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ALLOMETRY AND MODULARITY IN THE SKULL SHAPE OF FOUR SPECIES OF THE GENUS: *CTENOMYS* (Rodentia: Ctenomyidae)

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INTRODUCTION

Ecomorphology can be defined as the study of the relationship between the ecological role played by an organism (individual) and its morphological adaptations (Ricklefs, 1990), 2009). Thus, ecomorphological analysis has the basic premise that the positions of Species in morphological space correspond to their positions in ecological niche space (Ricklefs, 1990). Ecological niche that can be defined as the set of conditions and factors that limit the "functional space" occupied by a given Species, that is, the ecological niche is a concept of great abstraction and by definition multidimensional.

As for the morphological integration, the modules are sets of characters that can be genes, proteins or morphological elements, highly integrated with each other and little associated with the other elements. In empirical studies of morphological evolution, they are recognized by the presence and correlations between some parts of an organism and the absence of correlation between these and other parts of the same organism (Berg, 1960). The modular arrangement is considered the result of functional or ontogenetic relationships between characters (Falconer and Mackay, 1996).

Inferring the modularity patterns of complex morphological structures, that is, understanding how some characters share higher correlations with each other than with other characters, plays a fundamental role in understanding the morphological evolution of organisms. This is because this pattern can facilitate or constrain evolutionary changes (Schluter, 1996; Marroig and Cheverud, 2005; Pavlicev et al., 2008).

The analogies between variations in shape and size are called allometry (Gould 1966, 1977), and can be defined as differential rates of development between disparate measures or structures of an individual (Huxley, 1950). Allometry can be analyzed at at least three levels: ontogenetic allometry, which concerns the analyzed covariation in the extensions of a structure throughout the development of the individual; evolutionary allometry that discusses the covariation of differential size relationships between homologous structures of different Species and static allometry, which is related to the population variation of a structure at a given stage of the life span (Klingenberg, 1998).

Allometric patterns represent evolutionary changes in ontogenetic trajectories that comprise interruption or continuation along a conserved flow (ontogenetic scale), changes in early stages of development that result in different initial forms, and changes in direction (Klingenberg, 1998).

Therefore, the central idea of this report was to seek a greater understanding of how characteristics or morphological patterns observed in different groups of organisms in nature are "shaped" by the ecological context in which these organisms are inserted, that is, how environmental variables or the environment (ecological factors) are related to phenotypic variation, in this case, external morphological characteristics. In addition, this project aims to explore modularity patterns.

GOALS

The objectives of this work were to test whether there is allometry in the shape of the skull throughout the ontogenetic development of four species of rodent of the genus: *Ctenomys* (Blainville, 1826) occurring in South America. To test the presence and quantify the degrees of integration and morphological modularity in the shape of the skull among four Species of the genus:*Ctenomys*, two belonging to the Group: *Mendocinus* (*C. asutralis* and *C. flamarioni*)

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and two from the Group:*Torquatus* (C. *lami* and C. *minutus*) regarding the hypothesis of two or three modules along the ontogeny. Test the phylogenetic signal and verify that the patterns of evolution are the same among Species of the same phylogenetic group (*Torquatus* and *Mendocinus*).

METHODOLOGY

The individuals in the sample came from a photographic database that is part of the work of a master's project in Ecology linked to the Graduate Program in Ecology at the URI campus in Erechim. This database includes photos of dorsal and lateral views of skulls from specimens of the genus: *Ctenomys,* listed in scientific collections and museums in Brazil, Argentina and the United States. 439 skulls of four Species of the genus were analyzed: *Ctenomis*, *C. lami* (N = 94), *C. minutus* (N = 241), *C. flamarioni* (N = 53) and *C. australis* (N = 51). After the proper screening of this material, each photo received the digitization of a series of anatomical landmarks (morphological reference points, Figure 1) that was made with the TPSDig 2 program (Rohlf, 2010).

The coordinates of each anatomical landmark were superimposed by the Generalized Procrustes Analysis (GPA) method (Dryden and Mardia, 1998). GPA removes effects unrelated to size, position and orientation (Adams et al., 2004). Data analysis was performed in relation to centroid size (which is the square root of the sum of the squares of the distances from each anatomical landmark to the midpoint of the landmark configuration). As for the form, Procrustes residues were used. For the allometry test, a regression was performed between the centroid size and the Procrustes distances. Modularity hypothesis tests were performed through the frameworks anatomy of each skull and for the different views (dorsal and lateral). With the MorphoJ program, different hypotheses were generated, and those with greater statistical support will be kept for magnitude tests. The hypotheses tested were that the skull that was divided into two modules (rostrum and braincase), based on the embryonic origin of these tissues, and that of three modules (rostrum, zygomatic arches/frontal/palatal region and neurocranium), based on structures morpho-functional (Figure 2). Through PLS (Partial-Least Squares) tests the covariation between different modules can be measured. To quantify the strength of the association between modules, the RV coefficient was used, as it measures the association between two groups of variables, being a measure of integration between parts (Klingenberg and Marrugán-Lobón 2013).

