

UNIVERSIDADE FEDERAL DE MINAS GERAIS
Instituto de Ciências Biológicas
Programa de Pós-graduação Em Zoologia

Arthur Toledo Ramos Costa França

**BRAIN MORPHOLOGY DESCRIPTION AND COMPARATIVE ANALYSIS OF
AKODONTINI VORONTSOV, 1959 (RODENTIA: CRICETIDAE) RODENTS THROUGH
VIRTUAL ENDOCASTS**

Belo Horizonte
2024

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THROUGH VIRTUAL ENDOCASTS**

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Orientadora: Dr^a. Rafaela Velloso Missagia
Co-Orientador: Dr. Fernando Araújo Perini

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Brain morphology description and comparative analysis of Akodontini Vorontsov, 1959 (Rodentia: Cricetidae) rodents through virtual endocasts

ARTHUR TOLEDO RAMOS COSTA FRANÇA

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Na natureza tudo é indissociável (...)

Wuhu Siburu, Peneira de Arumã – Narrativa umuku masá desana,
Jaime Diakara

RESUMO

Os *endocasts* digitais surgiram como uma ferramenta essencial para o estudo da evolução do cérebro em diversos grupos de vertebrados. O presente estudo traz a primeira análise das relações entre tamanho e forma dos endocasts da tribo de roedores cricetídeos Akodontini, com foco na compreensão dos papéis que estruturas do cérebro, como os bulbos olfatórios, exercem na história natural destes roedores. A partir de imagens de microtomografias computadorizadas, analisamos a morfologia endocraniana de sete espécies de Akodontini com características ecológicas diversas: *Bibimys labiosus*; *Necromys lasiurus*; *Thaptomys nigrita*; *Akodon cursor*; *Blarinomys breviceps*; *Brucepattersonius iheringi*; e *Oxymycterus quaestor*. Espécies como *Blarinomys breviceps* possuem proporções maiores para os bulbos olfatórios, sugerindo capacidades olfativas acentuadas, o que seria importante para a detecção de presas abaixo do solo, correspondendo ao estilo de vida semi-fossorial e hábito predatório da espécie. Análises comparativas de espécies filogeneticamente próximas a *B. breviceps*, como *Brucepattersonius iheringi*, indicaram diversas similaridades na morfologia dos *endocasts*, principalmente em relação aos bulbos olfatórios. Ademais, diferenças nos valores do Quociente de Encefalização (QE) sugerem pressões evolutivas distintas entre os táxons de Akodontini. *Bibimys labiosus*, por exemplo, apresentou o maior QE, o que pode estar relacionado com características relacionadas com a utilização do habitat. O presente estudo evidencia a influência que fatores ecológicos como dieta e locomoção exercem na evolução da morfologia do cérebro de roedores Akodontini. Análises direcionadas para estruturas específicas do cérebro e o papel que exercem nas respectivas trajetórias evolutivas são essenciais para construir um maior entendimento das complexas relações entre morfologia do cérebro, ecologia e evolução em uma das tribos mais diversas de roedores da América do Sul.

Palavras-chave: rodentia; akodontini; endocast; morfologia; sigmodontinae

ABSTRACT

Virtual endocasts of the brain have emerged as an essential tool for understanding brain evolution across various craniate groups. This study presents the first comprehensive analysis of the relationships between endocast size and shape within the Akodontini tribe, with a focus on the role of brain structures such as the olfactory bulb in the clade's ecology and evolution. Using high-definition X-ray computed tomography, we analyzed the endocranial morphology of seven Akodontini species with varying diets and habitats: *Bibimys labiosus*; *Necromys lasiurus*; *Thaptomys nigrita*; *Akodon cursor*; *Blarinomys breviceps*; *Brucepattersonius iheringi* and; *Oxymycterus quaestor*. Our results indicate that species such as *Blarinomys breviceps* exhibit distinct olfactory bulb proportions, suggesting enhanced olfactory capabilities crucial for detecting prey underground, aligning with its semi-fossorial lifestyle. Comparative analysis with closely related species, such as *Brucepattersonius iheringi*, showed notable similarities in endocast morphology, particularly in olfactory bulb structure. However, differences in encephalization quotient (EQ) values suggest varying evolutionary pressures and ecological adaptations. For instance, *Bibimys labiosus* displayed the highest EQ, possibly reflecting its complex forested habitat. Our study underscores the influence of ecological factors like diet and locomotion on brain structure evolution in Akodontini. These findings highlight the need for further exploration of specific brain regions and their roles in species' ecological and evolutionary trajectories. This research contributes to a deeper understanding of the intricate relationships between brain morphology, ecology, and evolution in one of the most diverse rodent tribes.

Keywords: rodentia; akodontini; endocast; morphology; sigmodontinae

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LIST OF ACRONYMS

BM	Estimated body mass
CCT-UFMG Gerais	Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais
CLML	Cerebellum maximal length
CLW	Cerebellum width, not considering the paraflocculus
CRMH	Cerebrum maximal height
CRML	Cerebrum maximal length
CRMW	Cerebrum maximal width
CT	Computerized Tomography
E_c	Estimated brain volume for an animal with its body size
E_i	Real brain volume
EQ	Encephalization Quotient
EV	Endocranial Volume
MCN-M PUC-Minas	Coleção de Mastozoologia do Museu de História Natural da Pontifícia Universidade Católica de Minas Gerais
Mya	Million years
OH	Olfactory bulb height
OL	Olfactory bulb length
OV	Olfactory bulb volume
OW	Olfactory bulb width
PGLS	Phylogenetic Generalized Least Squares
QE	Quociente de Encefalização
TL	Total endocast length.

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1 INTRODUCTION

Rodents encompass almost 2700 species distributed in 35 families holding more than 500 genera, making them, by far, the most diverse mammalian order, representing approximately 40% of the world's extant mammal diversity (Kay & Hoekstra, 2008; Mammal Diversity Database, 2024). By comparison, Chiroptera, the second most diverse order, accounts for only 1500 species (Mammal Diversity Database, 2024). This staggering diversity is a result of high plasticity levels and diversification rates (Upham et al., 2019) that allowed the group to occupy most terrestrial environments throughout the world. Their immense ecological success is, among many factors, commonly associated with two things, their wide-ranging diet and, secondly, their propensity to breed (Kay & Hoekstra, 2008). Many rodents are typical r-strategists, favoring quantity over quality in offspring, and evolved extremely short generation times and extraordinary explorative and adaptive abilities (Spradling et al., 2001). Because of these evolutionary traits, rodents may be classified as a “model-group” for the studies of macroevolution and patterns of convergence (Hautier & Cox, 2015).

The main morphological trait of rodents is the single pair of open-rooted, chisel-shaped incisors, and a prominent diastema associated with the loss of the canine teeth. This configuration gives rodents the ability to gnaw, dig or chew virtually anything, depending on their conformation (Kay & Hoekstra, 2008). The increase in biting efficiency associated with these traits is a result of a forward shift of portions of the masseter muscle that pull the jaw forward from the zygomatic arch onto the rostrum. The earliest rodents and the living *Aplodontia rufa* (Rafinesque, 1817) have the protrogomorphic skull configuration. Extant rodent species diversified in three other different configurations: sciuromorphy, hystricomorphy and myomorphy (Cox et al., 2012; Swanson et al., 2019). In this context, it is relevant to note that the bite efficiency between these masseteric systems present in modern rodents is different: sciuromorphy improves gnawing efficiency, hystricomorphy improves chewing efficiency, and myomorphy improves both gnawing and chewing efficiency (Cox et al., 2012; Swanson et al., 2019).

Fossil material suggests that Rodentia evolutionary history dates back at least 55 Mya, in the Paleocene. Molecular clock analysis, however, points out that the first rodents probably diversified from other Glires (lagomorphs) at around 70 Mya, before the Cretaceous-Paleogene mass extinction (Kay & Hoekstra, 2008; Churakov et al., 2010). Rodent evolution may have

been significantly favored by their small size, short breeding cycles, and wide variety of niches. Consequently, they quickly became one of the most successful mammalian groups.



Figure 1 – Digital illustrations of the analyzed Akodontini species, based on Pardiñas et al. (2017): A – *Bibimys labiosus*; B – *Necromys lasiurus*; C – *Thaptomys nigrita*; D – *Akodon cursor*; E – *Blarinomys breviceps*; F – *Brucepattersonius iheringi*; G – *Oxymycterus quaestor*.

The superfamily of myomorph rodents Muroidea (Cox et al., 2012) includes the family Cricetidae, which is the second most diverse amongst all rodents, with almost 860 living species in about 156 genera distributed throughout the Americas and great part of Eurasia (Mammal Diversity Database, 2024). Out of the subfamilies of Cricetidae, Sigmodontinae Wagner, 1843 stands out (Patton, 2015), being the most diverse with more than 500 species and 94 genera (Mammal Diversity Database, 2024). The subfamily current range goes from Tierra del Fuego

in southernmost Argentina to southern North America (D'Elía & Pardiñas, 2015), encompassing virtually all habitats and altitudes throughout South and Central America, from sea level to nearly 5000m at the Andes. Most of Sigmodontinae diversity are endemic to Central and South America, with a great partmost of the genera being exclusively found in South America and adjacent Caribbean islands. They are present in all ecosystems, such as deserts, tropical rainforests, temperate forests, savannas, salt flats, scrublands and steppes (Hershkovitz, 1962; D'Elía & Pardiñas, 2015). Different phylogenetic studies have tried to elucidate Sigmodontinae evolutionary history, and they have been divided into different tribes with different compositions over the years (Reig, 1980; Smith & Patton, 1999; Jansa & Weskler, 2004; Leite et al., 2014; Cazzaniga et al., 2019). Initially, Sigmodontinae comprised seven clearly distinguished tribes (Reig, 1972), but according to more recent studies (Cazzaniga et al., 2019), Sigmodontinae is currently composed of 11 tribes.

Among Sigmodontinae, the tribe Akodontini Vorontsov, 1959 is the second most diverse (D'Elía & Pardiñas, 2015), behind only Oryzomyini Vorontsov, 1959. Over the years, the tribe went through different compositions. Initially, the group only included the genus *Akodon* Meyen, 1883 (Cockerell et al., 1914). Morphological similarities between other Sigmodontinae genera and *Akodon* were recognized afterwards (Tate, 1932), and only recently molecular data offered a well-supported phylogenetic hypothesis for the tribe (D'Elía 2003; Leite et al. 2014; Leite et al., 2015; Maestri et al., 2017; Stepan & Schenk, 2017), after years of disagreements in regards to their phylogenetic relationships (Tate, 1932; Vorontzov, 1959; Hoopper & Musser, 1964; Hershkovitz, 1966; Smith & Patton, 1991, 1993, 1999). Currently, according to molecular data, Akodontini encompasses lineages (Maestri et al., 2017, 2019; Stepan & Schenk, 2017) that represent an important radiation of rodents in South America, with species that are highly versatile, occupying a wide range of habitats (Reig, 1972, 1987; D'Elía & Pardiñas, 2015).

