STRUCTURAL ASSESSMENT OF ARCH-LIKE BONES: RODENTS' JAW AS A CASE STUDY

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ABSTRACT

Bone strength is determined by the mechanical properties of bone material, and the size and shape of the whole bone, *i.e.* its architecture. The mandible of vertebrates has been traditionally regarded as a beam oriented in relation to main masticatory loads, *i.e.* the longer dimension of its cross section being parallel to the load. Rodents follow this pattern but, in addition, their mandible possesses an intriguing arch-like shape that is apparent when seen in the lateral view. Little attention was given to the structural capacity of this trait. The central feature of an arch is that it can withstand a greater load than a horizontal beam. The objective of this study was to modeling the rodent mandible like an arch to evaluate its structural strength. The bending moment in an arch-like mandible was 15 to 25 % lower with respect to a beam-like mandible. Further, bending varies with mandible “slenderness” and incisor procumbency, a functionally relevant rodent trait. In the rodent *Ctenomys talarum* (Caviomorpha; Ctenomyidae), bone stress was substantially reduced when the mandible was modeled as an arch-like structure as compared with a beam-like structure, and safety factors were 11-34 % higher. The shape of rodents’ mandible might

work as an adaptation to high and repeatedly applied loads resulting from a unique feeding mode: gnawing.

Key words: bone architecture; mandible; *Ctenomys*; biomechanics; Rodentia

INTRODUCTION

Not infrequently, biological structures and certain man made devices share a common design due to restrictions imposed by physical laws. For example, the mandible of vertebrates can be regarded as a beam of expected orientation in relation to main loads imparted by teeth and muscles, namely the longer dimension of its cross section being parallel to the load (*e.g.* Hildebrand and Goslow, 2001). The mandible of rodents follows this general pattern but, in addition, it possesses an intriguing arch-like shape that is apparent when seen in the lateral view. Indeed, the rodent mandible seems to be "designed" following the shape of the elongated incisor roots which in some instances reach the proximity of the condyle (Cox and Hautier, 2015). While curved, ever-growing incisors for gnawing have been the subject of numerous studies (Ungar, 2010), little attention has been given to the structural capacity and distinctive architecture of rodent mandible. This is an important issue since it is subjected to both high and repeatedly applied loads resulting from a unique feeding mode: gnawing.

The mandible of vertebrates functions as a third-order lever: the in force and out-force are on the same side of the pivot (mandible articulation), being the out-force farther to the pivot than the in-force. During food processing, bending of the mandible mainly in the vertical plane results from this anatomical configuration (Fig.1). As other bones, the mandible must have adequate structural strength to withstand the stresses to which it is subjected during mastication (*e.g.* Thomason, 1991; Wroe and Milne, 2007; Cox et al., 2012). The strength of bones is determined by two different attributes, the mechanical properties of the bone material *per se*, and the size and shape of the whole bone, *i.e.* its architecture (Currey, 2006). This study focuses on the architecture of the mandible in rodents, one of the most speciose groups of mammals which also evolved a highly specialized masticatory apparatus (Feldhamer et al., 2007).

The central feature of an arch-like structure is that it can withstand a much greater load than a horizontal beam can support. This capacity results from the fact that a load applied on an arch has the effect of forcing the material together instead of apart thus eliminating tensile stresses (*e.g.* Curcio, 1968; Ambrose and Tripeny, 2012). Bone can resist compression but is weak when tensile stresses are applied to it (Currey, 2006). Hence, the hypothesis is proposed herein that the arch-like shape of rodents' mandible might work as an adaptation to increase strength against loads imparted by muscle action and reaction forces on teeth. Under this hypothesis it could be predicted structural material savings (*e.g.* bone) in the rodent mandible.

The other major feature, well known by former builders and architects, is that the slenderness of an arch-like structure (*i.e.* the quotient between *span* and *rise*; Fig. 2) affects its strength (O'Connor, 1994; Benaim, 2008). The "slenderness" of rodents' mandible is affected by incisor procumbency: how incisors are directed outward. Hence, follow the second hypothesis of the present study: incisor procumbency and mandible slenderness could affect its strength by changing the bending moment acting upon the rodent mandible.