For all statistical analyzes and for the generation of graphs, the MorphoJ program was used.

RESULTS AND DISCUSSIONS

ALOMETRIC

Regression analysis was significant for *C. lami* (p < 0,001) for Dorsal view, with size predicting 18.539% of shape. The skull of smaller individuals is more rounded while in larger individuals the skull is more elongated, mainly in relation to the elongation of the rostrum (Figure 3). For the Side view, the size influenced 9.292% of the shape. Smaller skulls have a proportionately shorter and lower rostrum while in larger skulls the rostrum is proportionately longer and deeper, and the cheek bone processes are more developed (Figure 4).

Regression analysis was significant for *C. minutus* (p < 0,001) for Dorsal view, with size predicting 14.227% of shape. The skull of smaller individuals is more rounded while in larger individuals the skull is more elongated, mainly in relation to the elongation of the

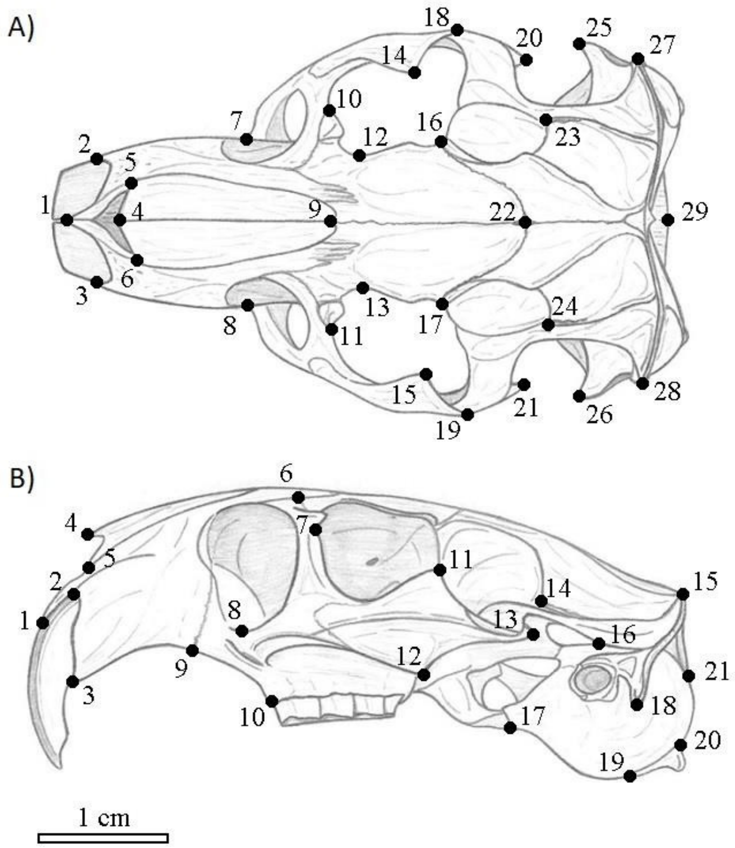

Figure 1: Location of anatomical landmarks in the skull of *Ctenomys* for dorsal (A) and lateral (B) views. The description of each anatomical landmark can be found in Annex 1 (Modified from Fornel et al., 2018).