These lineages comprises the genus *Akodon*, *Castoria* Pardiñas, Geise Ventura and Lessa, 2016, *Deltamys* Thomas, 1917, *Necromys* Ameghino, 1889, *Podoxymys* Anthony, 1929, *Thalpomys* Thomas, 1916, *Thaptomys* Thomas, 1916, *Oxymycterus* Waterhouse, 1837, *Juscelinomys* Moojen, 1965, *Blarinomys* Thomas, 1896, *Brucepattersonius* Hershkovitz, 1998, *Bibimys* Massoia, 1979, *Lenoxus* Thomas, 1909, *Kunsia* Hershkovitz, 1966 and *Scapteromys* Waterhouse, 1837. The adaptive types in Akodontini are highly diverse, with fossorial and semi aquatic specialized genera (*Blarinomys* and *Scapteromys*, respectively), the largest living

sigmodontine (*Kunsia*, *Gyldenstolpia*) and generalist cursorial species (such as *Akodon* and *Necromys*) (Hershkovitz, 1966; Reig, 1972, 1987; D'Elía & Pardiñas 2015).

However, one important aspect of Akodontini evolution and natural history is still poorly known: brain morphology, structure development, their association with the clade speciation process, and the role the brain and its subsequent structures have in the success of the tribe in occupying many diverse niches. As an alternative to the use of the brain in preserved specimens, many studies have conducted analysis of the endocranium (Bertrand & Silcox, 2016; Martinez et al., 2018; Ferreira et al., 2020; Bertrand et al., 2021). The endocranium is the part of the skull that shelters the olfactory bulbs, the cerebrum and the cerebellum, and which reflects the anatomy of the brain (Bertrand & Silcox, 2016). These structures are mirrored in the endocasts, which are basically molds of the internal anatomy of the cranial cavity and are currently one of the most versatile ways of assessing endocranium analysis. Traditionally, endocasts were achieved by filling the skull with latex, which eventually led to the possibility of breaking and damaging the specimen (Bertrand & Silcox, 2016; Holloway, 2018). However, with easier access to high-definition X-ray computed tomography scanners, this kind of information is now more readily available (Bertrand & Silcox, 2016; Czeibert et al., 2020). Endocast morphology analyses constitute an important tool for the studies of ecological and evolutionary relations within Craniata (Bertrand & Silcox, 2016; Bertrand et al., 2019; Ferreira et al., 2020; Bertrand et al., 2021; Villoldo et al., 2023). Furthermore, because they reflect brain anatomy, endocasts present variations according to ecological and evolutionary characteristics, such as locomotion and diet (Harvey & Krebs, 1990, Bertrand et al. 2019; Kerber et al., 2019).

Information regarding the species cognitive abilities may be related to ecological characteristics and are frequently assessed by the use of the encephalization quotient (EQ), which is the calculation of the proportion between real brain volume (E_i) and estimated brain volume for an animal with its body size (E_c) (Jerison, 1973; Aguirre et al., 2021), as specified in **Equation 1**.

Equation 1 - Encephalization Quotient Equation

$$EQ = \frac{E_i}{E_c}$$

In this regard, multiple studies have assessed the relations between various ecologies and behaviors and relative brain size in different mammalian groups throughout the years (Eisenberg & Wilson, 1978; Clutton-Brock & Harvey, 1980; Harvey et al., 1980; Eisenberg &

Wilson, 1981; Mace et al., 1981; Roth & Torington, 1982; Meier, 1983; Pilleri et al., 1984a; Gittleman, 1986; Bernard & Nurton, 1993; Shultz & Dunbar, 2006). Still, much of this work did not take into consideration the key factor of phylogenetic relationships, and used methods that could not discriminate important brain regions, such as the neocortex, responsible for sensory processing and integration, or the olfactory bulbs, associated with the sense of smell (Bertrand et al., 2021). Previous studies suggest that animalivorous species may present more developed olfactory bulbs (Martinez et al. 2018; 2020), while species with different locomotion methods may present differences in cerebellum size (Sultan & Glickstein, 2007; Camargo et al. 2019).

Considering the lack of information available for most Sigmodontinae species, in general, and the tribe Akodontini, in particular, the main objective of this study is to investigate the endocranium morphology of seven species of Akodontini rodents. Of these, one, *Bibimys labiosus* (Winge, 1887), tends to an herbivorous diet, with an apparent higher consumption of C4 plants (Maestri et al., 2016; Pardiñas et al., 2017; Missagia et al., 2019). Three show more generalist diets, including a diverse array of seeds, fruits, vegetation and occasional arthropods: *Necomys lasiurus* (Lund, 1841), *Thaptomys nigrita* (Lichtenstein, 1829) and *Akodon cursor* (Winge, 1887) (Maestri et al., 2016; Pardiñas et al., 2017; Missagia et al., 2019). The remaining three present more specialized diets, with a higher concentration and specializations towards carnivory, predated mainly arthropods and worms: *Blarinomys breviceps* (Winge, 1887), *Brucepattersonius iheringi* (Thomas, 1896) and *Oxymycterus quaestor* Thomas, 1903 (Maestri et al., 2016; Pardiñas et al., 2017; Missagia et al., 2019) (**Figure 1**).

For the specific objectives, we describe the main morphological characteristics of the endocasts of these species, assessing their differences and similarities regarding the group's phylogeny and EQ. Furthermore, we investigate differences in the volume and shape of the olfactory bulb, cerebrum and cerebellum, to associate the analyzed species ecology and natural history with these traits.

2 MATERIAL AND METHODS

The analyzed specimens came from two different collections in Brazil: the Centro de Coleções Taxonômicas of the Universidade Federal de Minas Gerais (CCT-UFMG) and the Coleção de Mastozoologia do Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN-M PUC-Minas). Vouchers from the CCT-UFMG and MCN-M PUC Minas were

scanned with a Skyscan 1174 Compact Desk-Top Micro-CT at the Laboratório de Biomateriais of the Escola de Engenharia of the UFMG. Specimens' vouchers are listed in **Table 1**.

Before generating the endocasts, the scanned dataset was aligned accordingly to the z-axis, y-axis and x-axis with the DataViewer software (Bruker, 2016). The endocasts were obtained through virtual processing of the Akodontini specimens CT Scan images on the 3DSlicer software (Fedorov et al., 2012). We utilized the SlicerMorph platform to achieve a better approach on morphometric tools (Rolfe et al., 2021). Digital endocasts were done manually, following the osseous boundaries of the skull, and smoothed out to remove any imperfections. Quantitative result analysis of the endocast volumes, discerning brain cavity and olfactory bulb, were calculated with the 3D Slicer "Segment Statistics" tool (Fedorov et al. 2012), following the proposed guidelines in Jerison (2012) and Bertrand and Silcox (2016).

Table 1 – Vouchers and localities of the analyzed Akodontini specimens

Species	Voucher	Locality
<i>Akodon cursor</i>	UFMG 6120	Rio Pomba, Minas Gerais, Brazil
<i>Bibimys labiosus</i>	MCN-M 2829	Serra do Salitre, Minas Gerais, Brazil
<i>Blarinomys breviceps</i>	UFMG 4033	Mariana, Minas Gerais, Brazil
<i>Brucepattersonius iheringi</i>	UFMG 6198	Serra do Itajaí National Park, Indaial, Santa Catarina, Brazil
<i>Necomys lasiurus</i>	UFMG 3916	RPPN Mata Samuel de Paula, Nova Lima, Brazil
<i>Oxymycterus quaestor</i>	UFMG 8128	Nova Lima, Minas Gerais, Brazil
<i>Thaptomys nigrita</i>	UFMG 6195	Serra do Itajaí National Park, Indaial, Santa Catarina, Brazil

After the quantitatives were obtained, it was necessary to obtain the real size of the brain (E_i) to calculate the EQ, following Gompertz (1902), Stephan et al. (1981), and Ferreira et al. (2022), in which the endocast volume (cm^3) is multiplied by 1,036, the cerebral gravity median (Gompertz, 1902), specified in **Equation 2**.

Equation 2 – E_i Equation

$$E_i = V (cm_3) \times 1,036$$

Jerison (1973) proposed the original EQ equation, in which $E_c = 0,12$ [body mass]^{0,67}. However, this equation had the intercept (0,12) too high for small mammals, based on extant species.

Eisenberg (1981) proposed an adaptation, in which the equation $E_c = 0,0553 [\text{body mass}]^{0,74}$ solved the intercept issue, although the slope (0,74) was too steep for rodents, which overestimated the EQ for small mammals and underestimated the EQ for larger mammals (Bertrand & Silcox, 2016). In this regard, the Pilleri et al. (1984b) equation was created specifically for rodents to obtain the estimated brain volume (E_c) for each specimen, in which the body mass is elevated to 0,6419, and multiplied by 0,00997, as specified in **Equation 3**. The Pilleri et al. (1984b) equation is ideal because the slope is lower, but the intercept is higher, when compared with Eisenbergs' (1981) equation. However, to allow for comparisons with other mammalian groups, results for the EQ to both Jerison (1973) and Eisenberg (1983) are also traditionally reported (Bertrand & Silcox, 2016).

Equation 3 - Pilleri et al. (1984b) E_c Equation

$$E_c = 0,00997 \times [\text{body mass}]^{0,6419}$$

To estimate body mass, since not always the material in scientific collections provide information on specimens' weight, we calculated a median weight based on literature data, (Maestri et al., 2017; Pardiñas et al., 2017) (**Table 2**).

Table 2 – Estimated body mass (BM), in g, from data available at Maestri et al., 2017 and Pardiñas et al., 2017 for the analyzed Akodontini species.

Species	BM (Maestri et al., 2017)	BM (Pardiñas et al., 2017)	Mean BM
<i>Akodon cursor</i>	48,7	43-50	47,23
<i>Bibimys labiosus</i>	30	23-26	26,33
<i>Blarinomys breviceps</i>	36	12,5-49	32,50
<i>Brucepattersonius iheringi</i>	43	40-45	42,66
<i>Necomys lasiurus</i>	28,8	20-67,5	38,76
<i>Oxymycterus quaestor</i>	-	100	100,00
<i>Thaptomys nigrita</i>	19,9	18-27	21,63

In addition to the EQ, we investigated the proportions between the obtained values and the species weight; the endocasts' whole volume with the individuals' weight; the part the olfactory bulb occupied in the endocast with the animal's weight; and further ratios calculated with linear measurements taken for the endocasts, as evidenced in **Figure 2**. Furthermore, Phylogenetic

Generalised Least Squares (PGLS) regressions were performed as a way of accessing trait correlations between the obtained proportions, accounting for the evolutionary association of analyzed species (Grafen, 1989; Martins & Hansen, 1997; Pagel, 1997, 1999; Rohlf, 2001), as specified by Symonds and Blomberg (2014). The utilized phylogeny was based on Upham et al. (2019), and the PGLS was performed within R statistical framework (R Core Team, 2024) with RStudio (RStudio Team, 2024) through the packages *ape* (Paradis et al., 2004), *caper* (Orme et al., 2012), *phytools* (Revell, 2012), and *geiger* (Pennell et al., 2014). The RStudio script is available in Appendix 1 – RStudio PGLS Script.