To test these hypotheses, the objectives of this study were: 1) To model the mandible of rodents as an arch-like structure in order to evaluate its structural strength, and to compare it with that of a beam–like mandible; 2) Analyze the relationship between incisor procumbency, mandible slenderness and bending moment; 3) To assess the structural strength for a real case, a mandible belonging to the chisel-tooth digging rodent *Ctenomys talarum*, for which there are measurements of bite force; and finally 4) To compare the amount of bone present in the mandible of different rodent species with other mammals.

MATERIAL AND METHODS

Modeling the rodent mandible like an arch.- The form of the rodent mandible, considering the hemi mandible in lateral view, was assumed to be a semicircular arch. The distance between the mandibular condyle and the tip of the incisor is, architecturally speaking, the *span* of an arch (Fig. 2). The maximum height of the mandible (*i.e.* the distance between the line connecting the condyle and the tip of the incisor, and the farthest point of the mandibular corpus in lateral view (Fig. 2) is assumed to be the *rise* of the arch (Benaim, 2008). The anterior *abutment*, which provides the thrust reaction force (Fig. 2) is supplied by the substrate/food being gnawed whereas the posterior is supplied by the glenoid fossa (thrust: the outward force exerted by an arch, Curcio, 1968).

In order to compare the strength of a rodent mandible to that of a theoretical beam-like mandible it was assumed that the type of bending to which the mandible is subjected consists of a *three point bending*, that is the in-force and out-force are on the same side of the pivot (mandibular articulation). Consequently, the method of sections and its equations of equilibrium (for example Ozkaya and Nordin, 1999) were used to calculate forces, moments, and stresses (see below).

$$\text{bending in a beam (section a)} = x \cdot R \qquad (1)$$

Where the bending in a beam is the product of the reaction force R at one end of the beam multiplied by distance to the section to being analyzed, x (Fig. 3).

In order to estimate the bending moment of different sections of the mandible when it is modeled as an arch, the following equation (Curcio, 1968) was used:

$$\text{bending in an arch (section a)} = \text{bending in a beam (a)} - HTR \cdot h \qquad (2)$$

Where HTR is the horizontal component of thrust reaction force TR which was trigonometrically calculated as: $HTR = TR \cdot \cos \alpha$ (α = angle determined by the tangent line at the incisor tip and the line connecting the incisor tip with the condyle; Fig. 2); h is the height of the arch in the section (a) (Fig. 3).

Though other values can be chosen, in the present analysis the mandibular span was set at 40 mm. The mandible was under a reaction force of 20 N applied upon the incisor. This value was chosen because it matches with those experimentally measured in living specimens using a bite force transducer (Becerra et al., 2011; 2013). The total length of the beam was the same as for the mandibular span, 40 mm. The height of the arch (h) at two sections, one quarter (10 mm) and in the middle (20 mm), were trigonometrically assessed.

Because muscle load is much greater than mandible mass, in the present analysis it was assumed that the weight of the mandible is negligible regarding to the production of bending.

Analyzing the relationship between incisor procumbency and bending moment.- Incisor procumbency (equivalent to angle α in Fig. 2) affects "mandibular slenderness", i.e. the quotient rise/span, and this in turn could affect bending moment through changing the direction of thrust (Benaim, 2008). For different values of incisor procumbency, within the range measured in different rodent species (Table 1), bending moments were estimated using equation (2). The relationship between incisor procumbency angle α and measurements of the mandibular arch is given by the following equation, which was obtained by deriving the function *arch of circle* in its intersection with the abscissa (which coincides with the line connecting the incisor tip and the condyle):

$$\alpha = \text{Procumbency angle} = \arctan\left(\frac{s}{\sqrt{\left(\frac{s^2}{8r}+\frac{r}{2}\right)^2-\frac{s^2}{4}}}\right) \qquad (3)$$

Where *s* is span (or condyle-incisive length) and *r* is rise (or maximum height of the mandible) (Fig. 2).

Lower incisor procumbency (angle α in Fig. 2) in the studied rodent species was calculated using equation (3). For this aim, the distance between the mandibular condyle and the tip of the incisor (= *span*), and the maximum height of the mandible (= *rise*) were measured using a digital calipers (0.01 mm).

