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Craniometric geographical variation in *Hylaeamys megacephalus* populations[1]

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ABSTRACT.- Mata P.S., Ribeiro M.S.L., Faria M.B. & Lima F.C. 2020. **Craniometric geographical variation in *Hylaeamys megacephalus* populations.** *Pesquisa Veterinária Brasileira 40(9):726-732.* Programa de Biociência Animal, Universidade Federal de Jataí, Cidade Universitária, BR-364 Km 195, Prédio da Pós-Graduação, Jataí, GO 75801-615, Brazil. E-mail: paoladamata@hotmail.com

Hylaeamys megacephalus (G. Fisher, 1814) presents great genetic diversity and wide geographical distribution, and occurs in both the Amazon and Cerrado biomes. Because of its generalist aspect, this species tolerates different eating habits and habitats. It occurs in flooded and dry areas and is predominantly terrestrial, which allows greater gene flow between populations even over long distances. Studies that seek a better understanding of morphological variations resulting from differences imposed by the environment throughout this species' distribution are still lacking. This study aimed to analyze the differences between *H. megacephalus* populations based on craniometry, investigating whether the environment has an influence on morphology. We analyzed a total of 142 specimens from three scientific mammal collections: National Museum, "Universidade Federal do Rio de Janeiro" (MN-UFRJ); "Laboratório de Biologia e Parasitologia de Mamíferos Reservatórios Silvestres", "Instituto Oswaldo Cruz", "Fundação Oswaldo Cruz"(LBCE-Fiocruz); and "Laboratório de Biodiversidade", "Universidade Federal de Goiás", "Regional Jataí" (LZE-UFG), and took 20 craniometric measurements. Craniometry was explored using unweighted pair group method with arithmetic mean (UPGMA), canonical variate analysis, and principal component analysis (PCA). The results led us to conclude that there are three craniometric groups of *H. megacephalus* with a tendency to differentiate as a result of geographical influences.

INDEX TERMS: Craniometry, geographic variation, *Hylaeamys megacephalus*, anatomy, morphological characters, skull, occurrence, rodent.

RESUMO.- [**Variação geográfica craniométrica em populações de *Hylaeamys megacephalus.***] Com grande diversidade genética e distribuição geográfica, *Hylaeamys megacephalus* (G. Fisher, 1814) ocorre tanto na Amazônia quanto no Cerrado. Visto seu aspecto generalista, esta espécie tolera diversos hábitos alimentares e habitats, ocorrendo em áreas inundadas ou não, sendo predominantemente terrestre, permitindo maior fluxo de genes entre as populações, mesmo em longas distâncias. Apresenta ampla distribuição, e carece de estudos que busquem um melhor entendimento sobre as variações morfológicas resultantes das diferenças impostas pelo meio ao longo de sua distribuição. O estudo teve como objetivo, analisar as diferenças entre as populações de *H. megacephalus*, com base na craniometria investigando se o ambiente interfere na morfologia. Analisamos um total de 142 espécimes oriundos de coleções científicas de mamíferos, do Museu Nacional, Universidade Federal do Rio de Janeiro (MN-UFRJ), Laboratório de Biologia e Parasitologia de Mamíferos Reservatórios Silvestres, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz (LBCE-Fiocruz) e Laboratório de Biodiversidade, Universidade Federal de Goiás, Regional Jataí, nos quais foram tomadas 20 medidas craniométricas. A craniometria foi explorada nas análises estatísticas de agrupamento de pares não ponderados com médias aritméticas (UPGMA), variação canônica e análise dos Componentes Principais (PCA). Os resultados encontrados nos levaram a concluir a existência de três grupos craniométricos da espécie de *H. megacephalus* com tendência a se diferenciarem, por influências geográficas.

TERMOS DE INDEXAÇÃO: Variação geográfica, craniometria, *Hylaeamys megacephalus*, anatomia, caracteres morfológicos, crânio, ocorrência, roedor.

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INTRODUCTION

The evolutionary success of rodents may be attributed to their small body size, high-rate and short-cycle reproduction, and wide range of dental characteristics (Rodrigues & Naehrer 2012). This specification is surprising, and it can be found in almost all non-marine habitats. The adaptive diversity of these animals is remarkable in ecology, as they occur in most ecosystems on the planet (Hautier et al. 2011, Arregoitia et al. 2017).