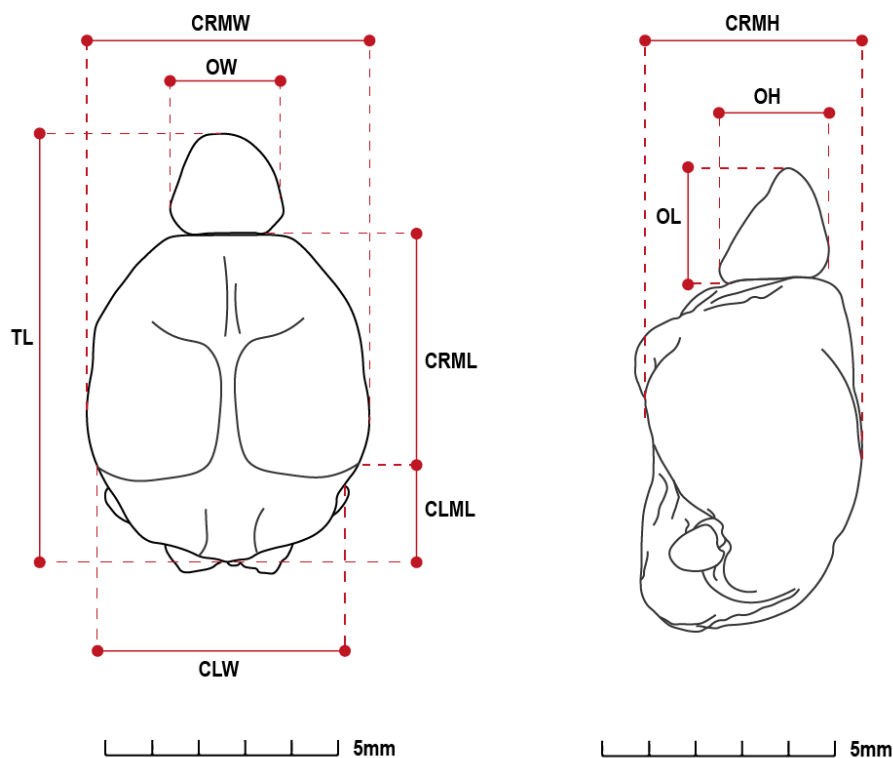
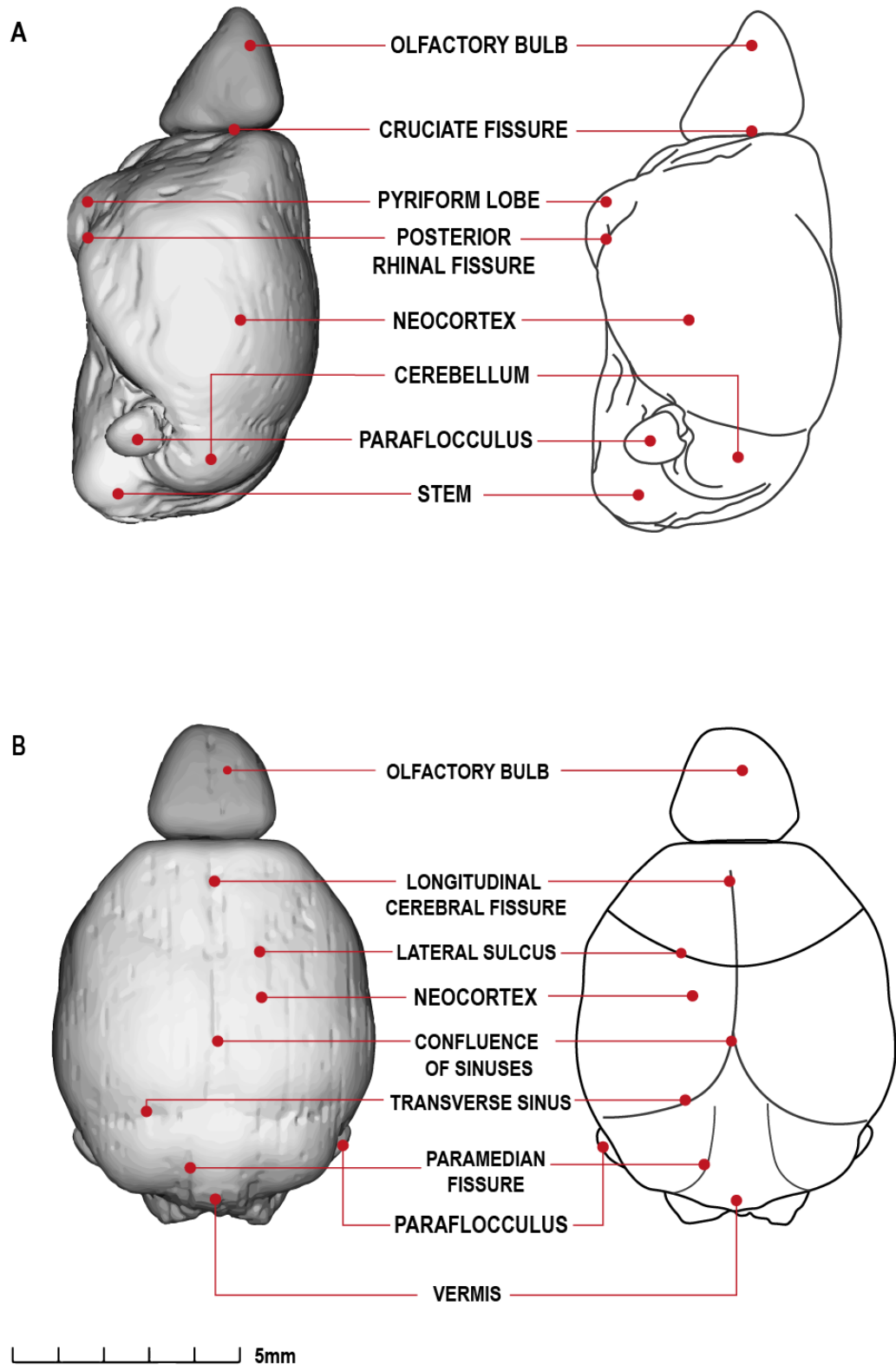


Figure 2 – Linear measurements taken, adapted from Bertrand & Silcox (2016). Illustration based on *Necromys lasiurus* – UFMG 3916.

Linear measurements were taken for every specimen, for total endocast length (TL), olfactory bulbs length (OL), olfactory bulbs width (OW), olfactory bulbs height (OH), cerebrum maximal length (CRML), cerebrum maximal width (CRMW), cerebrum maximal height (CRMH), cerebellum width, not considering the paraflocculus (CLW), and cerebellum maximal length (CLML), as shown in **Figure 2** (adapted from Bertrand & Silcox, 2016), with 3DSlicer measurement tools. Following these guidelines, the cerebrum delimitations correspond to the area of the neocortex. Additionally, linear measurements ratios were calculated to achieve a more robust approach on understanding the proportions the main structures of the brain measured herein occupy in a broader functional analysis. The calculated ratios were OL/TL,

CRML/TL, CLML/TL, CLW/CRMW, OW/CRMW and OH/CRMH. The morphological description of the brain followed, as a guideline, the structures specified in Cooper and Schiller (1975) and Bertrand and Silcox (2016), as shown in **Figure 3**.



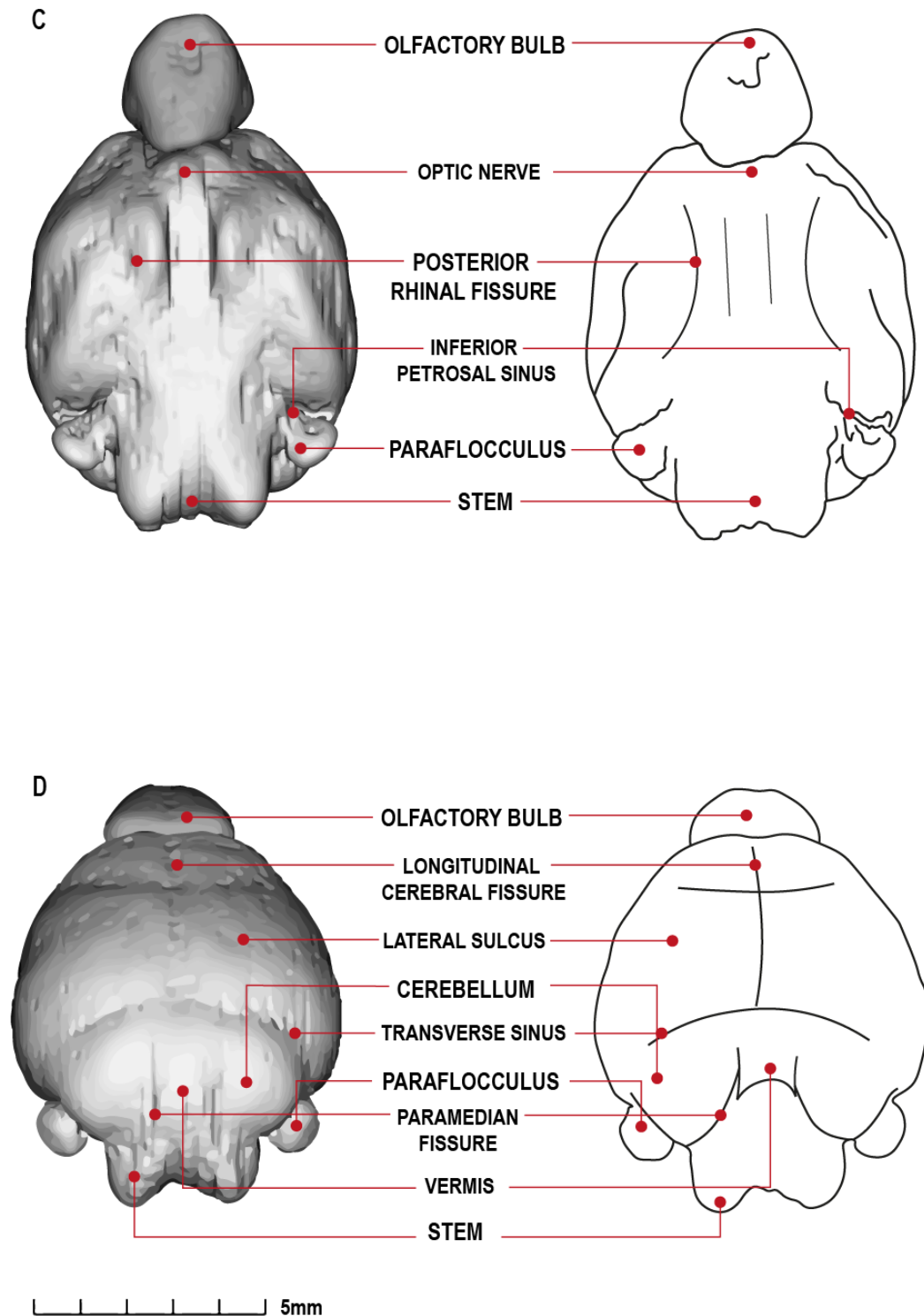


Figure 3 – Morphological structures of the Akodontini rodent brain, according to Cooper and Schiller (1975) and Bertrand and Silcox (2016), based on digital endocasts. Illustration based on *Necromys lasiurus* – UFMG 3916. A: lateral view; B: dorsal view; C: ventral view; D: posterior view.