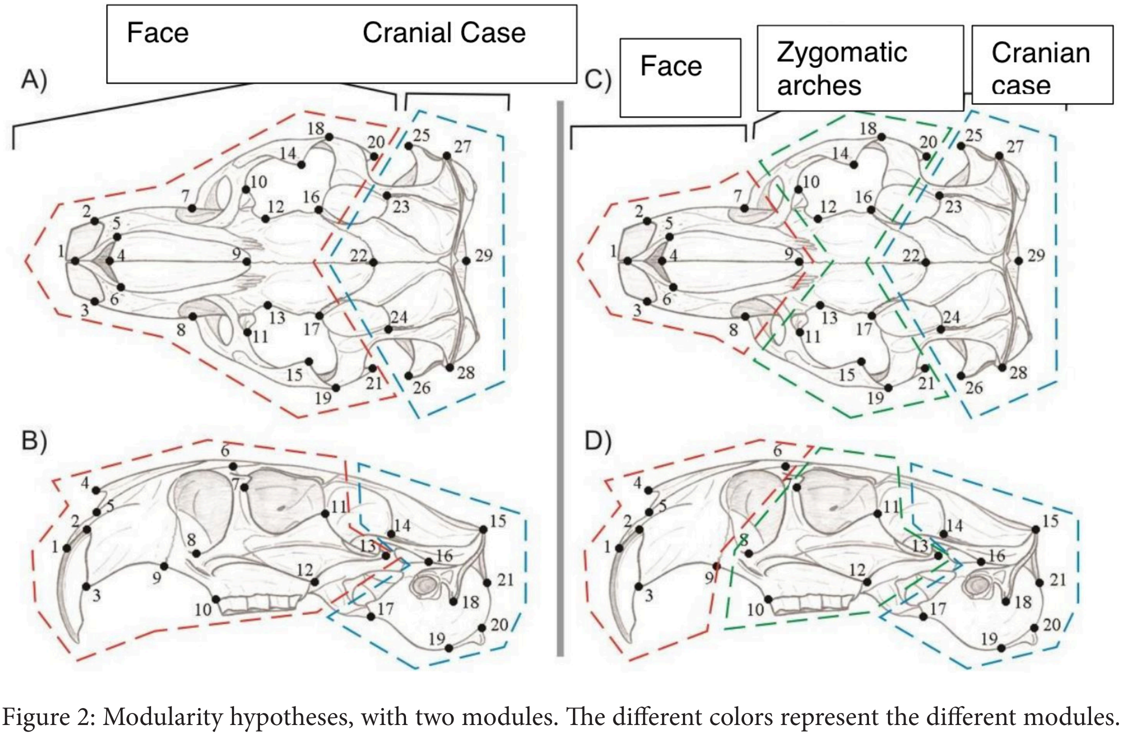

Figure 2: Modularity hypotheses, with two modules. The different colors represent the different modules. A) side view, B) side view. And three modules, C) side view, D) side view.

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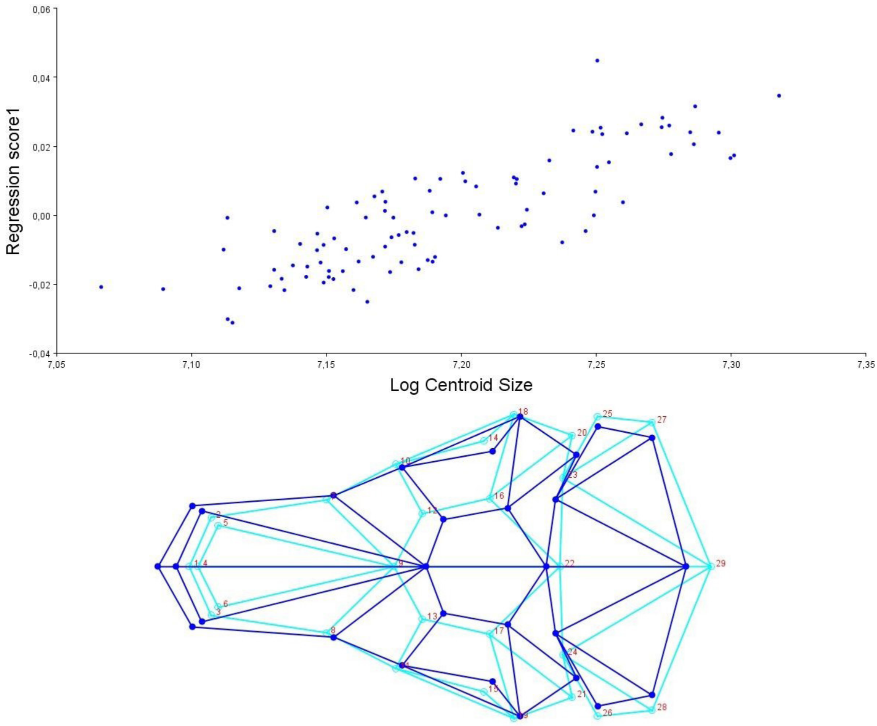

Figure 3: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis lami* in Dorsal view. The bottom Figure represents the configuration of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