Assessing the structural strength for a real case, the mandible of Ctenomys talarum.- Tensile and compression stress in a *C. talarum* (Thomas, 1898; Rodentia; Ctenomyidae) mandible, resulting from an incisor bite, were compared assuming an arch-like versus a beam-like structure of the same length. The mandible of an adult specimen of the species *C. talarum*, body mass 153 g, was scanned at Embrapa (San Pablo, Brasil; www.embrapa.br), using a Bruker microCT Skyscan1172. The distance between the mandibular condyle and the tip of the incisor (span) was of 30.2 mm. A series of 1860 projections were recorded covering 360° resulting in voxel sizes of 22 μmm. Reconstruction of the tomographic projection data was done using the NRecon Reconstruction 64-bit package (http://www.skyscan.be/). Different sections (Fig. 5) along the mandible, including the incisor, mandibular corpus, and angular process, were selected to estimate their structural strength. The section modulus of these mandible sections (dental roots were included) were assessed using the Moment Macro application of ImageJ 1.41 by W. Rasband—National Institute of Health, rsb.info.nih.gov/i. Stress in the selected sections were calculated using the equation (Alexander, 1989):

$$\text{Stress} = \frac{\text{bending moment}}{\text{section modulus}} \quad (4)$$

Estimations of bending moment in the selected sections were based upon biting forces experimentally measured in adult specimens (Becerra et al., 2011). As in other rodent species, *C. talarum* possesses a complex array of jaw adductor muscles which exert distributed loads at different locations of the mandible. For simplicity, based upon published anatomical studies (Woods, 1972; Vassallo, 1998), a common resultant of muscle forces was positioned one third of the distance from the condyle to the incisor tip (Fig. 5), hence a punctual load was assumed in the analysis. Reaction forces at the incisor and mandibular condyle were 19.1 N (Table 3 in Becerra et al., 2011) and 43.2 N, respectively, equilibrated by a jaw adductor force of 62.3 N (Fig. 5). These values were derived based upon the rotational equilibrium equation:

$$R_I \cdot M_I = MF \cdot M_M \quad (5)$$

Where R_I is the reaction force at incisor, M_I is the moment arm of R_I, MF is the assumed overall resultant of adductor muscle force and M_M is its moment arm (Fig. 5).

Safety factors were calculated using published values of ultimate strength of bone (133 MPa in tension; 193 MPa in compression; Currey, 2006) and dividing by stress values estimated for the different mandible sections (Alexander, 1989; Ozkaya y Nordin, 1999). It was assumed that the material properties of bone are constant along the length of the mandible.

Comparing the amount of bone in the mandible of rodents and other mammals.- A first approach to assess the amount of bone material present in the mandible of different mammal species, searching for possible structural material savings, can be done by weighing cleaned mandibles and using some measure of mandible size, for example the condyle-incisive length. These two variables were measured in museum specimens belonging to different mammalian species. One to four adult specimens of the following species housed in the Museo Municipal de Ciencias Naturales Lorenzo Scaglia (Mar del Plata; Argentina) were measured: Rodentia: Fam. Caviidae: *Cavia pamparum*; *Kerodon rupestris*; *Galea musteloides*; *Dolichotis pataginum*; *Hydrochoerus hydrochaeris; Microcavia australis*; Fam. Myocastoridae: *Myocastor coipus*; Fam. Chinchillidae: *Lagostomus maximus*; *Chinchilla lanigera*; Fam. Octodontidae: *Octodon degus*; *Spalacopus cyanus*; Fam. Ctenomyidae: *Ctenomys talarum*; *C. tuconax*; Fam. Cricetidae: *Akodon azarae*. *Holochilus brasiliensis*; *Scapteromys* sp.; Fam. Geomyidae: *Thomomys bottae*. Other mammal species: *Canis familiaris*; *Felis catus*; *Cerdocyon thous*; *Lycalopex gymnocercus*; *Oncifelis geofroyii*; *Galictis cuja*; *Mephitis mephitis*; *Conepatus chinga*; *Puma concolor*; *Panthera onca*; *Herpailurus yagouaroundi*; *Otaria flavescents; Leptonychotes weddellii*; *Tayassu pecari*; *Ozotoceros bezoarticus*; *Ovis aries*; *Dasypus* *hybridus*; *Callithrix* sp.; *Didelphis albiventris*. The amount of bone material in the studied species was assessed and compared by regression analysis assuming Model II (standardised major axis regression, SMA) (Sokal and Rohlf 1995; Warton et al., 2006) using the software SMATR (Falster et al., 2006).