3 RESULTS

3.1 Encephalization Quotient (EQ)

The estimated EQ for the generalized mammal is close to 1,0 (Perini et al. 2022). The median EQ using Pilleri et al. (1984b) equation for the Akodontini species was 1,08, which poses higher to the average EQ values for Myomorpha rodents - usually below 1,0 (Bertrand & Silcox, 2016) - and than the Rodentia mean EQ of approximately 0,98 (Boddy et al., 2012). Following the Pilleri et al. (1984b) equation, the highest EQ belonged to *Bibimys labiosus* (1,49), followed by *Necomys lasiurus* (1,11), *Thaptomys nigrita* (1,05), *Oxymycterus quaestor* (1,04), *Blarinomys breviceps* (1,04), *Akodon cursor* (1,01) and, lastly, *Brucepattersonius iheringi* with the lowest EQ (0,83) (**Table 3**). In this regard, the EQ didn't showcase major phylogenetic patterns (Maestri et al. 2017, 2019; Stepan & Schenk, 2017; Missagia et al. 2019). The EQ calculated according to the equations from Jerison (1973) and Eisenberg (1981) showed similar results, in which the highest value was found in *Bibimys labiosus* (0,11 and 0,19, respectively), and the lowest in *Brucepattersonius iheringi* (0,06 and 0,10, respectively). Quantitative values of endocranial volumes, olfactory bulb volumes and encephalization quotient are shown in **Table 3**. Furthermore, **Figure 4** illustrates the differences in encephalization quotients.

Table 3 – Endocranial volume (EV), olfactory bulb volume (OV), estimated body mass (BM), and Encephalization Quotient (EQ) from Jerison (1973), Eisenberg (1981) and Pilleri et al. (1984b).

Species	EV (cm ³)	OV (cm ³)	BM (g)	EQ (1973)	EQ (1981)	EQ (1984)
<i>Akodon cursor</i>	0,1160	0,0052	47,23	0,07	0,13	1,01
<i>Bibimys labiosus</i>	0,1167	0,0035	26,33	0,11	0,19	1,49
<i>Blarinomys breviceps</i>	0,0933	0,0048	32,50	0,08	0,13	1,04
<i>Brucepattersonius iheringi</i>	0,0892	0,0438	42,66	0,06	0,10	0,83
<i>Necomys lasiurus</i>	0,1113	0,0055	38,76	0,08	0,14	1,11
<i>Oxymycterus quaestor</i>	0,1926	0,0101	100,00	0,07	0,12	1,04
<i>Thaptomys nigrita</i>	0,0729	0,0034	21,63	0,08	0,14	1,05

The ratio between olfactory bulb volume (OV), and endocranial volume (EV) showed that the smallest olfactory bulb, proportionally, belongs to *Bibimys labiosus* (3%), despite having the highest EQ; while the largest belongs to *Blarinomys breviceps* and *Oxymycterus quaestor*

(5,2%), followed by *Necromys lasiurus* (5%), *Brucepattersonius iheringi* (4,9%), *Thaptomys nigrita* (4,6%) and *Akodon cursor* (4,5%).

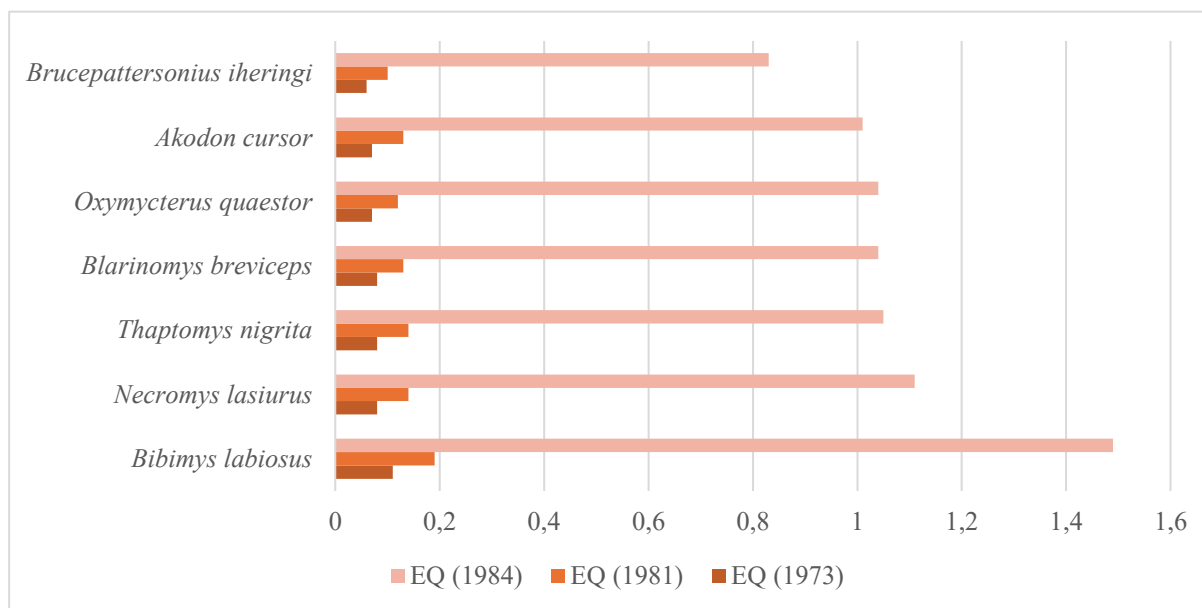


Figure 4 – Graphic representation of Encephalization Quotient (EQ) from Jerison (1973), Eisenberg (1981) and Pilleri et al. (1984b) between the analyzed species.

3.2 Phylogenetic Generalized Least Squares (PGLS)

PGLS analysis between Pilleri et al. (1984b) EQ values and specimens' body mass (**Figure 5**) corroborated the discrepancy found in *Bibimys labiosus* relatively large EQ, when in comparison with other Akodontini species, which was also found in the PGLS between the OV/EV ratio and BM (**Figure 6**). Proportionally, the insectivorous *Brucepattersonius iheringi* evidenced the smallest EQ/BM ratio. The remaining analyzed species stayed close to the expected EQ values.

In the PGLS analysis on the ratio between olfactory bulb and total endocast volume (**Figure 7**), *Bibimys labiosus* presented, again, the highest discrepancy, with a small OB compared to the total endocast. This is also evidenced in the morphological analysis and linear measurements presented in **Table 4** and **Table 5**. *Blarinomys breviceps* and *Brucepattersonius iheringi* stayed in relative proximity in this analysis, which is befitting their close phylogenetic relationships (Maestri et al. 2017, 2019; Steppan & Schenk, 2017). The more generalist *Necromys lasiurus* and *Akodon cursor* also shared similar endocranium proportions (Maestri et al., 2016; Pardiñas et al., 2017), even though they are not as closely related as *Blarinomys breviceps* and *Brucepattersonius iheringi* (Maestri et al. 2017, 2019; Steppan & Schenk, 2017).

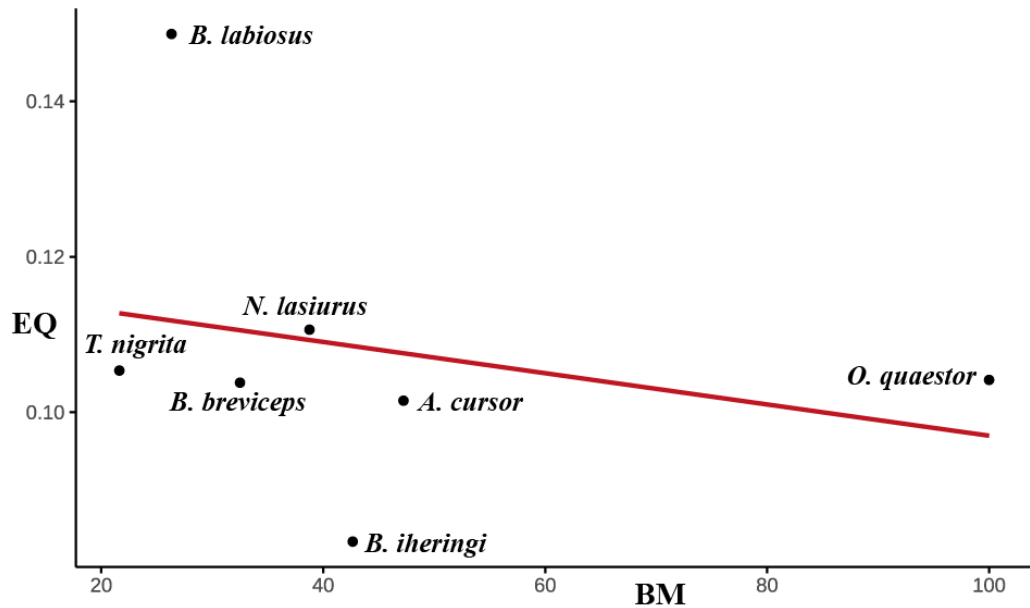


Figure 5 – Phylogenetic Generalized Least Squares (PGLS) analysis between encephalization quotient (EQ) and body mass (BM).

Endocranium proportions of the herbivorous *Bibimys labiosus* are closer to those of *Thaptomys nigrita*, which is more generalist (Maestri et al., 2016; Pardiñas et al., 2017). In the ratio between EV and OV (Figure 7), most analyzed specimens are, apparently, close to the regression line, except for *Bibimys labiosus* which shows a larger residual.

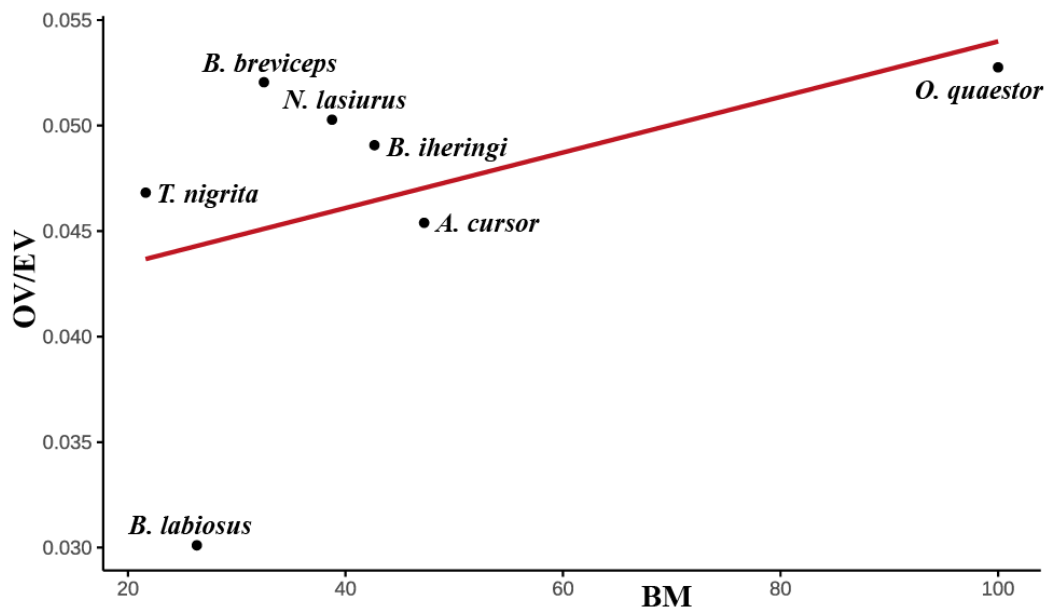


Figure 6 – Phylogenetic Generalized Least Squares (PGLS) analysis between olfactory bulb volume (OV) and endocranium volume (EV) with body mass (BM).