Hylaeamys megacephalus (G. Fisher, 1814) (Azara's broad-headed oryzomys or large headed rice rat) presents great genetic diversity and wide geographical distribution, and occurs in both the Amazon and Cerrado biomes, forming three clades in three different regions: one in the Cerrado and two in the Amazon (north and south of the Amazonas River). Genes of the clade belonging to the south of the Amazonas River are closer to those of the clade that inhabits the Cerrado, suggesting an allopatric divergence in which historical and ecological factors have an influence on the distribution and diversification of species (Miranda et al. 2007, Machado et al. 2019).

Because of its generalist aspect, *H. megacephalus* tolerates several eating habits and habitats. It occurs in flooded and dry areas and is predominantly terrestrial, which allows greater gene flow between populations even over long distances. This rodent has a wide distribution, and studies that seek a better understanding of morphological variations resulting from differences imposed by the environments are still lacking (Emmons & Feer 1997, Bonvicino et al. 2008, Percequillo et al. 2008, Rocha et al. 2011, Paglia et al. 2012, Rocha et al. 2014, Patton et al. 2015).

Morphological variation in these animals can be explained by different ecological and/or evolutionary mechanisms, such as intraspecific and sexual selection. Size and shape are critical biological attributes of organisms, resulting from the interaction between genes and environment. Usually, a large fraction of the variability of morphometric data is related to the size of individuals, which can result in changes in the associated shape (Kardong 2014).

This study aimed to analyze the differences between *H. megacephalus* populations based on craniometry, investigating whether the environment has an influence on morphology.

MATERIALS AND METHODS

Samples. Cranial morphology was assessed in 142 specimens from three mammal scientific collections: 63 from the National Museum, "Universidade Federal do Rio de Janeiro" (MN-UFRJ), 49 from the"Laboratório de Biologia e Parasitologia de Mamíferos Reservatórios Silvestres", "Instituto Oswaldo Cruz", "Fundação Oswaldo Cruz" (LBCE-Fiocruz), and 30 from the "Laboratório de Biodiversidade", "Universidade Federal de Goiás", "Regional Jataí" (LZE-UFG) (Table 1). They are distributed over 27 Brazilian municipalities: seven in the Amazon and 20 in the Cerrado biomes. For statistical analysis, locations with fewer than five specimens were grouped into the closest geographical region (Table 2 and Fig.1).

Quantitative analysis. The samples were analyzed in January 2018 at the MN-UFRJ and LBCE-Fiocruz, and in July 2018 at the LZE-UFG. Adult individuals of both sexes were analyzed. Age was classified according to the third molar eruption criterion (Fig.2). Cranial dimensions were measured following an adaptation from Voss (1988) and Manduca (2008) using a digital precision (0.01 mm) caliper. Twenty measurements were taken (Table 3 and Fig.3-5).

Statistical analysis. Cluster analysis was performed using the unweighted pair group method with arithmetic mean (UPGMA) (Sneath & Sokal 1973). The cut-off point was established using the k-means clustering analysis to favor interpretation of score distribution patterns in the multivariate space. Subsequently, we performed canonical variate analysis, for discriminatory morphometric trends, and principal component analysis (PCA), based on the covariance matrix of the logarithmically transformed data used to determine the main independent trends in craniometric variation. The 20 craniometric variables were analyzed using the R software and descriptive statistics (mean and standard deviation). Small population samples (<5 specimens) were grouped into larger samples from the closest geographical location (Fig.1).

