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MANDIBULAR ALLOMETRY IN *HYDROCHOERUS HYDROCHAERIS* (LINNAEUS, 1766) (HYDROCHERINAE, CAVIIDAE)

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ABSTRACT

The mammalian masticatory apparatus is a highly plastic region of the skull and thus subjected to singular ontogenetic trajectories. Here we present the first descriptive allometric pattern study of mandible among the capybara (Hydrochoerus hydrochaeris), based on the study of 37 specimens. Allometric changes in shape were analyzed using geometric morphometrics techniques and the pattern of allometry was visualized. A multivariate regression of the shape component on size, estimated by the logarithm of centroid size, appeared as highly significant. Therefore, a major component of shape variation in these mandibles is related to the attainment of adult size (i.e., growth).

KEY-WORDS: Capybara; Jaw; Ontogeny; Rodentia; Scaling.

INTRODUCTION

Being the mammalian masticatory apparatus a highly plastic region of the skull, rodents are some of the most highly specialized mammals in this respect (Hautier *et al.*, 2011). A defining characteristic of rodents is the grossly enlarged pair of incisors, seen in both the upper and lower jaws, which are open-rooted and continue to grow throughout life (Hautier *et al.*, 2011). These specializations, plus a small number of cheek teeth used for chewing, are associated with a specialized musculature (Schumacher, 1961). To cope with the demands imposed by such an unusual dentition and propaliny (*e.g.*, the mandible can be moved fore and aft) (Cox *et al.*, 2012), the masticatory musculature of rodents has become highly specialized. The masseter is the dominant jaw-closing muscle, forming between 60% and 80% of the masticatory musculature (Sisson *et al.*, 1982), and is divided into

three layers in rodents: the *musculus masseter* (with a *pars superficialis* and a *pars profunda*) and the *musculus zygomaticomandibularis* (sometimes termed the medial masseter).

Rodents have two feeding modes, gnawing at the incisors and chewing at the molars, but owing to a mismatch between the cranial and mandibular lengths, the incisors and molars cannot be in occlusion at the same time (Jamniczky & Hallgrímsson, 2009; Tagliaro *et al.*, 2009). Thus, the two feeding modes are mutually exclusive, and the mandible must be moved anteriorly and posteriorly with respect to the cranium.

Variations in the masseter complex, and the associated modifications of the skull, have traditionally been used as diagnostic characters to classify rodents (Parés-Casanova *et al.*, 2015). The masseter extends its origin onto the rostrum and this can be done in one of three ways, referred to as sciuroomorphy,

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hystricomorphy and myomorphy. Differences of muscle and skull morphology between the three groups confer benefits or costs on biomechanical performance (e.g., biting efficiency) (Panchetti *et al.*, 2008). The hystricomorphs, encompassing South American rodents plus some Old World forms such as porcupines, jerboas and capybara, have extended the zygomaticomandibularis muscle up through the orbit and anteriorly on to the rostrum through the enlarged infraorbital foramen. Its morphology produces a more effective grinding action at the molars.

Despite a recent revival of developmental studies investigating the early development and patterning of the cranial musculature in mammals (Smith, 2006; Goswami, 2006; Wilson & Sánchez-Villagra, 2011) little is known about the late development and post-natal growth of the cranial system (but see, e.g., Abdala *et al.*, 2007), and even less about the development of the associated musculature (Wainwright *et al.*, 1976; Dias *et al.*, 2011). From a functional perspective, however, such studies can provide profound insights into the selective patterns operating during early ontogeny, which ultimately determine the adult form of an organism (e.g., Herrel *et al.*, 2008) and may help to understand the systematic position of taxa characterized by highly derived anatomical features.

Morphometrics is defined as the quantitative description, analysis and interpretation of shape and variation of structures in biology (Richtsmeier *et al.*, 2002; Galan, 2016). In a fundamental area of research, unlike the analytical approaches, the geometric one is aimed at comparison of the shapes (Reyment, 2010). Moreover, morphometric studies have played an important role in resolving taxonomic problems (Cardini & Thorington, 2006).