On the other hand, the PGLS analysis between OV and BM did not evidence any discrepancies considering the expected proportions, with all analyzed specimens close to the regression line (Figure 8).

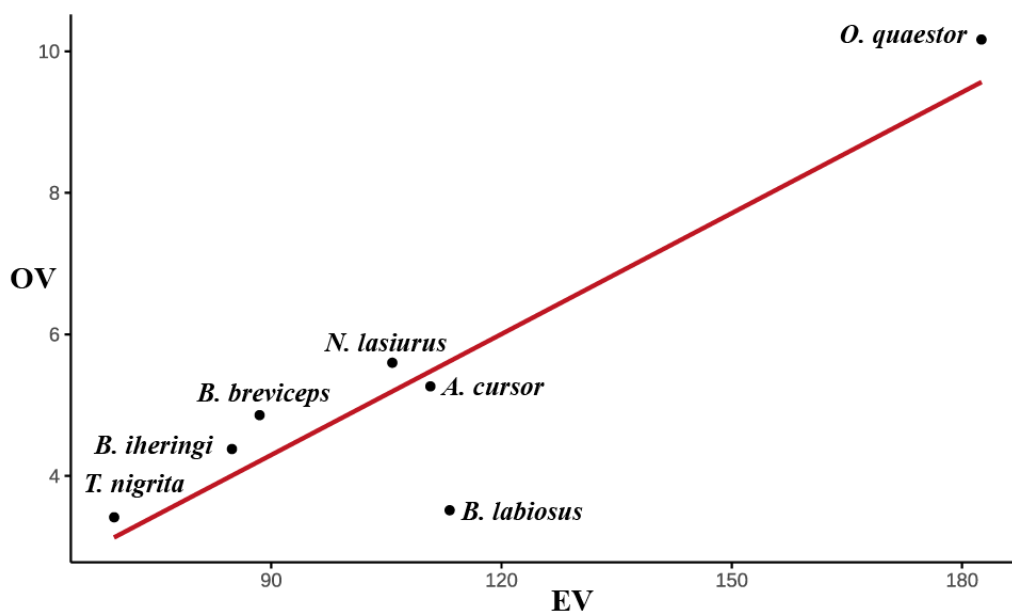


Figure 7 – Phylogenetic Generalized Least Squares (PGLS) analysis between olfactory bulb volume (OV) and endocast volume (EV).

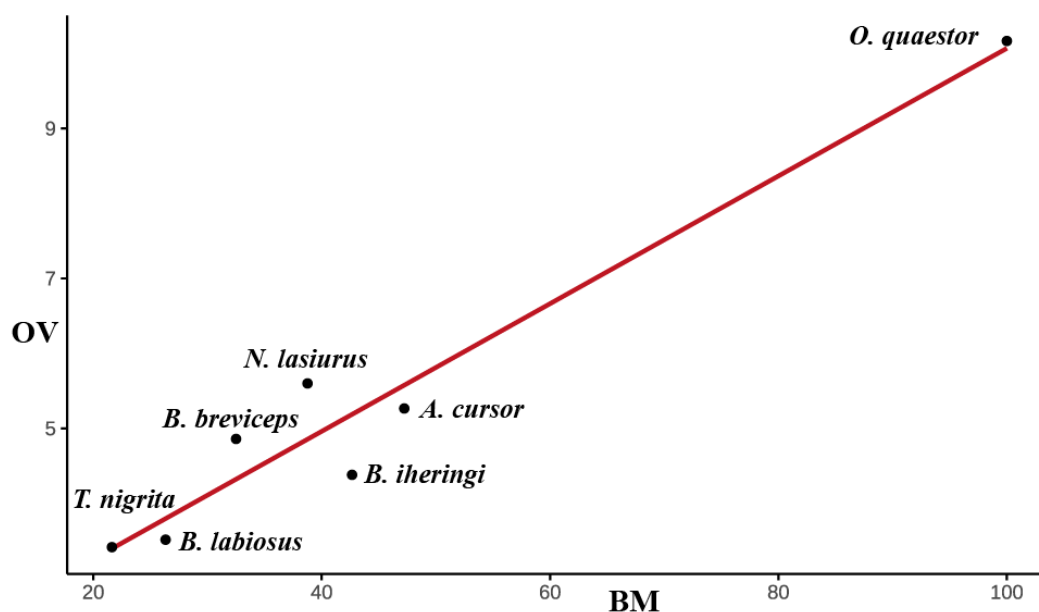


Figure 8 – Phylogenetic Generalized Least Squares (PGLS) analysis between olfactory bulb volume (OV) and body mass (BM).

3.3 Linear Measurements and Morphological Analysis

The olfactory bulb accounted for 19% of the total endocast length in *Bibimys labiosus*, *Brucepattersonius iheringi* and *Oxymycterus quaestor*, being the smallest ratios of all

considered species. *Thaptomys nigrita* presents the highest proportion with 26%, followed by *Necromys lasiurus* (24%), and, lastly, by *Akodon cursor* and *Blarinomys breviceps*, both with 21%. When considering olfactory bulb width, in comparison with the total cerebrum/neocortex width, *Bibimys labiosus* also evidenced the smallest ratio (34%), followed by *Necromys lasiurus* (40%), *Akodon cursor* (42%), *Thaptomys nigrita* (43%), *Oxymycterus quaestor* (46%), *Brucepattersonius iheringi* (48%) and *Blarinomys breviceps* (51%). Furthermore, the olfactory bulb height was also the smallest in *Bibimys labiosus* with 45% of the height identified for the cerebrum, followed by *Brucepattersonius iheringi* (48%), *Oxymycterus quaestor* and *Akodon cursor*, both with 50%, *Thaptomys nigrita* (52%) and, lastly, *Blarinomys breviceps*, with 55% of the accounted height (Table 5).

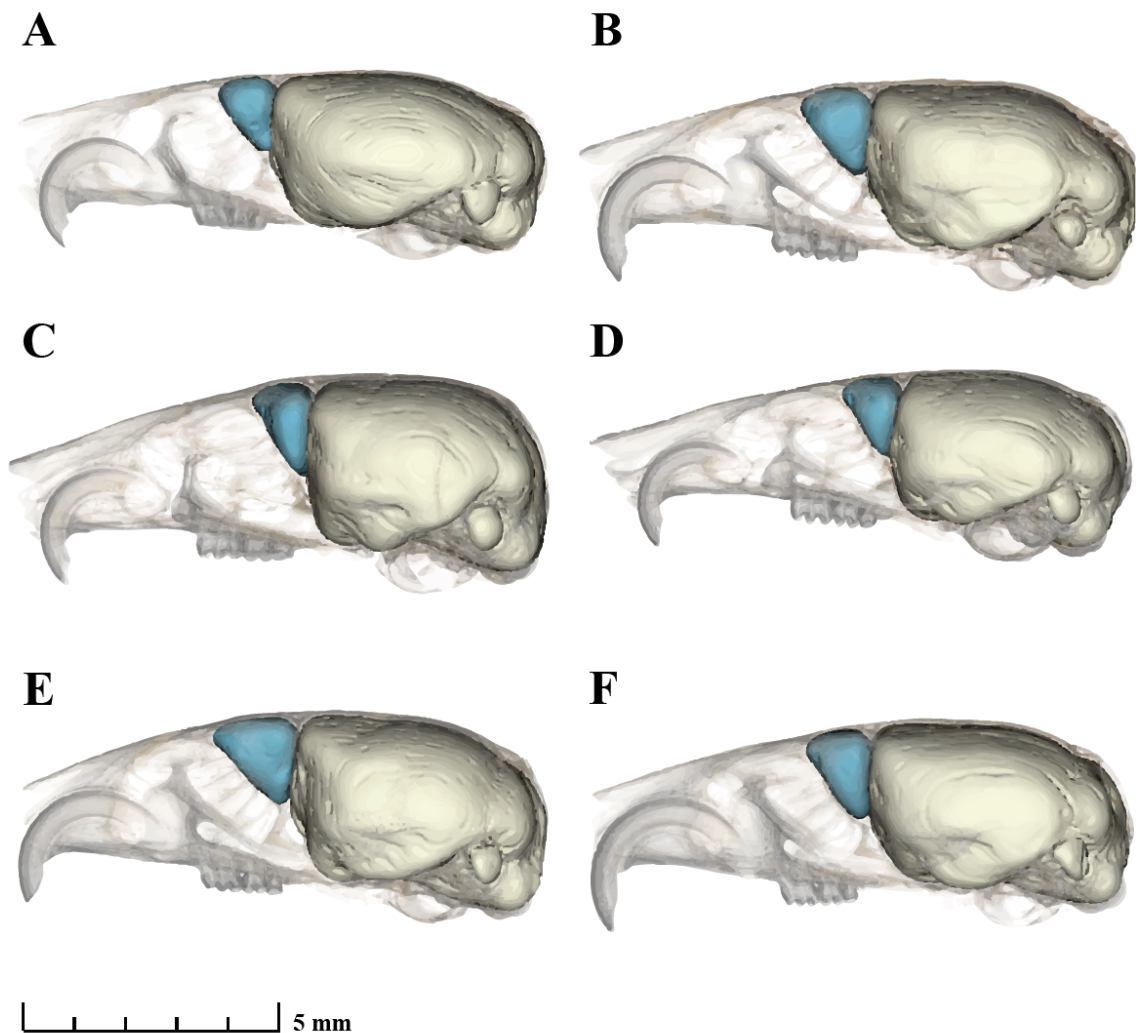


Figure 9 – Lateral view of the endocasts within the skull of: A – *Bibimys labiosus*; B – *Akodon cursor*; C – *Blarinomys breviceps*; D – *Brucepattersonius iheringi*; E – *Necromys lasiurus*; and F – *Thaptomys nigrita*. Blue area represents the olfactory bulb and, the gray area, the remaining structures of the brain. The confluence of these areas corresponds to the cruciate fissure.

Regarding the position of the olfactory bulbs in the skull, *Akodon cursor*, *Necromys lasiurus* and *Bibimys labiosus* present the cruciate fissure above and before the M3, ending approximately above and in the middle of the M1. *Blarinomys breviceps*, *Brucepattersonius iheringi*, and *Oxymycterus quaestor* cruciate fissure start further above and before the M3 and end above and between M2 and M1. *Thaptomys nigrita* cruciate fissure starts even further before, in the M3, and ends almost at the start of M1 (**Figure 9** and **Figure 14**). *Oxymycterus quaestor* voucher (UFMG 8128) is preserved in liquid, and the endocast contains musculature artifacts. In this regard, the corresponding lateral view is presented in the Appendix 2 – Lateral view of the endocast of *Oxymycterus quaestor* Thomas, 1903.