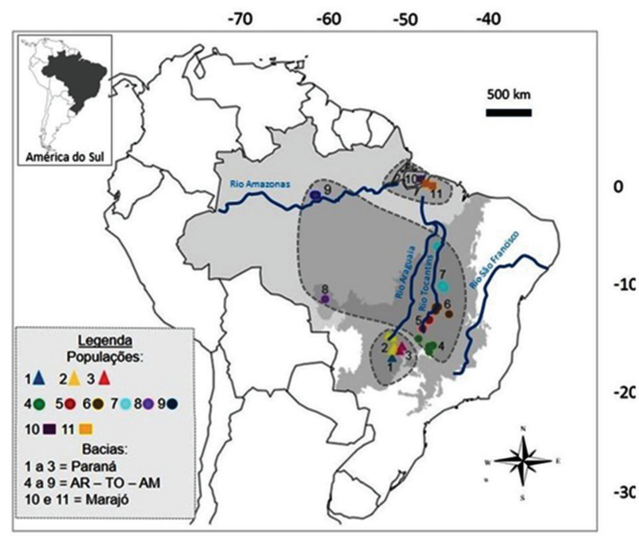

Fig.1. Distribution map of the collected *Hylaeamys megacephalus* samples, where each color and number indicates the geographically grouped populations and the symbols show the groups in the UPGMA analysis.

Fig.2. Microphotograph of the molar teeth showing the third molar (3M) eruption in *Hylaeamys megacephalus*, specimen 079 LZE, ventral view.

Table 1. Origin of the *Hylaeamys megacephalus* specimens analyzed

Number	Institution	Morphoclimatic domain	Latitude	Longitude	Municipality	State*
6986, 6987, 8566, 9456, 7003, 7471, 7491, 8511, 9442	LBCE	Cerrado	18º 57' 55" S	51º 55' 35" W	Aporé	GO
8754, 8751, 8752, 8755	LBCE	Cerrado	17° 37' 59" S	47° 46' 42" W	Campo Alegre de Goiás	GO
8718	LBCE	Cerrado	16º 57' 44" S	49º 13' 41" W	Hidrolândia	GO
8768	LBCE	Cerrado	17° 43' 19" S	48° 09' 35"W	Ipameri	GO
13523, 13522, 13524, 13542, 13519, 13027, 13024, 13023, 13028,13031	LBCE	Cerrado	11º 49' 26" S	46º 37' 42" W	Novo Jardim	TO
13004, 13005, 13025, 13059, 13029, 13030, 13084, 13437, 13526, 13543, 13467, 13070, 13065	LBCE	Cerrado	11° 37' 40"S	46° 49' 14"W	Dianópolis	TO
18587	LBCE	Cerrado	18° 15' 47"S	48° 09' 04" W	Cumari	GO
12194, 12152, 12158, 12172	LBCE	Cerrado	12° 59' 22" S	58° 45' 51" W	Sapezal	MT
54, 78, 80, 82,83, 87, 89, 90, 92, 96, 129, 144, 154,156, TX 03, 79, 141	LZE	Cerrado	17º 52' 53"S	51º 42' 52" W	Jataí	GO
165	LZE	Cerrado	18º 17' 56" S	51º 08' 43" W	Aparecida do Rio Doce	GO
167	LZE	Cerrado	16º 57' 24" S	51º 48' 37" W	Caiapônia	GO
177	LZE	Cerrado	16º 43' 13" S	52º 19' 10" W	Doverlândia	GO
221, 245, 251, 255, 212, 213, 217, 219, 256	LZE	Cerrado	17º 47' 53" S	50º 55' 41" W	Rio Verde	GO
69	LZE	Cerrado	18º 57' 55" S	51º 55' 35" W	Aporé	GO
20880, 20882, 20883, 20886, 20888, 20889, 20890, 20892, 20877, 20878, 20695, 20893, 20895, 20897, 2098, 20899, 20900, 20901, 20904, 20911, 20913, 69002, 75119	Museu Nacional -UFRJ	Amazônia	03° 06' 07"S	60º 01' 30"W	Manaus	AM
10289, 10288	LBCE	Amazônia	01° 00' 41"S	48° 57' 48"W	Cachoeira do Arari	PA
69185	Museu Nacional -UFRJ	Amazônia	00° 58' 29"S	62° 55' 27" W	Barcelos	AM
84037	Museu Nacional -UFRJ	Amazônia	01° 40' 27"S	47° 46' 16" W	Capim	PA
84036, 84035, 84034, 84033, 84031, 84030, 84032	Museu Nacional -UFRJ	Amazônia	01° 27' 21"S	48° 30' 16" W	Belém	PA
46867, 46861, 46863	Museu Nacional -UFRJ	Cerrado	14° 07' 57"S	47° 30' 36"W	Alto Paraíso	GO
46864, 46870	Museu Nacional -UFRJ	Cerrado	13° 47' 51"S	47° 27' 30"W	Cavalcante	GO
43013, 43014, 43009, 43015, 43011, 43016, 43012, 43018, 43019, 43020, 43021, 46860, 81655, 81658	Museu Nacional -UFRJ	Cerrado	13° 46' 35"S	47° 15' 53"W	Teresina de Goiás	GO
81664, 81665, 81666, 81669, 81670, 81671, 81672, 81673, 81674, 81675, 81676	Museu Nacional -UFRJ	Cerrado	15° 03' 22"S	48° 09' 41"W	Mimoso de Goiás	GO
81701	Museu Nacional -UFRJ	Cerrado	15º 55' 25" S	48º 48' 31" W	Corumbá de Goiás	GO
10855	LBCE	Cerrado	14° 29' 16"S	46° 06' 47"W	Mambaí	GO
6858, 6799, 6852	LBCE	Cerrado	18º 18' 22" S	51º 57' 44" W	Serranópolis	GO