RESULTS

Arch-like vs. beam-like mandibles.- Depending on the location of the section being analyzed, reduction in the bending moment in an arch-like mandible with respect to a beam-like mandible can reach 15-25 % for mandibles approaching 70° of incisor procumbency (Fig. 4b).

Effect of procumbency.-The bending moment acting on a rodent mandible modeled as an arch varies with incisor procumbency which affects mandible slenderness. The lowest values of bending occur near 60° of incisor procumbency (Fig. 4a). As shown in Table 1, the species *Dolichotis patagonum*, whose lower mandible is shaped as a slender arch, is near this value of procumbency. The bending moment increases when procumbency approaches 90°. Hence, the mandible of *Octodon degus* and *Myocastor coipus* (Table 1) may experience the highest values of bending moment. (Fig. 4).

Structural strength for a real case.- The cross section of the mandible of the rodent *C. talarum*, at different places along it, varies both in shape as well as in bone thickness (Fig. 5). Estimated values of tension and compression stress vary from 5 to 40 MPa depending on the section considered (Table 2). The stress values were 13-25 % lower when the mandible was modeled as an arch-like structure as compared with a beam-like structure. Accordingly, safety factors were 11-34 % higher when the mandible was modeled as an arch (Table 2).

Saving of structural material.- Although there is considerable overlap between data points, the amount of bone present in the mandible seems to be lower in species of rodents, especially those of smaller body size, as compared with the sample of mammals. In fact, the y-intercept of rodents' fitted line was lower than that of other mammals (Fig. 6). A test for common slope across groups produced significant differences (P=0.03) between SMA regressions of rodents *vs.* other mammals.

DISCUSSION

Analyzing the capacity to avoid structural failure of different skeletal parts has been the focus of recent research on evolutionary morphology (Soons et al., 2010). The mandibular apparatus of rodents, which is adapted to process hard food items, is particularly capable of producing strong bite forces (Van Daele et al., 2009; Becerra et al., 2012; Vassallo and Antenucci, 2015). Therefore it must be able to withstand large reaction forces received on incisors, molars, and jaw condyle. Further, due to repeated loading resulting from gnawing, fatigue can be expected in different regions of the skull and mandible. In line with this, there is evidence that in the blind mole-rat *Myospalax*, continuous physical pressures of digging on incisors lead to cell and tissue fatigue, resulting in perforation of the palatal bone in ageing individuals (Zuri and Terkel, 2001). How the loads transmitted to the bones in different regions of the skull and mandible resisted during chewing? As stated above, the mechanical properties of biological materials are, *per se*, an important factor in bone strength (Currey, 2006). For example, it has been shown that adaptive changes in the incisor enamel microstructure are related to the use of the incisors to dig in certain rodent species, a behavior known as chisel-tooth digging (Vieytes, 2007). Energy absorption by viscoelastic cranial sutures is another mechanism to withstand the loads produced during chewing (Herring, 2008). On the other hand, the size and shape of the bone itself, *i.e.* its architecture, is the other factor involved in structural strength (*e.g.* Rayfield et al., 2001).

The objective of this study was to model the rodent mandible like an arch in order to evaluate its structural strength. The results show that the bending moment may be substantially reduced in a mandible if it has an arch-like shape rather than a beam–like shape. Depending on the mandible section being considered, and taking into account interspecific variation in “incisor procumbency-arch slenderness”, the reduction in bending moment can reach values between 15-25 %. This fact is consistent with the hypothesis that the arch-like shape of rodents’ mandible might work as an adaptation to increase strength against loads imparted by both muscle action, and reaction forces on teeth.