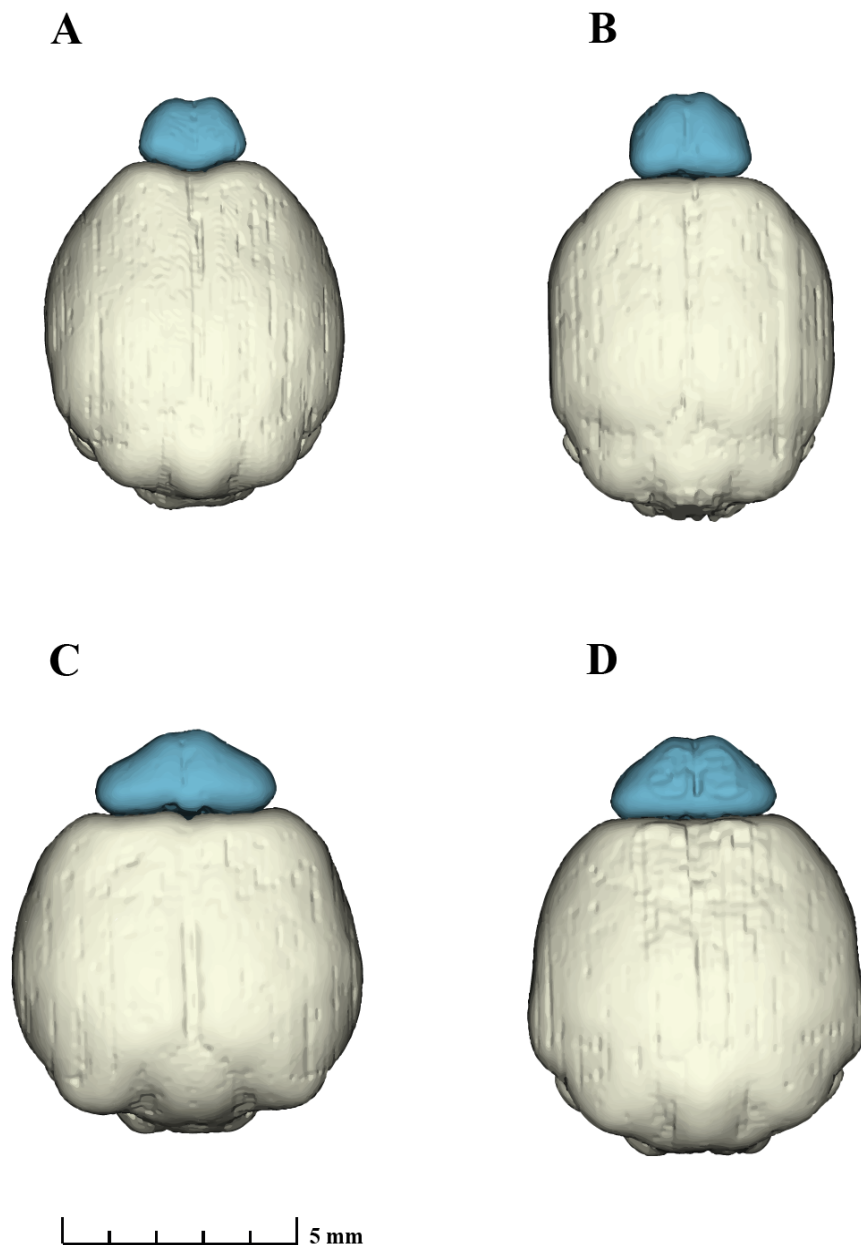


Figure 10 – Dorsal view of the endocasts of: A – *Bibimys labiosus*; B – *Akodon cursor*; C – *Blarinomys breviceps*; D – *Brucepattersonius iheringi*.

Concerning the neocortex and structures of the cerebrum, *Bibimys labiosus* had the longest ratio when compared with the total endocast length, occupying approximately 70% of it. *Brucepattersonius iheringi* followed with 67%, *Blarinomys breviceps* and *Oxymycterus quaestor* with 66% and in *Akodon cursor*, *Necromys lasiurus* and *Thaptomys nigrita* it accounted for 62% of the total endocast length.

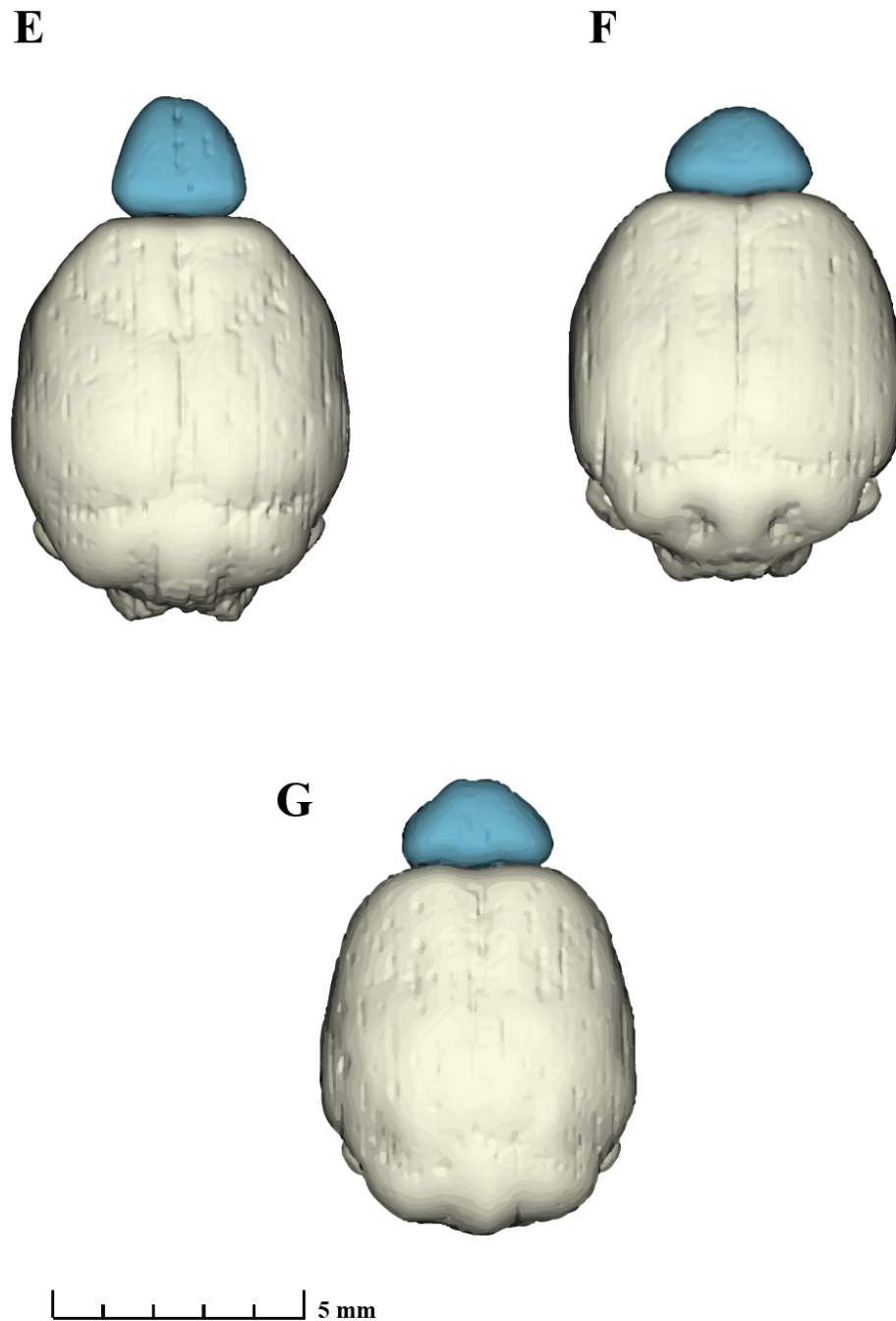


Figure 11 – Dorsal view of the endocasts of: E – *Necromys lasiurus*; F – *Thaptomys nigrita*; G – *Oxymycterus quaestor*.

When analyzing the morphological structure of the neocortex, *Akodon cursor* has a cerebrum maximal width of 6,07 mm (Table 4), with a lateral sulcus occupying a larger portion of the endocast than the transverse sinus, which gives the endocast an octagonal shape (Figure 10 and Figure 11). *Necromys lasiurus* has similar features, differentiated mainly by the accentuated prominence of the longitudinal cerebral fissure, and a wider transverse sinus than the lateral sulcus. *Bibimys labiosus*, with a proportionally long maximal width of 6,40 mm, evidences a conical shape towards the cruciate fissure, with almost no sign of the lateral sulcus.