By using the geometric morphometric approach, variation in form can be captured and the allometric and non-allometric components can be disentangled (Zelditch *et al.*, 2012). In this study, we analyzed patterns of allometric variation in mandible size and shape of a hystricomorph species, *Hydrochoerus hydrochaeris*, the capybara, the largest member of the order *Rodentia*.

The capybara is a semi-aquatic rodent of South America (Cueto, 1999). Adult weighs from 27 to 79 kg, and is up to 50 cm tall and 100-130 cm in length (Cueto, 1999; Chacón *et al.*, 2013). It is found from Panama Canal through northeastern Argentina (Cueto, 1999; Ulloa, 2005). It is a selective grazer preferring grasses, but also including aquatic vegetation, grains, melons and squashes (Ulloa, 2005). Three species of capybara are currently recognized: *Hydrochoerus hydrochaeris*, the lesser capybara *H. ishtmius*, and

an extinct species from Argentina, *H. ballesterensis* (Ojasti, 1973; Vaughan *et al.*, 2000).

MATERIAL AND METHODS

Data collection

We examined 37 specimens of *Hydrochoerus hydrochaeris* held in the collections of the *Departamento de Biología* of the *Universidad del Valle* in Cali (Colombia) and *Instituto de Ciencias Naturales* of the *Universidad Nacional de Colombia*. Every specimen had been taxonomically identified to the species level, and were initially collected for other studies. As sex information was not available for all specimens studied, we performed all our analyses irrespective of sex.

Mandible landmarks obtention

Digital images of left lateral hemimandibles were taken with a Nikon D1500 digital camera equipped with an 18-105 mm Nikon DX telephoto lens. Each mandible was placed in the center of the optical field, with body oriented parallel to the image plane. The 13 landmarks on the left hemimandible (lateral aspect) were digitized by using TpsDig ver. 2.26 software (Rohlf, 2016). The landmarks chosen were present on all specimens and were considered to sufficiently summarize the morphology of the lateral aspect of hemimandible – alveolus, tips of processes, and point of maximum curvature of structures – (Cardini & Slice, 2004) (Fig. 1). Moreover, they can be used as the carrier of biological hypotheses of different morphogenetic mandibular units. Since the mandible is constituted by a unique dentary bone of relatively simple shape, most of the landmarks taken were of type 2 (e.g., it is supported only by geometric, not histological evidence; for instance, the maxima of curvature) (Bookstein, 1991).

Statistical analyses

To obtain information on shape with differences related to size, position and orientation removed (Rohlf, 2005). The data were first superimposed on Bookstein's shape coordinates by IMP CoordGen8 (Sheets, 1998). We used centroid size (CS), the square root of the summed squared distances of each landmark from the centroid of the landmark configuration as a geometric measure of mandible size (Rohlf, 2005). Subsequently, mandibular form of each specimen was



1. Most dorsal point of the edge of the articular surface condyle.
2. Most ventral part of sigmoid notch.
3. Tip of coronoid process.
4. Point that is at the maximum concavity between most dorsal point of the edge of the articular surface condyle and most nuchal point of post-condylar process.
5. Most nuchal point of post-condylar process.
6. Point that is at the maximum concavity between the post-condylar process and the angular process.
7. Tip of the angular process.
8. Perpendicular ventral projection of the most dorsal point of the edge of the articular surface condyle.
9. Ventral point of concavity of the ventral margin of the mandible that meets the vertical projection of tip of coronoid process.
10. Ventral point of the mandibular symphysis that meets the vertical projection of most ventral part of diastema.
11. Most rostro-dorsal point of the mandibular symphysis.
12. Most ventral part of diastema.
13. Most rostral point of the margin of the premolar row.

FIGURE 1: Lateral mandible view of *Hydrochoerus hydrochaeris*. Thirteen landmarks were used to capture mandibular shape. Mandibles were aligned by their tooth row to a stable plane.

represented by CS, and by multidimensional shape vector in linearized Bookstein's shape space.

For the smallest shape variation around the point of tangency, the best point of tangency is the sample mean form. TpsSmall ver. 1.33 software (Rohlf, 2015b) was used to assess this correlation between the 2D distances to the Euclidean distances in that tangent space. The correlation was very close to linear for all of the data ($r = 1.000$; slope, $b = 0.999$), suggesting that tangent space was an adequate approximation to Kendall's shape space (e.g., the mathematical properties of the shape space for landmark configurations) and that no specimens deviated appreciably from the linear regression line (Rohlf, 2005). Thus, although the mandible is not a perfect flat object, we considered that the two-dimensional approach implied quite a limited loss of information, and we proceeded with the morphometric analyses.