LBCE = Laboratório de Biologia e Parasitologia de Mamíferos Reservatórios Silvestres, LZE = Laboratório de Biodiversidade; *GO = Goiás, TO = Tocantins, MT = Mato Grosso, AM = Amazonas, PA = Pará.

Table 2. Number of samples, place of origin, and number of specimens analyzed

Samples	Specimen location and quantity
1	Aporé - GO (10)
2	Caiapônia - GO (01), Doverlânida - GO (01), Jataí - GO (17), Serranopólis - GO (03)
3	Aparecida do Rio Doce - GO (01), Rio Verde - GO (09)
4	Campo Alegre de Goiás - GO (04), Cumari - GO (01), Hidrolândia - GO (01), Ipameri - GO (01)
5	Corumbá de Goiás - GO (01), Mimoso de Goiás - GO (11)
6	Alto Paraíso - GO (03), Cavalcante - GO (02), Goiatins - TO (01), Mambaí - GO (01), Teresina de Goiás - GO (14)
7	Dianopólis - TO (13), Novo Jardim - TO (10)
8	Sapezal - MT (04)
9	Manaus - AM (21), Santa Isabel - AM (01)
10	Barcelos - AM (01), Cachoeira do Arari - AM (02)
11	Bélem - PA (07), Capim - PA (01)

State: GO = Goiás, TO = Tocantins, MT = Mato Grosso, AM = Amazonas, PA = Pará.

RESULTS

A total of 11 populations were observed and arranged in three cranial groups listed by hydrographic basins: Marajó Island, Paraná, and Araguaia-Tocantins/Amazonas River (Fig.1). Statistical analysis (UPGMA) showed that the populations from the Paraná and Araguaia-Tocantins/Amazonas River basins are more similar to each other compared with the those from the Marajó Island (Fig.6).

As in the UPGMA analysis, canonical variate analysis also showed discriminatory morphometric trends with formation

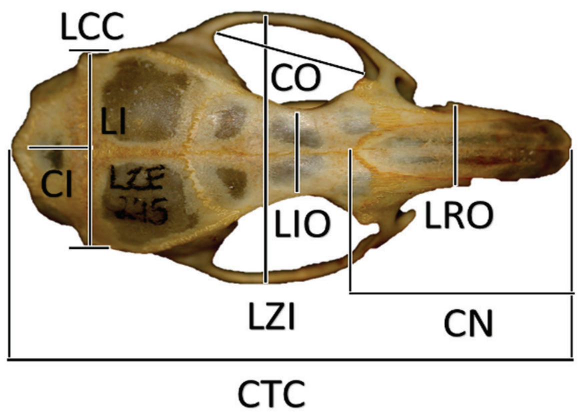

Fig.3. Dorsal view of the skull of *Hylaeamys megacephalus*, specimen 080 LZE. Total skull length (CTC), nasal length (CN), rostral width (LRO), interorbital width (LIO), zygomatic arch width (LZI), orbital length (CO), interparietal width (LI), skull width (LCC), interparietal length (CI).