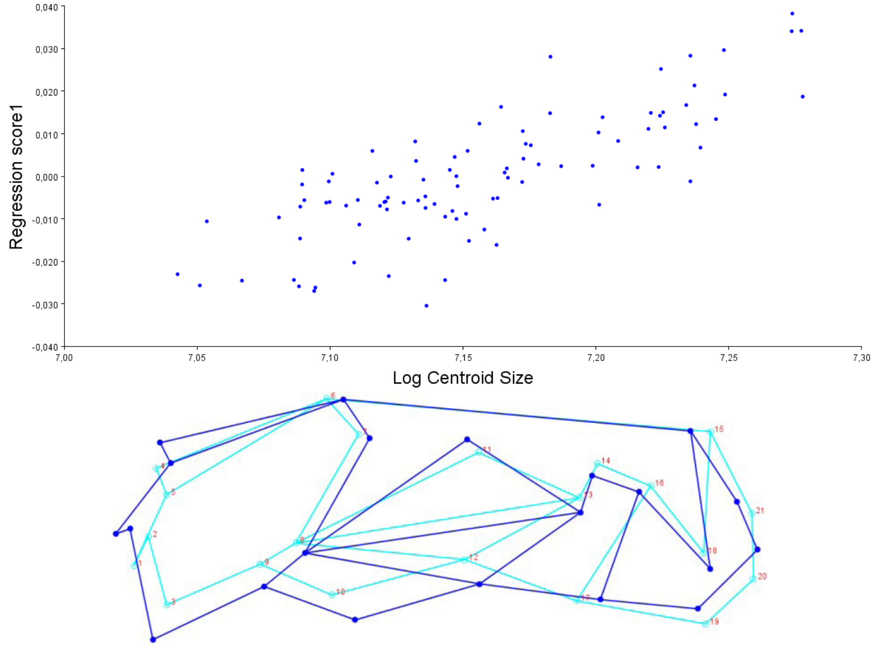

Figure 4: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis lami* in side view. The bottom Figure represents the configuration of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

rostrum (Figure 5). For the Side view, the size influenced 6.811% of the shape. Smaller skulls have a proportionately shorter and lower rostrum while in larger skulls the rostrum is proportionately longer and deeper, as well as a more developed superior jugal process (Figure 6).

Regression analysis was significant for: *C. flamarioni* ($p < 0{,}001$) for Dorsal view, with size predicting 18.777% of shape. The skull of smaller individuals is more rounded while in larger individuals the skull is more elongated, mainly in relation to the elongation of the rostrum (Figure 7). For the Side view, the size influenced 15.308% of the shape. Smaller skulls have a proportionately shorter and thinner rostrum while in larger skulls the rostrum is proportionately longer and deeper, and the cheek bone processes are more developed (Figure 8).

Regression analysis was significant for: *C. australis* ($p < 0{,}001$) for the Dorsal view, with the size predicting 14.650% of the shape. The skull of smaller individuals is more rounded while in larger individuals the skull is more elongated, mainly in relation to the elongation of the rostrum (Figure 9). For the Side view, the size influenced 14.828% of the shape. Smaller skulls have a lower and less developed region of the rostrum, giving a more curved appearance. In larger animals, the rostrum is more developed and higher, giving a more straight profile to the skull (Figure 10).

The four Speciess presented significant allometry and with very similar values for the Dorsal view for the four Speciess. However, for the side view of the skull, the R^2 value was more similar among Species of the same group. (Grupo *torquatus*: *C. lami* = 9,292; and *C.minutus* = 6,811; Group *mendocinus*: *C. flamarioni* = 15,308; and *C. australis* = 14,828) and more different between the two groups. Therefore, the allometry seems to be phylogenetically constrained with Species more similar to each other within the same group and Species more different between groups, that is, from different evolutionary lineages.

MODULARITY

We found different results for the modularity test between different views of the skull, between different modules and between different Species. In Table 1, we can see that for the two-module hypothesis for the Dorsal view of the skull only: *C. minutus* and *C. flamarioni* showed significant modularity ($P < 0.05$). For Side view, the two-module hypothesis was significant only for: *C. lami* and *C. minutus* (Table 1). As for the three-module hypothesis, none of the Species presented a significant result for the Dorsal view of the skull. However, Side view showed significance for the three-module hypothesis only for*C.minutus* and *C. flamarioni* (Table 1).

CONCLUSION

The study aimed to test whether there is allometry in the shape of the skull throughout the ontogenetic development of four rodent species of the genus: *Ctenomys* and to test the presence and quantify the degrees of integration and morphological modularity in the shape of the skull among four species of the genus: *Ctenomys*, two belonging to the Group: *Mendocinus* (*C. asutralis* and *C. flamarioni*) and two from the Group:*Torquatus* (C. *lami* and C. *minutus*). It was concluded that there is allometry for the four species, however, there is a phylogenetic restriction, since *C. lami* and *C. minutus* were more similar to each other and differed from *C. flamarioni* and *C. australis*. Therefore, allometry is phylogenetically restricted within the genus: *Ctenomys*.