Size and shape variation

To explore variation in mandibular shape among specimens and to visualize its changes, we conducted a Principal Component Analysis (PCA) on the covariance matrix of the shape variables. The PCA analysis was performed using PAST Package ver. 2.17c (Hammer *et al.*, 2001).

Analysis of allometry and removing the effect of size

To assess the effect of size on shape, we regressed the shape of the collection of specimens (captured as coordinates of landmarks) onto size (CS, log transformed) as independent variable using *TpsRegr* ver. 1.36 software (Rohlf, 2015a).

RESULTS

The results of multivariate regression of shape variables (20 coordinates) on log CS revealed that shape variation could be clearly explained by allometry (Generalized Goodall F-test: $F = 7.4662$, $df = 22, 770$, $p = 0.0000$). Thus, our analyses indicated significant shape changes according to size changes. The position of the specimens in the morphospace defined by the first two axes obtained by PCA analysis of mandible shape variables and visualization of related, mandibular shape changes are presented in Fig. 2. The first two axes explained 54.8% ($PC1 + PC2 = 33.5 + 21.3\%$) of the total observed variance. An additional 42.3% of variance was spread across PC3-PC23. Jolliffe cut-off was $8.734E-05$. Both axes tended to distinguish between small specimens (understood as young animals) and bigger ones (understood as old animals). This suggests that most of the variation is driven by shape changes during growth.

Individual regressions of shape on centroid size display the pattern of allometric shape variation within the size range observed (Fig. 3). As such, allometry therefore explains a substantial part of shape variation and plays an important role in determining that main modifications are located in the ramus (landmarks 4, 5, 6 and 8) and in ventral part of the corpus (landmarks 9 and 10) and diastema (landmarks 12 and 13) (Fig. 4).

DISCUSSION

For *H. hydrochaeris* there are papers concerning gastrointestinal parasites, blood parasites, anatomical studies on miology, habitats, diets and potential use of food, morphophysiology of urogenital system... but none is concerning (at least to author's knowledge) to allometry. This is the first study of allometry of capybara focused on mandible using geometric morphometric methods. These methods can be defined as the quantitative description, analysis and interpretation of shape and variation of structures in biology. In a fundamental area of research, unlike the analytical approaches, the geometric one is aimed at comparison of the shapes.

In the sample studied of *H. hydrochaeris* there appeared a positive allometry, e.g., mandibular shape did vary according to mandibular size. Our analyses determined that mandibles exhibit positive allometry, whereby the relative size of mandibles becomes greater with increasing body size, indicating a functional dissociation with age (if the shape were the same throughout the life of animals, mechanical considerations, such the relative engulfment capacity and the specific physical forces at play during the feeding process, it would not increase allometrically with body size). A major component of shape variation in the mandibles of *H. hydrochaeris* is thus related to the attainment of adult size (i.e., postnatal growth). As an integral component of the craniomandibular apparatus, mandibles play an