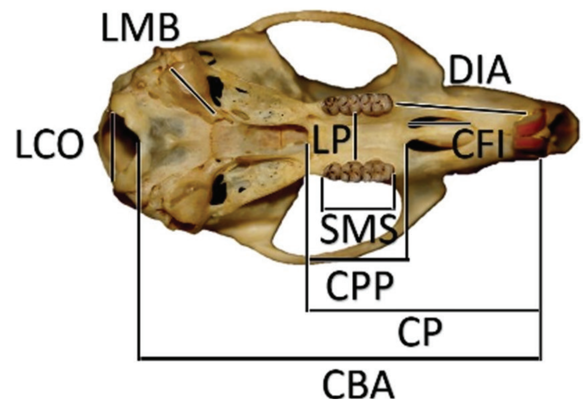

Fig.4. Ventral view of the skull of *Hylaeamys megacephalus*, specimen 080 LZE. Cranial base length (CBA), palatal length (CP), palatal bridge length (CPP), upper molar teeth series (SMS), palatal width (LP), incisive foramen length (CFI), diastema (DIA), maximum bulla width (LMB), distance between the occipital condyles (LCO).

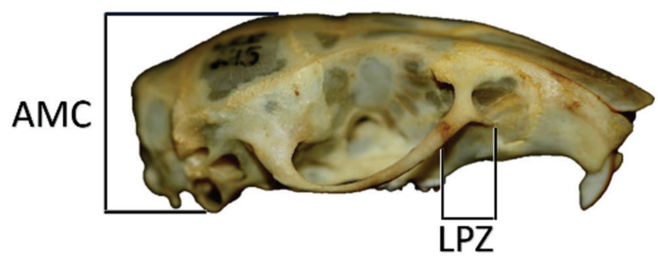

Fig.5. Lateral view of the skull of *Hylaeamys megacephalus*, specimen 080 LZE. Zygomatic plate width (LPZ), maximum skull height (AMC).

Table 3. Cranial characters represented by their acronyms, meaning and description

Acronyms	Meaning	Description
AMC	Maximum skull height	Distance between the basisphenoid-basioccipital suture and the frontoparietal suture.
CBA	Cranial base length	Distance between the posterior border of the incisor alveolus and the anterior border of the foramen magnum.
CFI	Incisive foramen length	Distance between the anterior border and the posterior border of the incisor foramen.
CI	Interparietal length	Anteroposterior distance of the median axis of the interparietal.
CN	Nasal length	Distance between the anterior border of the nasal and the nasofrontal suture.
CO	Orbital length	Internal distance between the frontal and maxillary sutures to the root of the squamous cell present in the zygomatic arch.
CP	Palatal length	Distance between the posterior border of the incisor alveolus and the border of the palate.
CPP	Palatal bridge length	Distance between the posterior border of the incisor foramen and the border of the palate.
CTC	Total skull length	Maximum distance measured between the anterior border of the nasal and the posterior border of the occiput.
DIA	Diastema	Distance between the posterior alveoli of the incisors and the anterior alveoli of the first molar.
LCC	Skull width	Width between the anterior regions of the squamous suture and the occiput.
LCO	Width between occipital condyles	Greater distance between the outer borders of the occipital condyles.
LI	Interparietal width	Maximum distance between the lateral borders of the interparietal.
LIO	Interorbital width	Minimum interobital distance.
LMB	Maximum bulla width	Maximum distance between the junction of the basisphenoid and basioccipital sutures and the outer border of the bulla.
LP	Palatal width	Width between the molar series measured between the first and second molars.
LPZ	Zygomatic plate width	Distance measured at the base of the zygomatic plate from the anterior to the posterior limit.
LRO	Rostral width	Rostrum width measured at the height of the infraorbital foramen.
LZI	Zygomatic arch width	Greater distance between the lateral borders of the zygomatic arch.
SMS	Upper molar teeth series	Distance between the border of the anterior alveolus of the first molar and the border of the posterior alveolus of the third molar.

of three population groups: Araguaia-Tocantins/Amazonas River, Paraná, and Marajó Island. However, in the discriminatory analysis, these three groups overlapped regarding craniometry, with a tendency to segregate (Fig.7).

In PCA, the first component, axis 1 (PC1), synthesizes the dorsal metrics (CTC, IOL, CN, LZI, LCC, and CO) and corresponds to 27.7% of the variation, whereas the second component, axis 2 (PC2), synthesizes the ventral metrics (CFI, SMS, CP, LCO, and CBA) and represents 8.5% of the variation (Fig.8). The most significant morphometric differences were found in the ventral metrics, making them the main component responsible for distinction between the samples.