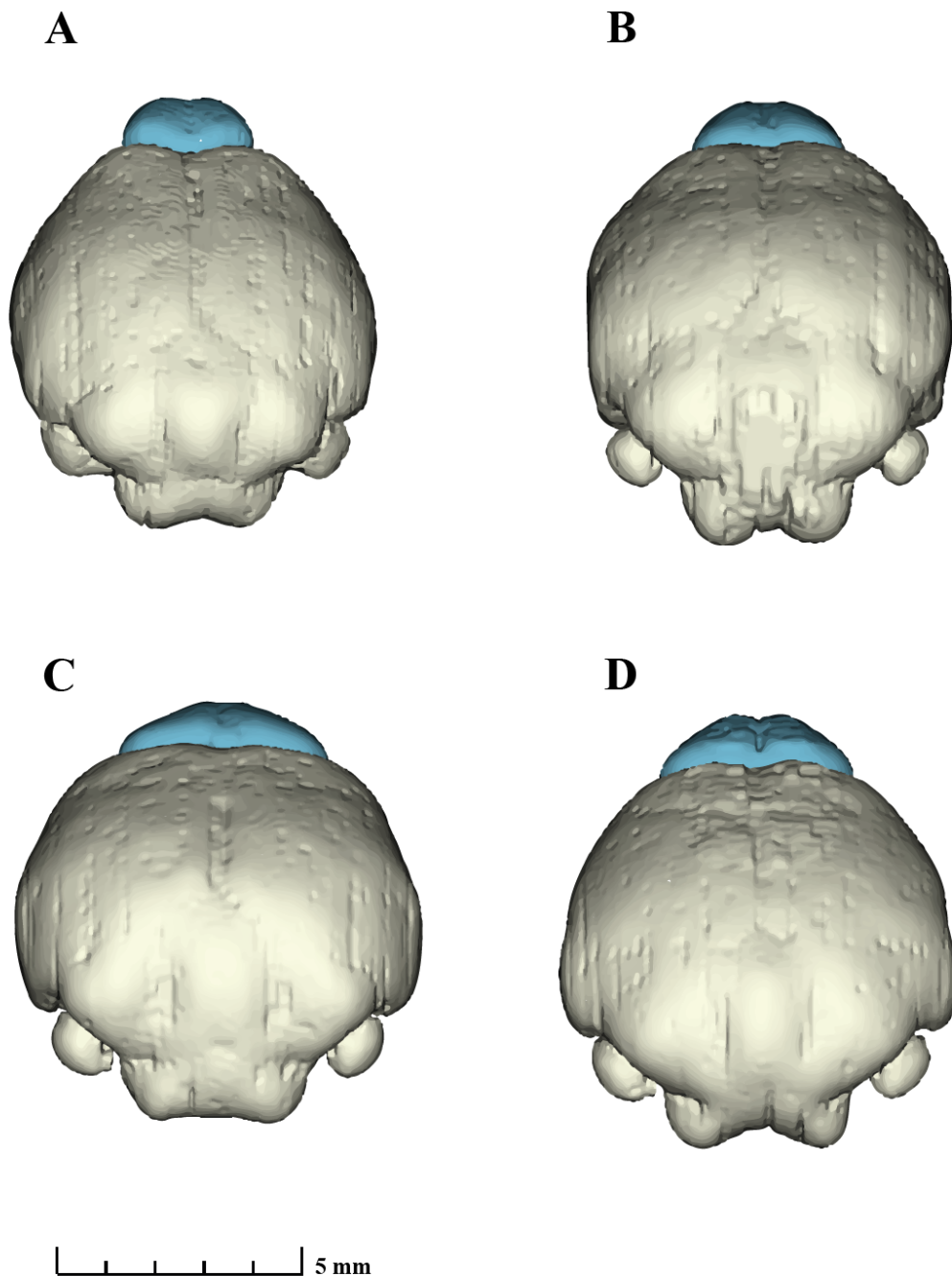


Figure 12 – Posterior view of the endocasts of: A – *Bibimys labiosus*; B – *Akodon cursor*; C – *Blarinomys breviceps*; D – *Brucepattersonius iheringi*.

Furthermore, the cruciate fissure in *Bibimys labiosus* is not straight, which is reflected in a highlighted curved feature in the neocortex of this species. *Blarinomys breviceps* and *Brucepattersonius iheringi* are similar to each other, with a cerebrum width of 6,22 mm and 6,08 mm, and length of 4,48 and 4,79, respectively, with proportionally shorter cerebrums accounting for only 72% and 79% in the ratio between cerebrum maximal length to cerebral maximal width, when compared to *Oxymycterus quaestor*, for which it accounts for 94%, proportionally the longest cerebrum. *Blarinomys breviceps* also has a prominent feature in this part of the endocast, which is a large and wide longitudinal cerebral fissure before the transverse sinus. *Thaptomys nigrita* has a relatively smoother surface, with wide longitudinal cerebral fissure, however, with a longer cerebrum than *Blarinomys breviceps* and *Brucepattersonius iheringi*. *Oxymycterus quaestor*, besides having a long cerebrum of 94% length to width ratio, also has longer measurements in general, being the largest species analyzed (**Table 4**).

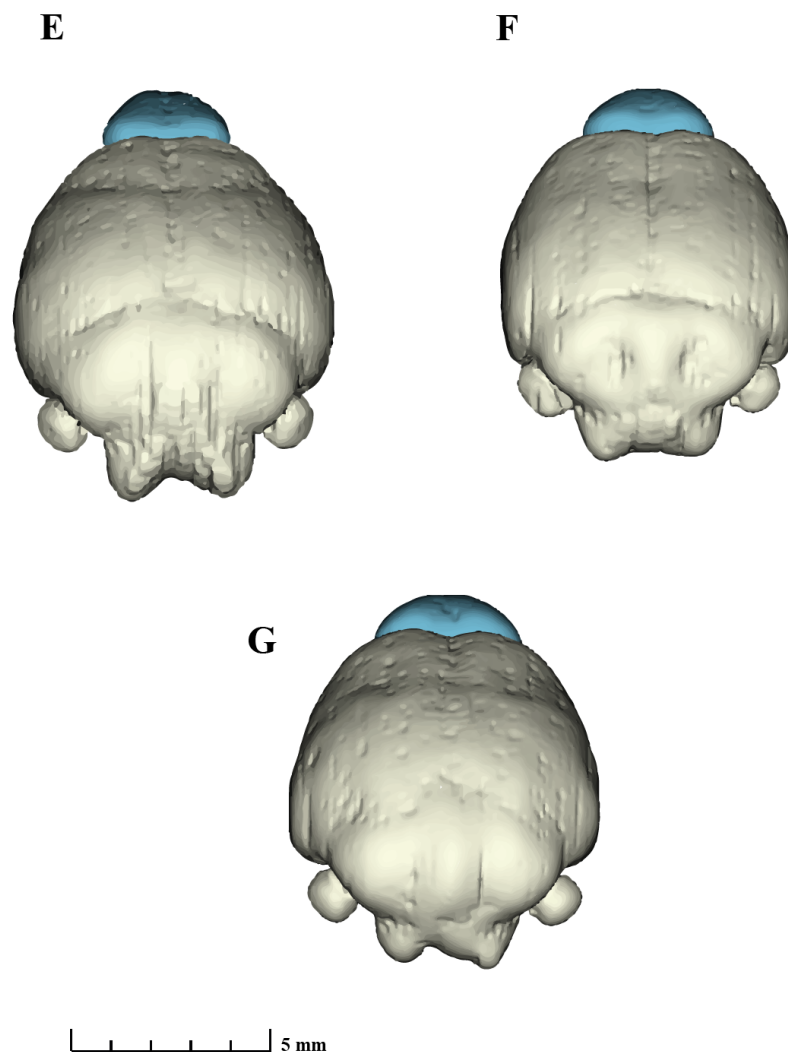


Figure 13 – Posterior view of the endocasts of: E – *Necromys lasiurus*; F – *Thaptomys nigrita*; G – *Oxymycterus quaestor*.

Table 4 – Linear measurements taken, adapted from Bertrand & Silcox (2016). Measurements are in mm. TL: total endocast length; OL: olfactory bulbs length; OW: olfactory bulbs width; OH: olfactory bulbs height; CRML: cerebrum maximal length; CRMW: cerebrum maximal width, CRMH: cerebrum maximal height; CLW: cerebellum width, not considering the paraflocculus; CLML: cerebellum maximal length.

Species	TL	OL	OW	OH	CRML	CRMW	CRMH	CLW	CLML
<i>Akodon cursor</i>	8,65	1,83	2,54	2,07	5,34	6,07	4,10	4,93	1,48
<i>Bibimys labiosus</i>	8,40	1,56	2,19	1,76	5,85	6,40	3,94	4,44	0,99
<i>Blarinomys breviceps</i>	6,77	1,40	3,20	2,05	4,48	6,22	3,72	4,67	0,88
<i>Brucepattersonius iheringi</i>	7,17	1,36	2,94	1,77	4,79	6,08	3,65	4,79	1,02
<i>Necomys lasiurus</i>	8,68	2,05	2,39	2,11	5,42	5,95	3,99	4,84	1,21
<i>Oxymycterus quaestor</i>	10,44	2,03	3,35	2,36	6,84	7,28	4,73	5,42	1,57
<i>Thaptomys nigrita</i>	7,10	1,84	2,23	1,84	4,41	5,22	3,51	4,11	1,26

Considering the cerebellum and associated structures (**Figure 12** and **Figure 13**), *Thaptomys nigrita* showed the highest ratio for cerebellum maximal length and total endocast length (18%), followed by *Akodon cursor* (17%), *Oxymycterus quaestor* (15%), *Necomys lasiurus* and *Brucepattersonius iheringi* (14%), *Blarinomys breviceps* (13%), and *Bibimys labiosus* (12%). When comparing the cerebellum width, not considering the paraflocculus, and cerebrum width, the ratio is greater in *Akodon cursor* and *Necomys lasiurus* (81%), followed by *Brucepattersonius iheringi* and *Thaptomys nigrita* (79%), *Blarinomys breviceps* (75%), *Oxymycterus quaestor* (74%) and *Bibimys labiosus* (69%).

Table 5 – Ratios in % amongst linear measurements taken, adapted from Bertrand & Silcox (2016). TL: total endocast length; OL: olfactory bulbs length; OW: olfactory bulbs width; OH: olfactory bulbs height; CRML: cerebrum maximal length; CRMW: cerebrum maximal width, CRMH: cerebrum maximal height; CLW: cerebellum width, not considering the paraflocculus; CLML: cerebellum maximal length.

Species	OL/ TL	OW/CR MW	OH/CR MH	CRML/ TL	CRML/CR MW	CLML/ TL	CLW/CR MW
<i>Akodon cursor</i>	21%	42%	50%	62%	88%	17%	81%
<i>Bibimys labiosus</i>	19%	34%	45%	70%	91%	12%	69%
<i>Blarinomys breviceps</i>	21%	51%	55%	66%	72%	13%	75%
<i>Brucepattersonius iheringi</i>	19%	48%	48%	67%	79%	14%	79%
<i>Necomys lasiurus</i>	24%	40%	53%	62%	91%	14%	81%
<i>Oxymycterus quaestor</i>	19%	46%	50%	66%	94%	15%	74%

<i>Thaptomys nigrita</i>	26%	43%	52%	62%	84%	18%	79%
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For the cerebellum, the paramedian fissure and the confluence of sinuses presented to be the main points of diagnosis, as these structures varied the most. *Necromys lasiurus* has relatively straight paramedian fissures, similar to those of *Thaptomys nigrita*. In dorsal view, the cerebellum of *Blarinomys breviceps* is almost non identifiable because of the near absence of the transverse sinus in the endocast, being also extremely short (0,88 mm), similar to *Brucepattersonius iheringi*. However, *Brucepattersonius iheringi* does not have an evident confluence of sinuses, which is also a distinct feature.

4 DISCUSSION

Rodent ecology information is usually scarce due to, amongst other factors, relatively little trapping success, cryptic and nocturnal habits of most species and, in the case of specialized insectivorous species, relatively low abundance (Rickart et al., 1991; Rickart et al., 2011; Heaney et al., 2013; Martinez et al., 2018). Virtual endocasts of the brain have proved to be an important and useful tool on understanding the evolution of the brain - and its relation to ecology - in a wide array of groups (Bertrand & Silcox, 2016; Martinez et al., 2018; Bertrand et al., 2019; Boscaini et al., 2020; Early et al., 2020; Hall et al., 2021; Weisbecker et al., 2021; Villoldo et al., 2023). This study provides the first insight into the relationships between endocast size and shape for the Akodontini tribe. The results presented herein compiled the EQ for seven species within the tribe, of which the insectivorous *Brucepattersonius iheringi* evidenced the smallest values, while the herbivorous *Bibimys labiosus* evidenced the highest. PGLS analyses showcased *Bibimys labiosus* as having the most divergent quantitative values, while most species seemed to be within expected values. Also, the PGLS analysis between olfactory bulb volume and endocast volume with body mass for *Blarinomys breviceps* highlighted the species proportionally large olfactory bulb. Additionally, we did a morphological description of the species endocasts, with notes on the proportions between the structures, in which great discrepancies were found in more specialized species, such as a wide and short olfactory bulb in *Blarinomys breviceps* and *Brucepattersonius iheringi*, and a proportionally short olfactory bulb in *Bibimys labiosus*. As previously stated, rodent ecology information is, usually, scarce. The gathered morphological information provided here might help elucidate aspects of natural history and behavior of the analyzed species with inferences regarding their ecology.