Ecological and behavioral factors affect rodents’ incisor procumbency. For example, the incisors of subterranean tooth-digging rodents are strongly projected forward to improve the angle of attack against the soil (Mora et al., 2003). Table 1 shows that mandibular incisor procumbency, in different rodent species, vary between 90 to 70 degrees. This fact determines, at one end, a mandible which resembles a semicircular *roman* arch (incisor procumbency = 90°) or, at the other end, the shape of a slender arch (incisor procumbency ~ 70°). Results in Fig. 4 show that slender rodent mandibles probably experience lower bending stresses. It has been shown that the reduction of bending moment in slender architectural arches is due to an increase in the horizontal component of thrust (see Fig. 2, 3; Curcio, 1968).

Contrary to what happens with an architectural arch where the size and shape of its cross section remains approximately constant throughout, all along the mandible of *Ctenomys*, and presumably in other mammals, the amount of bone that must withstand loads varies greatly (Fig. 5). In the anterior part of the mandible it is formed solely by the incisor (Fig. 5 section a), while at the level of diastema the incisor is surrounded by alveolar bone (Fig. 5 section b). The cross section of the mandible is massive where it houses the roots of the molars and incisors (Fig. 5 section c), contrary to the thin angular process (Fig. 5 section d). Given this variation in the amount of bone in different sections of the mandible, estimated values of tension and compression stress (calculated based on experimentally obtained bite forces from Becerra et al., 2011) vary between 5.4 to 40.9 MPa (compression), and 5.4 to 42.6 MPa (tension) (Table 2). Safety factors calculated at sections corresponding to the incisor and angular process were lower than those for the diastema and mandibular corpus where the cross section of the mandible is massive. In general, estimated safety factors in *Ctenomys* mandible (range 6.9-28.3) were greater than to those obtained by Thomason and Russell (1986) for the rostrum of the marsupial *Didelphis* (range 1.8-11). Maybe this difference is related to the fact that, in addition to strong bite events, the mandible of rodents would confront fatigue due to repeated loading from gnawing. In both studies safety factors were greater than those calculated for long-bones, which vary from 1.4 to 5 according to a study by Biewener (1983).

The significant differences observed in the amount of bone present in the mandible of different rodent species (arch-like mandibles) with respect to other mammalian species (beam-like mandibles) (Fig. 6) indicate that in the former, there would be bone material savings which is what might be expected under the arch hypothesis. This is a striking fact because the data available so far indicate that rodents, despite their relatively small size, are among the mammals capable of exercising proportionately higher bite forces (*e.g.* Becerra et al., 2014) and, consequently, the mandible and other cranial structures must withstand high loads. Here it was shown that an arch shaped mandible can convert these high loads in relatively lower bending moments.

CONCLUSIONS

Some researchers have drawn attention to the curvature of certain bone elements, and its functional implications. For example, Bertram and Biewener (1988) suggests that the longitudinal curvature that characterize the long bones of terrestrial mammals increases the predictability of the pattern and distribution of stresses compared with straight long bones, which is of importance to cope a highly variable loading environment. A reduction of the bending moment might be an important factor influencing the design of bone subjected to both high and repeatedly applied loads. Arch-shaped bones might be found in vertebrate species more often than usually thought (Cubo et al., 1999; Macintosh et al., 2015). It is worth noting that it is not necessary that a structure possess a pure geometrical form (*e.g.* parabola, catenary, semicircular) to perform as an arch (Benaim, 2008). Therefore, this analysis could be extended to the study of bone morphology and its mechanical properties in other vertebrate species.

ACKNOWLEDGMENTS

I thank Philip Cox and Nick Milne for comments on earlier drafts, to Federico Becerra for his help with section modulus estimations, and to Adriá Casinos for discussions. Financial support PIP 2014-2016 from CONICET.

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FIGURE LEGENDS

Fig. 1 Carnivore mandible (Felidae) subjected to three point bending. The mandible is shown turned upside down for ease of comparison with a beam. M: temporalis muscle force (for simplicity, the line of action is sketched vertically); MC: mandibular condyle; R_C: reaction force at the canine; R_{MC} : reaction force acting upon the mandibular condyle. Note that the in-force (M) and out-forces exerted by dental elements are on the same side of the pivot (mandibular condyle), a condition known as third-order lever. Insert: complete skull with mandible.