The structured morphological groups point to a strong relationship between the populations from the Amazonas River and Tocantins-Araguaia basins, and a less intense relationship between the Araguaia-Tocantins/Amazonas River and Paraná basins. In turn, the Araguaia-Tocantins/Amazonas River and Paraná basins alone show more significant craniometric differentiation when compared with each other. The isolated populations from the Marajó Island also proved to be different from the others. However, we emphasize that, because the data referring to the Marajó Island present a low number of analyzed specimens, they may have induced separation of the analyses, causing a deviation.

As for the craniometric characters evaluated for *Hylaeamys megacephalus*, the mean varied between a minimum of 2.62 (LP) and a maximum of 31.10 (CTC) and the standard deviation ranged from 0.29 (IOL) to 2.52 (LZI), as shown in Table 4.

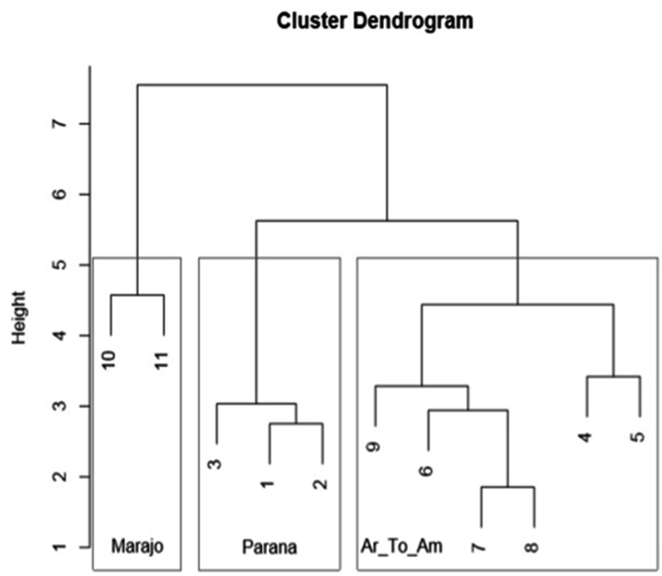

Fig.6. Cluster dendrogram of the *Hylaeamys megacephalus* populations according to craniometry by hydrographic basin.

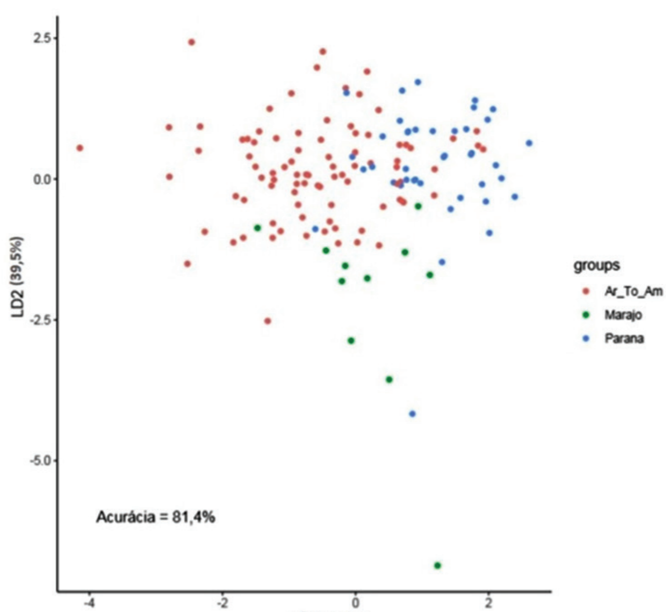

Fig.7. Canonical variate analysis discriminating the three population groups by hydrographic basin.

