique Lessa. This work was supported by the Agencia Nacional de Investigación e Innovación (ANII) and PEDECIBA.

References

- Alexander, R. McN. 1981: Factors of safety in the structure of animals. *Science Progress* 67, 109–130.
- Alexander, R. McN. 1985: The maximum forces exerted by animals. *Journal of Experimental Biology* 115, 231–238.
- Alexander, R. McN. 1990: *Animals*, 520 pp. Cambridge University Press, Cambridge.
- Bargo, M.S., Vizcaíno, S.F., Archuby, F.M. & Blanco, R.E. 2000: Limb bone proportions, strength and digging in some Lujanian Mylodontid ground sloths. *Journal of Vertebrate Paleontology* 20, 601–610.
- Blanco, R.E. 2008: The uncertainties of the largest fossil rodent. *Proceedings of the Royal Society of London* 275, 1957–1958.
- Bondesio, P. 1978: La presencia del género *Carlesia* (Rodentia, Dinomyidae, Eumegamyninae) en la formación Arroyo Chasicó (Plioceno Temprano), Provincia de Buenos Aires. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia' 2*, 198–206.
- Christiansen, P. 2007: Evolutionary implications of bite mechanics and feeding ecology in bears. *Journal of Zoology* 272, 423–443.
- Christiansen, P. & Wroe, S. 2007: Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology* 88, 347–358.
- Collins, L.R. & Eisenberg, J.F. 1972: Notes on the behaviour and breeding of pacaranas (*Dinomys branickii*) in captivity. *International Zoo Yearbook* 12, 108–114.
- Cooper, G. & Schiller, A.L. 1975: *Anatomy of the Guinea Pig*, 417 pp. Harvard University Press, Cambridge.
- Druzinsky, R.E. 2010a: Functional Anatomy of incisal biting in *Aplodontia rufa* and sciuriform rodents-Part1: masticatory muscles, skull shape and digging. *Cells Tissues Organs* 191, 510–522.
- Druzinsky, R.E. 2010b: Functional Anatomy of incisal biting in *Aplodontia rufa* and sciuriform rodents-Part 2: Sciuriformity is efficacious for production of force at the incisors. *Cells Tissues Organs* 192, 50–63.
- Edgeworth, W. 1935: *The Cranial Muscles of the Vertebrates*, 493 pp. Cambridge University Press, Cambridge.
- Ellis, J.L., Thomason, J.J., Kebreab, E. & France, J. 2008: Calibration of estimated biting forces in domestic canids: comparison of post-mortem and *in vivo* measurements. *Journal of Anatomy* 212, 769–780.
- Fernández de Alvarez, E. 1958: Sobre nuevos restos de Eumegamysops praependens (Amegh.) Kragl. *Revista de la Asociación Geológica Argentina* 13, 87–104.
- Freeman, P.W. & Lemen, C.A. 2008: A simple morphological predictor of bite force in rodents. *Journal of Zoology* 275, 418–422.
- Greaves, W.S. 1995: Functional predictions from theoretical models of the skull and jaws in reptiles and mammals. In Thomason, J. (ed.): *Functional Morphology in Vertebrate Paleontology*, 1–277. Cambridge University Press, Cambridge.
- Kraglievich, L. 1926: Los grandes roedores terciarios de la Argentina y sus relaciones con ciertos géneros pleistocenos de las Antillas. *Anales del Museo Nacional de Historia Natural* 34, 121–135.
- Kraglievich, L. 1930: Descripción de un interesante roedor eumegámido descubierto en el Uruguay. *Gyriabruss teisseirei*, n. sp. *Revista de la Sociedad de Amigos de la Arqueología* 4, 21–224.
- Kraglievich, L. 1932: Diagnósis de nuevos géneros y especies de roedores cávidos y eumegámidos fósiles de la Argentina. Rectificación genérica de algunas especies conocidas y adiciones al conocimiento de otras. *Anales de la Sociedad Científica Argentina* 114, 155–181 211–237.
- Lessa, E.P. & Patton, J.L. 1989: Structural constraints, recurrent shapes, and allometry in pocket gophers (genus *Thomomys*). *Biological Journal of the Linnean Society* 36, 349–363.
- Lessa, E.P. & Stein, B.R. 1993: Morphological constraints in the digging apparatus of pocket gophers (Mammalia: Geomyidae). *Journal of the Linnean Society* 47, 439–453.
- McHenry, C.R., Wroe, S., Clausen, P.D., Moreno, K. & Cunningham, E. 2007: Supermodeled sabercat, predatory behavior in *Smilodon fatalis* revealed by high-resolution 3D computer simulation. *Proceedings of the National Academy of Sciences* 104, 16010–16015.
- Meers, M.B. 2002: Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behaviour. *Historical Biology* 16, 1–12.
- Millien, V. 2008: The largest among the smallest: the body mass of the giant rodent *Josephoartigasia monesi*. *Proceedings of the Royal Society of London* 275, 1953–1955.
- Mones, A. 1986: Palaeovertebrata Sudamericana. Catálogo Sistemático de los Vertebrados Fósiles de América del Sur. Parte I. Lista preliminar y bibliografía. *Courier Forschungsinstitut Senckenberg* 82, 1–625.