Fig. 2 The mandible of rodents modeled like an arch. A mouse mandible is shown turned upside down to highlight the analogy with the arch in architecture. TR: thrust reaction force; HTR and VTR: horizontal and vertical components of thrust reaction force, respectively; AP: angular process; MC: mandibular condyle. α = incisor procumbency: angle determined by the tangent at incisor tip. Photography on the left: *Casa del Puente*, by Architect Amancio Williams, City of Mar del Plata, Argentina.

Fig. 3 Forces and parameters producing bending in an arch and a beam. “a”: section in which the bending stress is analyzed; x: distance between section "a” and the end of the arch or beam; h: arch height in the section “a”. R: reaction force. TR, HTR and VTR: ibid Fig. 2.

Fig.4 a: Bending moment in an arch-like rodent mandible under a reaction force of 20 N resulting from an incisor bite, at one quarter (10 mm) and at half of its length (20 mm). Condyle – incisive length = 40 mm (see Methods). b: Reduction (%) in bending moment in an arch-like mandible with respect to a beam-like mandible. Rectangle: reduction in bending for the range of measured incisor procumbencies in Table 1.

Fig. 5 Mandible of *Ctenomys talarum* and cross sections taken into account to estimate tension and compression stresses. 4, 7, 13 and 26 mm: distances from the tip of the incisors to each section. Sections: a, incisor; b, diastema; c, molars; d, angular process. R_I: reaction force at incisor; R_{MC}: reaction force at mandibular condyle; MF: adductor muscle force resultant. M_I and M_M are the moment arms of R_I and MF, respectively. Scale bar: 1 cm.

Fig. 6 Amount of bone material present in the mandible of different mammal species. A common slope test yielded significant differences (P=0.03) between the regression of rodents *vs*. other mammals.