On the other hand, the modularity in the shape of the skull did not show any clear pattern suggesting that there must be other

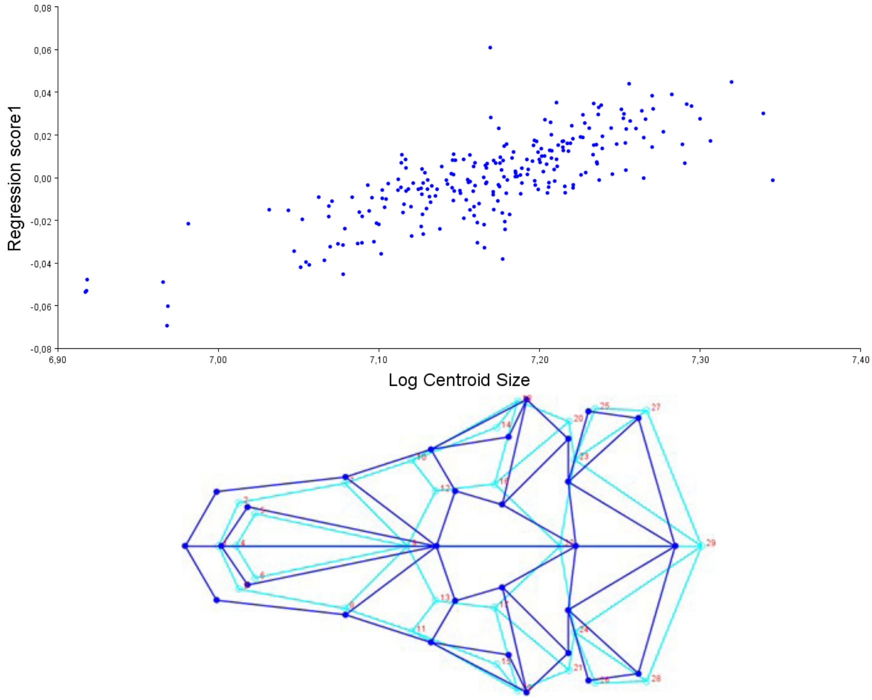

Figure 5: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis minutus* in Dorsal view. The bottom Figure represents the configuration of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

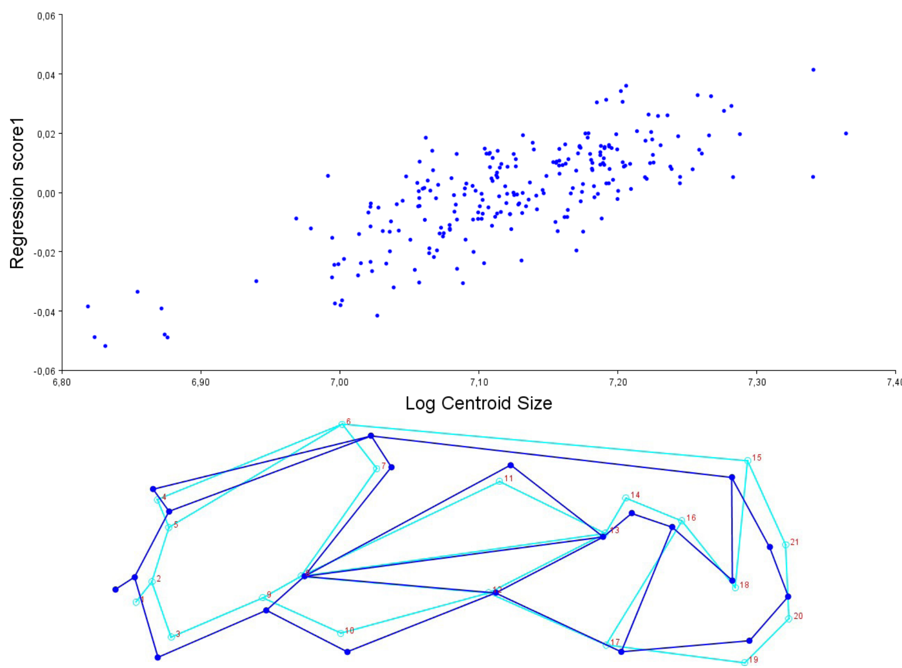

Figure 6: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis minutus* in side view. The bottom Figure represents the configuration of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