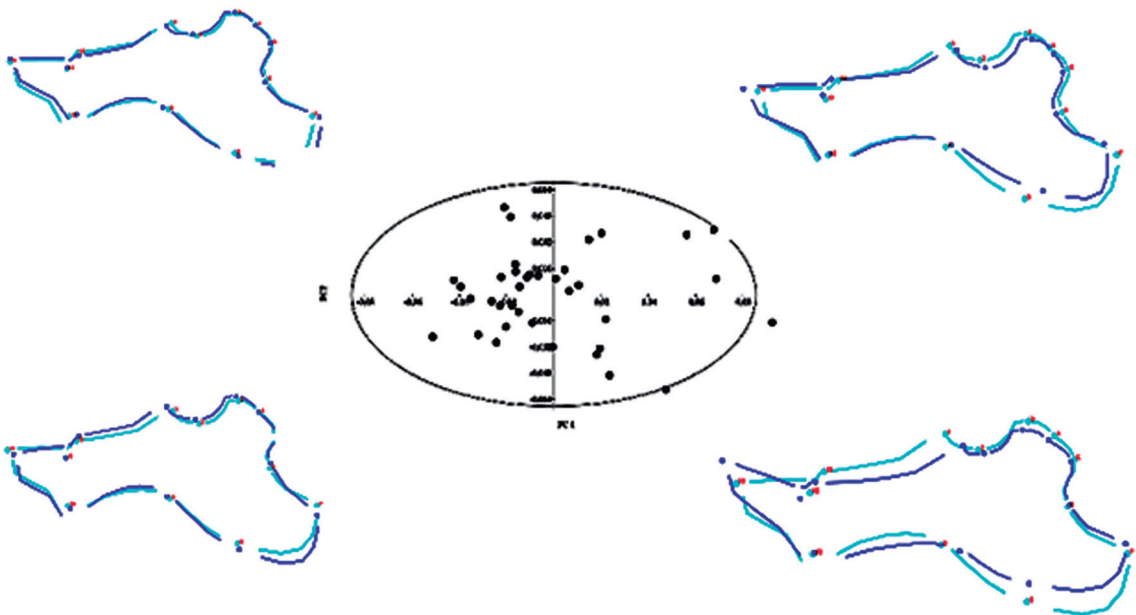


FIGURE 2: Principal Component Analysis scatter plot for first two axes, which explained 54.8% ($PC1 + PC2 = 33.5 + 21.3\%$) of the total observed variance, for *Hydrochoerus hydrochaeris* mandibles ($n = 37$). Ellipse is 95% confidence. Each dot represents one specimen. The major patterns of morphological variation in the pooled sample are reflected. Jolliffe cut-off was $8.734E-05$.

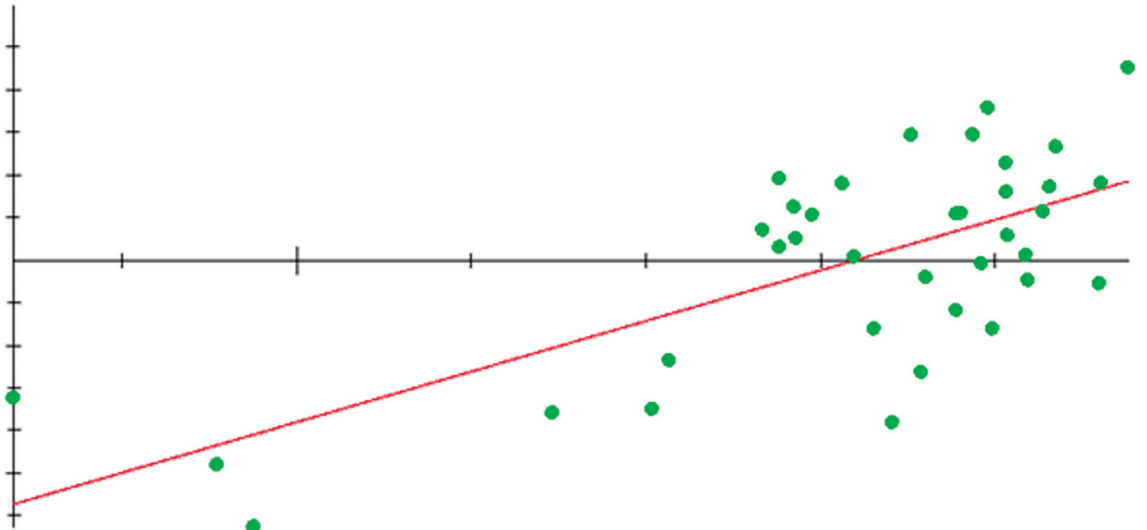


FIGURE 3: Multivariate regression of shape variables (26 coordinates, Y-axis) on log CS (X-axis) for *Hydrochoerus hydrochaeris* mandibles. It revealed that shape variation is clearly explained by allometry. Generalized Goodall F-test: $F = 7.4662$, $df = 22, 770$, $p = 0.0000$. Each dot represents one specimen ($n = 37$).