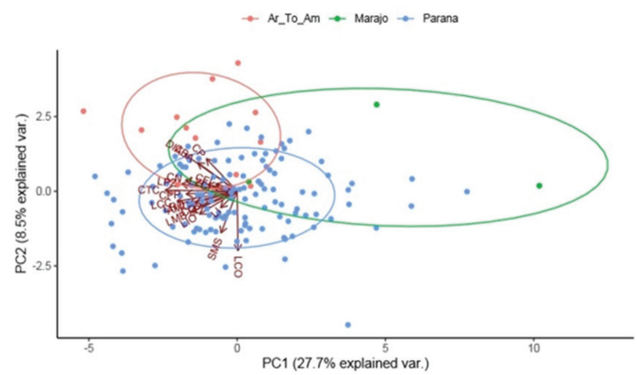

Fig.8. Principal component analysis (PCA) between the *Hylaeamys megacephalus* populations showing the craniometric characters. Principal components: axis 1 (PC1) synthesizes the dorsal metrics, representing 27.7% of the variation; axis 2 (PC2) synthesizes the ventral metrics, corresponding to 8.5% of the variation.

Table 4. Mean and standard deviation of the 20 craniometric characters of the *Hylaeamys megacephalus* samples

Craniometric characters	Mean	Standard deviation
CTC	31.10	1.34
LIO	5.18	0.29
CN	12.83	0.86
CFI	4.23	0.41
DIA	8.16	0.66
LZI	15.21	2.52
LCC	11.83	0.45
LRO	6.00	0.50
SMS	4.68	0.34
LPZ	3.64	0.32
CP	13.68	1.41
CPP	6.95	0.45
LCO	3.46	0.54
CBA	24.52	2.02
CI	4.04	0.54
LI	9.80	0.80
LP	2.62	0.29
CO	9.25	0.53
AMC	9.13	0.42
LMB	5.23	0.49

The Araguaia-Tocantins and Amazonas River basins presented higher CP, DIA and CBA values than the Paraná basin, with these characters related to internal morphology. In contrast, the Paraná basin showed higher SMS values than the Araguaia-Tocantins/Amazonas River basin, with differences also related to internal morphological variables. The Marajó Island basin population groups differ from the other two groups with respect to external variables (CPP, CTC, LPZ, LMB, LIO, AMC, and LRO), with lower values for these variables observed in the first.

DISCUSSION

According to Marroig (2007), a simple increase in skull size can lead animals to consume larger and harder food items or become more resistant to explore new environments and niches. Our results suggested that the morphological characteristic is associated with the environment where the species lives. For this reason, we correlated the craniometric results to the hydrographic basins.

Most of the variables involved in these morphometric differences are associated with the general structure of the skull. The SMS and CP measures, for example, directly contribute to the adaptation of the oral cavity structure, allowing changes in food acquisition habits. Differences in shape can mean functional differences performed by the same parts, revealing different responses when subjected to the same selective pressure (Schmidt-Nielsen 1984, Van Valkenburgh 1994).

Measurement variations should be interpreted so that the components that represent structural measures can and, usually, play an essential role in functional adaptation. Over time, such adaptations have enabled individuals to develop specializations. In this case, the skull shape is highly valuable for these interpretations, because the differences in length and width, such as in the palate, oral cavity or molar teeth series, directly represent the possibility of restructuring the diet.

Analysis of the craniometric similarity between the *Hylaeamys megacephalus* populations from the Araguaia-Tocantins and Amazonas River basins, population 9, located north of the Amazonas River, is craniometrically similar to the other populations of the Cerrado biome (Fig.1 and 6). Thus, our results compared the genetic data reported by Miranda et al. (2007) and Machado et al. (2019), who stated that genes of the clade belonging to the south of the Amazonas River are closer to those of the clade that inhabits the Cerrado, suggesting an allopatric divergence.

This difference between morphological and genetic data can be explained by the use of markers, since the changes observed in morphological characteristics occur through a relatively slower process compared with those in genetic characteristics. The contrast between these data can be justified by geographical influences, despite the strong geographical barrier exerted by the Amazonas River, which affects gene flow. This isolation directly affects two speciation components: the development and establishment of divergence between different forms of discontinuity (Mayr 1970).

Thus, differences between species are influenced by geographical variations and, whether morphological, physiological or ecological, they are potentially isolating mechanisms that reinforce the distinction between two populations (Pearson 2007).

CONCLUSION

Morphological analysis shows the existence of three craniometric groups of *Hylaeamys megacephalus* with a tendency to differentiate as a result of geographical influences.

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Conflict of interest statement.- The authors have no competing interests.

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