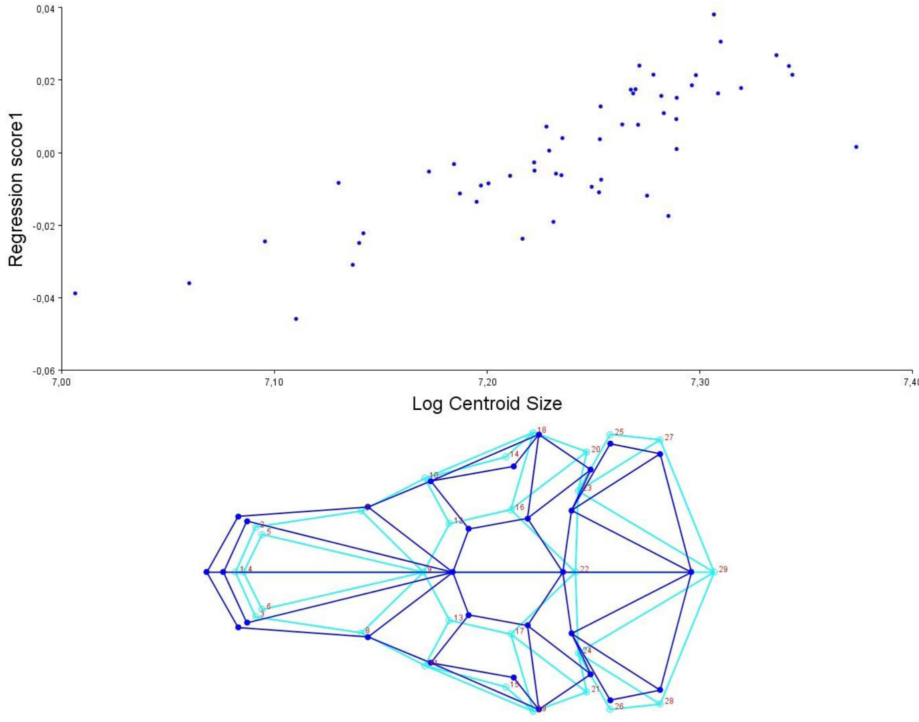

Figure 7: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis flamarioni* in Dorsal view. The bottom Figure represents the configuration of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

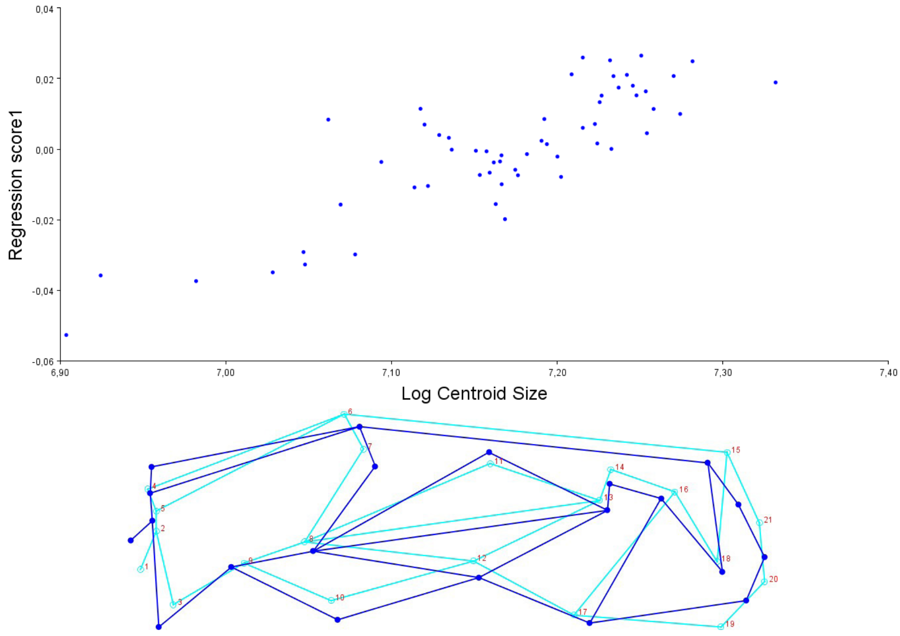

Figure 8: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis flamarioni* in side view. The bottom Figure represents the configuration of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