- Mones, A. 1997: Estudios sobre la familia Dinomyidae, II. Aportes para una osteología comparada de *Dinomys branickii* Peters, 1873 (Mammalia: Rodentia). *Comunicaciones Paleontológicas del Museo Nacional de Historia Natural de Montevideo* 29, 1–40.
- Naples, V. 1987: Reconstruction of cranial morphology and analysis of function in the Pleistocene ground sloth *Nothrotheriops shastense* (Mammalia, Megatheriidae). *Contributions in Science* 389, 1–21.
- Nies, M. & Ro, J.Y. 2004: Bite force measurement in awake rats. *Brain Research Protocols* 12, 180–185.
- Pascual, R. 1967: Familia Dinomyidae. In Borrello A.V. (ed.): *Paleontografía Bonaerense*, 123–127. Comisión de Investigación Científica, volumen 4 (Vertebrata), La Plata.
- Paula Couto, C. de. 1951: Uma espécie do género *Tetrastylus* Ameghino, 1886, em Lagoa Santa. *Boletim do Museu Nacional (nova série, Geologia)* 15, 1–16.
- Pocock, R.I. 1926: The external characters of a young female *Dinomys branickii* exhibited in the Society's Gardens. *Proceedings of the Zoological Society of London* 96, 221–230.
- Rinderknecht, A. & Blanco, R.E. 2008: The largest fossil rodent. *Proceedings of the Royal Society of London* 275, 923–928.
- Saban, R. 1968: Musculature de la tête. In Grassé P.P. (ed.): *Traité de Zoologie*, 1–870. Masson & Cie, Paris.
- Sanborn, C.C. 1931: Notes on *Dinomys*. *Field Museum of Natural History, Zoological Series* 18, 149–155.
- Schulman, G. 1906: Ubre die ventrale Facialmuskulatur einiger Säugetiere, besonders der Monotremen. *Festschrift für Palmen* 18, 4–67.
- Shipley, L.A., Illius, A.W., Danell, K., Hobbs, N.T. & Spalinger, D.E. 1999: Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. *Oikos* 84, 55–68.
- Therrien, F. 2005a: Mandibular force profiles of extant carnivorans and implication for the feeding behaviour of extinct predators. *Journal of Zoology* 267, 249–270.
- Therrien, F. 2005b: Feeding behaviour and bite force of sabre-toothed predators. *Zoological Journal of the Linnean Society* 145, 393–426.
- Thomason, J.J. 1991: Cranial strength in relation to estimated biting forces in some mammals. *Canadian Journal of Zoology* 69, 2326–2333.
- Tullberg, T. 1899–1900: Ueber das System der Nagethiere: Eine Phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 18, 1–514.
- Turnbull, W.D. 1970: Mammalian masticatory apparatus. *Fieldiana (Geology)* 18, 149–356.
- Turner, A. & Antón, M. 1996: *The Big Cats and Their Fossil Relatives*, 234 pp. Columbia University Press, New York.
- Vizcaíno, S.F. & De Iuliis, G. 2003: Evidence for advanced carnivory in fossil armadillos (Mammalia: Xenarthra: Dasypodidae). *Paleobiology* 29, 123–138.
- Vizcaíno, F.S., Zárate, M., Bargo, M.S. & Dondas, A. 2001: Pleistocene burrows en the Mar del Plata area (Argentina) and their probable builders. *Acta Paleontológica Polonica* 46, 289–301.
- White, T.G. & Alberico, M.S. 1992: *Dinomys branickii*. *Mammalian Species* 410, 1–5.
- Windle, B.C.A. & Parson, F.G. 1899: On the myology of the Edentata. *Proceedings of the Zoological Society of London* 1, 314–339 2, 990–1917.
- Woods, C.A. & Hermanson, W. 1985: Myology of Hystricognath rodents: an analysis of form, function, and phylogeny. *NATO ASI Series, (A: Life Sciences)* 92, 515–548.
- Wroe, S., McHenry, C. & Thomason, J.J. 2005: Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society of London, B* 272, 619–625.
- Zárate, M.A., Bargo, M.S., Vizcaíno, S.F., Dondas, A. & Scaglia, O. 1998: Estructuras biogénicas en el Cenozoico tardío de Mar del Plata (Argentina) atribuibles a grandes mamíferos. *AAS Revista* 5, 95–103.