Fig. 1

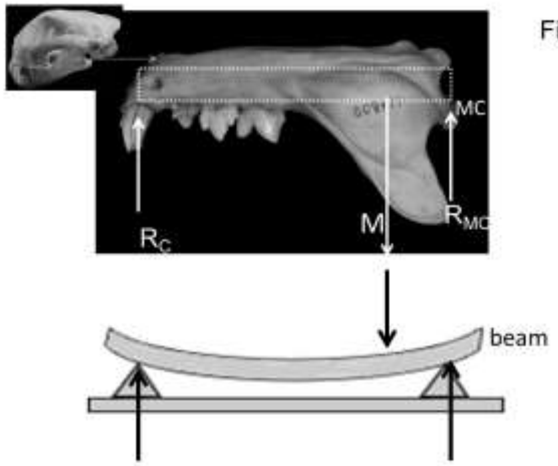


Fig. 2

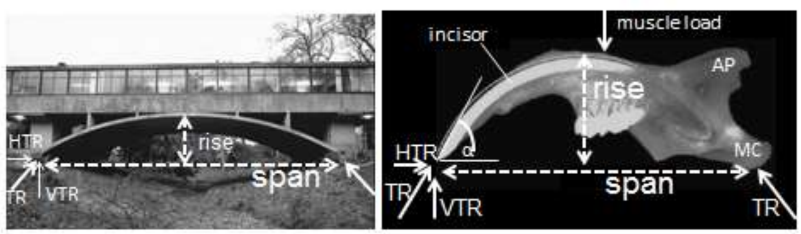
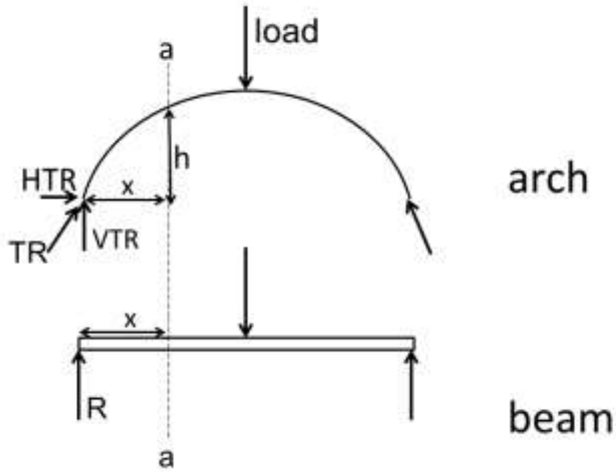
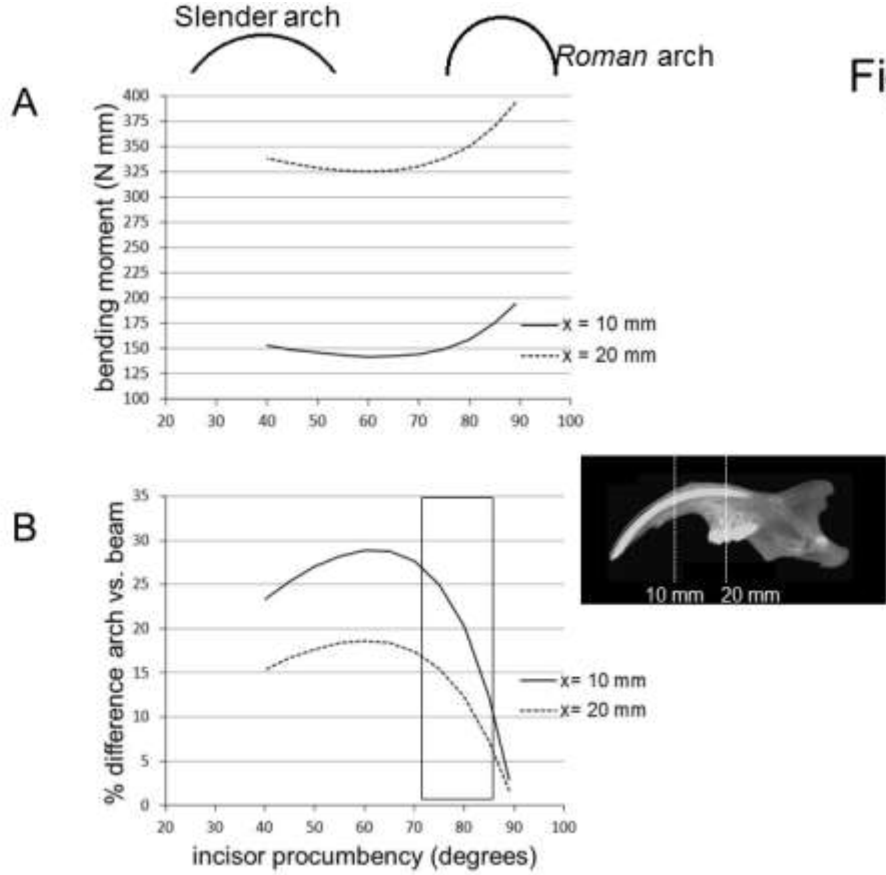


Fig. 3

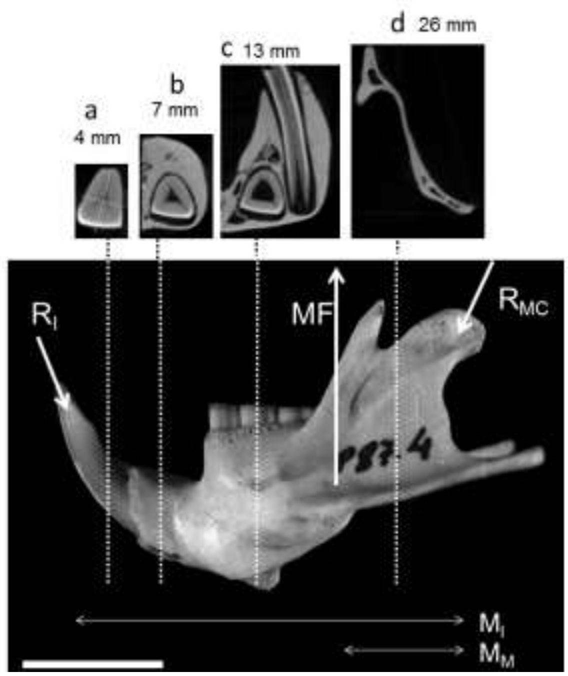




Slender arch
Roman arch
A
bending moment (N mm)
x = 10 mm
x = 20 mm
B
% difference arch vs. beam
x= 10 mm
x= 20 mm
incisor procumbency (degrees)
10 mm
20 mm