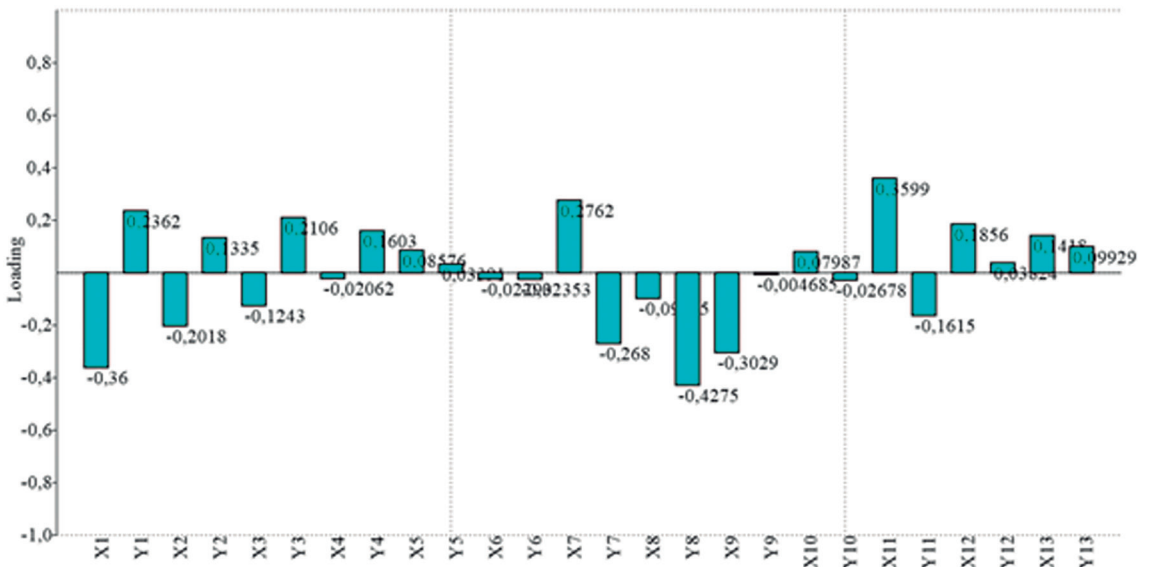


FIGURE 4: Loadings for Principal Component 1 for the 13 mandibular landmarks analyzed (PC1 = 33.5% of the total observed variance). Landmarks that contributed less to variation are located in the ramus (landmarks 4, 5, 6 and 8) and in ventral part of the corpus (landmarks 9 and 10) and diastema (landmarks 12 and 13).

important role in feeding mechanics. So the detected growth pattern seems to be related to dental eruption: the body must become elongated along its whole length to provide space for the additional teeth developed in this part, and the depth of the body must then increase, owing to increased growth of the alveolar part, to afford room for the roots of the teeth. Bony parts which enable the jaw to withstand the powerful action of the masticatory muscles (muscular attachment points) change less. Thus, the forces produced by the action of the masticatory muscle are not affected by mandibular size.

These robust scaling relationships also would allow to predict mandible shape from fragmentary remains in the capybara. Furthermore, if the evolution of morphology is arguably the evolution of allometry, its changes in different sloth species could also contribute to a better understanding of *Hydrochoerus* evolutionary relationships.

In conclusion, mandibular muscle mass increases during postnatal development and growth, as does the force-generating capacity of the jaw adductor muscles (notably the masseter complex).

RESUMEN

El aparato masticatorio de los mamíferos es una región altamente plástica del cráneo y, por ello, sujeta a trayectorias ontogénicas singulares. En este estudio presentamos el primer estudio descriptivo del patrón alométrico de la mandíbula en el capibara (*Hydrochoerus hydrochaeris*), basado en el estudio de 37 especímenes. Los cambios alométricos en la forma pura fueron analizados mediante técnicas de morfometría geométrica, permitiendo la visualización del patrón de alometría. Una regresión multivariada de la forma pura sobre el tamaño, estimado por el logaritmo del tamaño del centroide, apareció como altamente significativo. De ello, deducimos que la variación de la forma pura en la mandíbula está relacionada con la llegada al tamaño adulto, es decir, con el crecimiento.

PALABRAS-CLAVE: Capibara; Mandíbula; Ontogenia; *Rodentia*; Escalado.

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