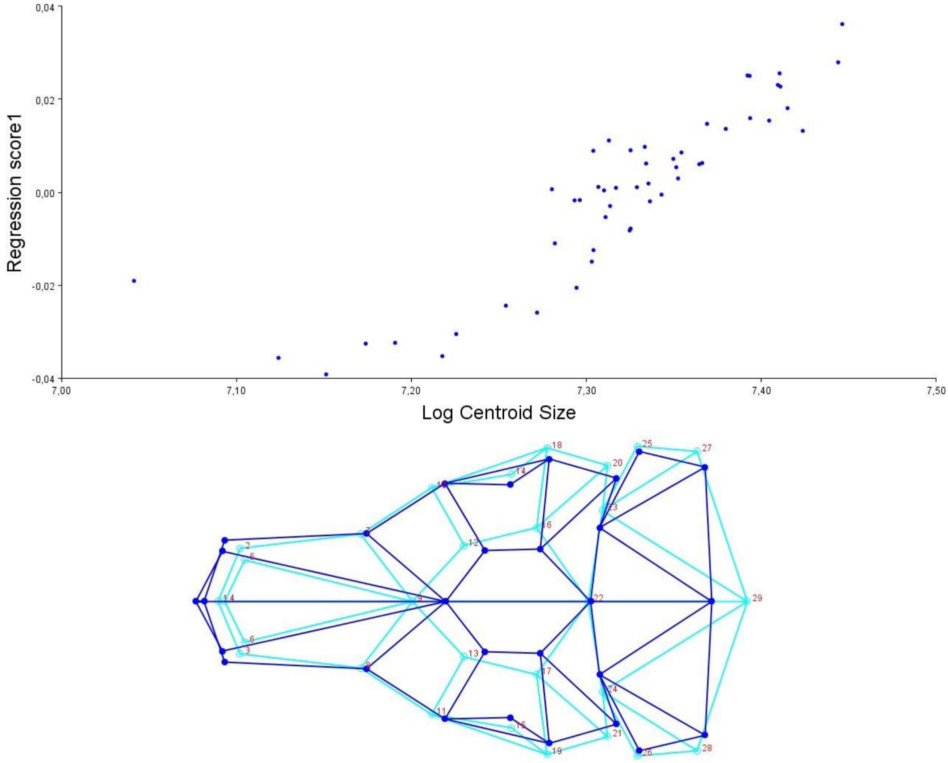

Figure 9: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis australis* in Dorsal view. The bottom Figure represents the configuration of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

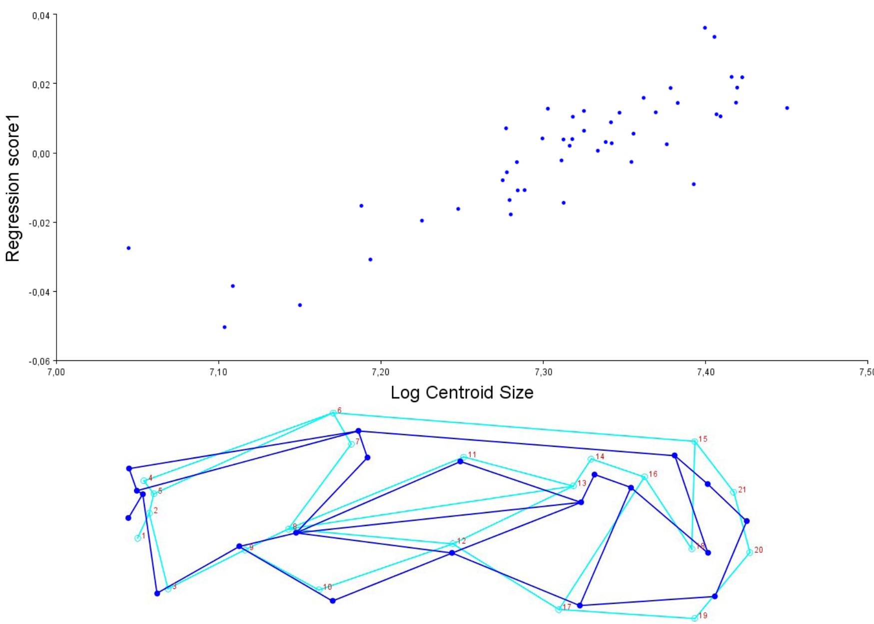

Figure 10: Regression between skull size (x-axis, log centroid size) and skull shape (y-axis) for juveniles and adults of *Ctenomis australis* in side view. The bottom figure represents the conFiguretion of anatomical landmarks along the allometry trajectory, with the light blue line representing the end with smaller skulls and the dark blue line representing the end with larger skulls.

Two modules:				
	Dorsal view		Side view	
Species	RV coefficient	*P*	RV coefficient	*P*
C. lami	0,352639	0,134831	0,271014	0,005254
C. minutus	0,20409	0,016327	0,242772	0,000073
C. flamarioni	0,360756	0,018182	0,390603	0,082591
C. australis	0,184643	0,229299	0,429608	0,080128
Three modules:				
	Dorsal view		Side view	
Species	RV coefficient	*P*	RV coefficient	*P*
C. lami	0,359405	0,242567	0,282991	0,225692
C. minutus	0,241031	0,151136	0,229155	0,023634
C. flamarioni	0,450904	0,563636	0,317892	0,033139
C. australis	0,19574	0,1121	0,388482	0,44349

Table 1: Values of RV coefficient and Significance Value, in relation to dorsal and lateral views of the skull of four Species of the genus *Ctenomis* in relation to the hypotheses of two and three modules.

factors (for example, environmental) besides the evolutionary history that influence the morphological integration in the genus: *Ctenomys*.

MATERIALS SENT FOR PUBLICATION

To date, no works have been submitted for publication. However, we intend to write and submit an article with these data to Revista Perspectiva by the end of the year.