Fig. 4

Fig. 5



a
4 mm
b
7 mm
c 13 mm
d 26 mm
R_I
MF
R_MC
M_I
M_M

Fig. 6

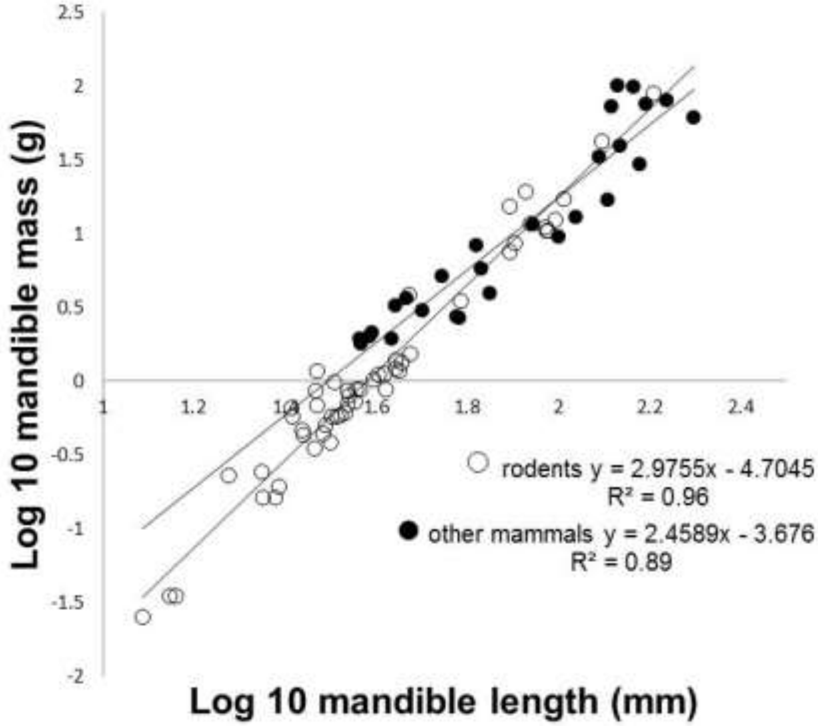

2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
1
1.2
1.4
1.6
1.8
2
2.2
2.4
Log 10 mandible mass (g)
Log 10 mandible length (mm)
rodents y = 2.9755x - 4.7045
R² = 0.96
other mammals y = 2.4589x - 3.676
R² = 0.89

Table 1. Measurements of arch curvature and incisor procumbency in the mandible of different rodent species. Condyle-incisive length, and maximum height of the mandible = *span* and *rise* of the mandibular arch, respectively (see Fig. 2). * lagomorpha ** values supplementary to *Thomas' angle* (Landry 1957).

Species	Condyle-incisive length (mm)	maximum height of the mandible (mm)	Incisor procumbency (degrees)**
Dolichotis patagonum	93.7	24.6	71°
Myocastor coipus	84.6	32.8	82.7°
Lagostomus maximus	78.2	22.1	73.3°
Chinchilla lanigera	43.7	13.2	74.6°
Octodon degus	26.1	11	85.1°
Hydrochoerus hydrochaeris	180	55	75.6°
Cavia aperea	42.6	13.6	77°
Ctenomys talarum	29.7	10.9	81.1°
Akodon azarae	16.2	5.1	76.3°
*Oryctolagus cuniculus**	75	23	75.7°

Table 2.- Stress experienced at different sections (a, b, c, d; see Fig. 5) of a rodent mandible (*Ctenomys talarum;* Caviomorpha; Ctenomyidae), and percentage difference assuming a beam versus arch-like structure for the jaw. Safety factors based upon bone ultimate strength of 133 MPa (tension) and 193 MPa (compression) (Currey, 2006).

Jaw section		4 mm a			7 mm b			13 mm c			26 mm d		
		beam	arch	%	beam	arch	%	beam	arch	%	beam	arch	%
Stress	Tension (MPa)	25.7	19.2	25.3	10.2	8.2	19.6	6.2	5.4	12.9	57.2	42.6	25.5
	Compression (MPa)	20.9	15.6		10.1	8.1		6.3	5.4		55.0	40.9	
Safety factor	Tensión	5.2	6.9	32.7	13.1	16.3	24.4	23.9	26.6	11.3	2.3	3.1	34.8
	Compression	9.2	12.4		19.2	23.9		25.4	28.3		3.5	4.7	