OTHER ACTIVITIES OF UNIVERSITY INTEREST

Participation in the academic week of the Biological Sciences course from June 1st to 3rd, 2022 at URI Campus de Erechim.

WORK CONTINUITY OR DEPLOYMENT PERSPECTIVES

It is intended to continue this project considering that the scientific initiation scholarship has been renewed for another year. In addition, we intend to analyze other views of the skull, such as the ventral view and the lateral view of the mandible of these same four species of the genus: *Ctenomys.*

REFERENCES

Adams, D. C., Rohlf, F. J., e Slice, D. E. 2004. Geometric Morphometrics: ten years of progress following the "revolution**". Ital J Zool** 71: 5-16.

Berg, R. L. 1960. The ecological significance of correlation pleiades. **Evolution** 14: 171-180.

Dryden, I.L. e Mardia, K.V. 1998. **Statistical Shape Analysis**. John Wiley & Amp; Sons, Inc., New York.

Fornel, R; Cordeiro-Estrela, P; Freitas, T. R.O. In: Skull shape and size variation within and between mendocinus and torquatus groups in the genus *Ctenomys* (Rodentia: Ctenomyidae) in chromosomal polymorphism context. **Genetics and Molecular Biology**. 41(1): 263-272; 2018.

Falconer, D. S.; Mackay, T. F. C. 1996. **Introduction to quantitative genetics.** Longman Group Limited, 4.ed. Edinburg. 464p.

Futuyma, D. 2009. **Biologia Evolutiva**, 3ed. Ribeirão Preto: Funpec editora.

Gould, S. J. 1977. **Ontogeny and phylogeny**, Belknap Press of Harvard University. Cambridge Massachusetts. 502p.

Huxley, J. S. 1950. Relative growth and form transformation. **Proceedings of Royal Society of London** 137:465-469.

Klingenberg, C. P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. **Biological Reviews**. 79-123.

Klingenberg, C. P.,; J. Marugán-Lobón. 2013. Evolutionary covariation in geometric morphometric data: analyzing integration, modularity and allometry in a phylogenetic context. **Systematic Biology**, 62:591–610.

Marroig, G. e Cheverud, J. M. 2005. Size as line of least evolutionary resistance: Diet and adaptive morphological radiation in new worl monkeys. **Evolution**, 59:1128-1142.

Pavlicev, M. J. P., Kenney-Hunt, E. A., Norgard, C. C., Roseman, J. B. W., Cheverud, J.M. 2008. Genetic variation in pleiotropy: Differential epistasis as a source of variation in the allometric relationship between long bone lengths and body weight. **Evolution**,62:199-213.

Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. **Evolution,**5:1766-1774.

ANNEX

Annex 1: Anatomical description of the landmarks used in this study for the skull of the genus Ctenomys (See Figure 1).

Dorsal view of the skull: 1- anterior suture point between the premaxillary; 2-3 anterolateral end of the incisor socket; 4- anterior end of the suture between the nasals; 5-6 most anterior point of the suture between nasal and premaxillary; 7-8 most anterior point of the root of the zygomatic arch; 9- suture between nasal and frontal; 10-11 anterolateral end of the lacrimal bone; 12-13 point of smaller width between the frontals; 1415 tip of the tip of the superior jugal process; 16-17 anterolateral end of the suture between frontal and scoamozal; 18-19 lateral end of the suture between jugal and scoamozal; 20-21 tip of posterior jugal process; 22- suture between frontal and parietal; 23-24 anterolateral end of the suture between parietal and scoamozal; 25-26 anterior tip of the external auditory meatus; 27-28 point of maximum curvature of the mastoid apophysis; 29- most posterior point of the midplane occipital bone.

Side view of the skull: 1- most anterior point of the premaxillary; 2- most anterior point of the incisor alveolus; 3- most inferior point of the incisor alveolus; 4- most anterior point of the nasal bone; 5- most anterior point of the suture between the nasal bone and the premaxilla; 6- suture between frontal, premaxillary and maxillary in the superior root of the zygomatic arch; 7- most inferior point of the suture between the lacrimal and the maxilla; 8- most inferior point of the infra-orbital foramen in the inferior root of the zygomatic arch; 9- lowest point of the suture between premaxillary and maxillary; 10- most anterior point of the premolar alveolus; 11- upper end of the jugal process; 12- lower end of the jugal process; 13- posterior tip of the jugal process; 14- medial point between the parietal and squamosal suture; 15-upper end of the lambdoidal crest; 16- anterior tip of the suture between squamosal and tympanic bulla; 17- lower end of the suture between the pteridoid and the tympanic bulla; 18- lower end of the mastoid process; 19- anterior border of the paraocipital process; 20- posterior border of the paraoccipital apophysis; 21- posterior end of the insertion between the occiput and the tympanic bulla.