Previous studies evidenced that turbinal bone proxies may relate to olfactory capabilities, although there is no study showing a clear relation between olfactory performance and size of the olfactory bulb in rodents. In this regard, Martinez et al. (2018) found that highly specialized vermivorous species - with higher olfactory capabilities to detect prey underground, especially in leaf litter (Heth & Todrank, 2007; Martinez et al., 2018) - show an increase in the surface area and complexity of olfactory turbinals when compared to generalist and carnivorous species. Amongst the insectivorous species analyzed herein, *Blarinomys breviceps* is also semi-fossorial, moving through the leaf litter (Geise et al. 2008, Missagia & Perini, 2018). In this regard, the species didn't present considerable difference in the olfactory bulb length when compared with generalist species; however, *Blarinomys breviceps* did show the proportionally widest and highest olfactory bulb. Also, the PGLS analysis between olfactory bulb volume (OV) and endocast volume (EV) with body mass (BM) evidenced that *Blarinomys breviceps* have the largest ratio, with the olfactory bulb proportionally occupying the largest part of the total endocast volume amongst all analyzed specimens.

This information corroborates with the pattern of development observed in associated olfactory structures in muroid rodents with similar behavior, such as the Philippine endemics *Chrotomys* Thomas, 1895 (Heaney et al., 2016; Martinez et al., 2018). Of the analyzed specimens, *Brucepattersonius iheringi* is the closest relative of *Blarinomys breviceps* (Maestri et al., 2017, 2019; Stepan & Schenk, 2017). In this regard, the species did present many endocast morphological similarities: both have relatively short and wide olfactory bulbs, as well as the whole endocranium, which is somewhat expected, especially in *Blarinomys breviceps*, as it differs from other Akodontini due to the shortening of the skull in the braincase region (Missagia & Perini, 2018). *Brucepattersonius* Hershkovitz, 1998 is a genus of specialized insectivorous rodents endemic to the Atlantic Rainforests of South America, and with some species sympatric with *Blarinomys breviceps*, including *B. iheringi* (Vilela et al., 2015; Abreu et al., 2023). *Brucepattersonius iheringi* presented the lowest EQ of all analyzed specimens (0,83 according to the Pilleri et al., 1984b equation) in all applied equations (Jerison, 1973; Einsenberg, 1981; Pilleri et al., 1984b).

In fact, considering the Pilleri et al. (1984b) equation, the EQ for *Blarinomys breviceps* (1,04) is closer to *Oxymycterus quaestor* (1,04) and *Thaptomys nigrita* (1,05). These findings suggest that, although *Brucepattersonius iheringi* is more closely related to *Blarinomys breviceps* (Maestri et al., 2017, 2019; Stepan & Schenk, 2017; Missagia et al., 2019), and

morphologically closer to *Oxymycterus quaestor* (Missaglia & Perini, 2018), the species have a considerable difference in EQ values from both, being more similar to the more generalist *Thaptomys nigrita*.

Considering locomotion, Pilleri et al. (1984b) points out that rodents with lower EQ are usually fossorial, with medium EQ, terrestrial or semiaquatic, and with higher EQ, arboreal. From what is currently known for the analyzed dataset, which do not include arboreal species, the terrestrial *Bibimys labiosus* did show the highest EQ (1,49). Bertrand and Silcox (2016) and Pilleri et al. (1984b) point out that, amongst Rodentia, Sciuromorpha has the highest EQ values, with an average of 1,22, which is lower than the identified for *Bibimys labiosus*. Also, *B. labiosus* usually inhabits relatively complex environments, such as the Atlantic Rainforest and dense ecotone formations within the Cerrado biome (Pardiñas et al., 2017) and species that live in environments that poses higher complexity, such as forested habitats, usually have a larger relative brain size (Eisenberg & Wilson, 1978; Mace et al., 1981; Meier, 1983; Bertrand et al., 2021). It is, however, important to notice that the average EQ from Pilleri et al. (1984b) was not conducted with the use of digital endocasts, which should be considered when making inferences from these results. Also, it is important to consider linear measurements of the major brain structures to assess their role in the species ecology, behavior and evolution, in association with the EQ, since the latter can be affected by factors like activity period (Pilleri et al. 1984b).

One major morphological characteristic of *Bibimys labiosus* lies in the proportionally small ratio between olfactory bulb width and length and total length and width of the endocast (19% and 34% respectively) in comparison with the remaining species, even with the high EQ. As suggested by Bertrand et al. (2019), more elongated olfactory bulbs might be related with a better sense of smell, which can be proved useful when living in the ground. We believe that, in *Bibimys labiosus*, the small olfactory bulb size might be correlated with diet and the lack of need to identify prey through smell. Speculatively, for *Bibimys labiosus*, there might be a relationship between the small olfactory bulb and further development of brain structures associated with other senses, such as sense of touch, as evidenced by the enlarged labial region covered with vibrissae of this species, but this hypothesis should be further analyzed.

Furthermore, fossoriality might heavily influence the overall shape of the endocast, even more than other locomotor behaviors, because of functional demands associated with a reduction in the cruciality of vision (Bertrand et al., 2019; Bertrand et al., 2021), as larger brains can be

energetically costly (Williams & Herrup, 1988). Usually, these differences are noticeable with relatively smaller brains, as well as the structures of the neocortex, olfactory bulbs and paraflocculi (Bertrand et al., 2019; Bertrand et al., 2021). Indeed, the proportions between cerebrum maximal length and cerebrum maximal width evidenced itself to be the smallest in *Blarinomys breviceps* (72%), followed by *Brucepattersonius iheringi* (79%). As previously mentioned, information regarding many rodent species ecology is scarce and, in this regard, so is that of *Brucepattersonius iheringi*. Noticeably, the unique short and wide olfactory bulb structure of *Blarinomys* and *Brucepattersonius*, associated with the small neocortex, might indeed be related to their insectivorous diet and the inferred semi-fossorial locomotion habits. However, there is not enough information regarding the possibility of *Brucepattersonius* being semi-fossorial, which should be considered in further analysis considering the species ecology. The phylogenetic proximity of *Blarinomys* and *Brucepattersonius* must also be considered when analysing endocast similarities between these two species. Therefore, it is still unclear which structures of the olfactory bulb are directly related to these evolutionary and ecological traits.

Despite being insectivorous with highly specialized morphological structures associated with this diet, *Oxymycterus quaestor* did show the highest proportions between cerebrum maximal length and cerebrum maximal width (94%), closer to those of more generalist species such as *Bibimys labiosus* (91%), *Necromys lasiurus* (91%) and *Akodon cursor* (88%). In this regard, the neocortex is, in summary, the area in which the integration between sensory and motor information happens (Martin, 1990). The identified similarities between the midbrain in the endocast of *Blarinomys breviceps* and *Brucepattersonius iheringi* contrast with the cranial and, probably ecological, similarities of the latter with *Oxymycterus* (Missaglia & Perini, 2018), as the endocast of *Oxymycterus delator* did present many differences. Taking this into consideration, it is possible to infer that phylogenetic inertia may have played a stronger influence on the the brain morphology of *Blarinomys* and *Brucepattersonius* than ecological and adaptive pressures. However, it is important to notice that, as stated by Bertrand and Silcox (2016), interpreting the midbrain structures can be complicated, as it can reflect a wide array of specializations in neocortical functions. These functions might have developed in response to many different factors, such as vision, hearing, memory, motor skills and cognition (Jerison, 1973; Christensen & Evans, 1979; Kaas, 2020; Bertrand et al., 2024). Species with high levels of social behavior, for example, are reported to have larger neocortices (Michener, 1983; Matějů & Kratochvíl, 2013; Bertrand et al., 2021). This might be justified as some areas of the midbrain

are associated with intraspecific communication, i. e., in this regard, the major influence on neocortex size is related to specific areas related to these traits, and not the overall size of the structure. In time, such differences might be impossible to identify in endocasts (Bertrand et al. 2021).

5 CONCLUSION

We provided, herein, the first insights into the relationships between endocast size and shape in the Akodontini tribe, with descriptions of the brain structures, their differences, and EQ. The brain structure's role in the ecology and evolution of this clade were not yet tested, and is subject to further investigations, as stated in the discussion. Notably, *Blarinomys breviceps* and *Brucepattersonius iheringi* exhibit a proportionally larger and more complex olfactory bulb, which may suggest enhanced olfactory capabilities for detecting prey. This is consistent with similar findings in other specialized insectivorous rodents. The results observed for *Bibimys labiosus* can also be targeted as further points to understand in the morphological context of the brain structures, as it presented a considerably large EQ with the smallest olfactory bulb, which might also be associated with the use of different senses when searching for resources, such as a more developed vibrissae.

This study highlights the importance of considering individual brain structures and their relationships to specific ecological and behavioral traits. It is, however, also important to notice, that the endocasts do not provide every information we need to understand the corresponding brain structures. Further investigations, considering an increase in analyzed specimens and species, might help us elucidate questions that are yet to be answered regarding Akodontini evolutionary history, ecology and behavior, mainly on rare, cryptic species.

Furthermore, elucidating the specific brain structures and their functions is of major relevance to better understand the ecological and behavioral adaptations observed in these rodents. Such studies could enhance our understanding of the evolutionary pressures shaping brain morphology and function in diverse environments.

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7 APPENDICES

7.1 Appendix 1 – RStudio PGLS Script

```
library(phytools)
```

```
library(geiger)
```

```
library(caper)
```

```
library(ggplot2)
```

```
library(ape)
```

```
setwd("C:/User")
```

```
print(getwd())
```

```
caminho_arquivo <- "trRod.nexus"
```

```
if (file.exists(caminho_arquivo)) {
```

```
  print("Arquivo encontrado")
```

```
  dados <- read.nexus(caminho_arquivo)
```

```
} else {
```

```
  print("Arquivo não encontrado")
```

```
}
```

```
tree <- read.nexus("trRod.nexus")
```

```
data <- read.csv("quantitativos.csv", header = TRUE, sep = ";")
```

```
data2 <- read.csv("quantitativos.csv", header = TRUE, sep = ";", row.names = 1)
```

```

colnames(data)[which(colnames(data) == "bulbo")] <- "OV"

colnames(data)[which(colnames(data) == "endocranio")] <- "EV"

colnames(data)[which(colnames(data) == "weight")] <- "BM"

colnames(data)[which(colnames(data) == "eq")] <- "EQ"

colnames(data)[which(colnames(data) == "bulbo.endo")] <- "OV_EV"

print(colnames(data))

cd <- comparative.data(data = data, phy = tree, names.col = "X", vcv = TRUE, vcv.dim = 3,
warn.dropped = TRUE)

italic_species <- function(name) {

  bquote(italic.(.(name)))

}

# Modelo PGLS 1: OV x EV

m1 <- pgl(OV ~ EV, cd, lambda = "ML", param.CI = 0.95)

summary(m1)

# ggplot para o Modelo 1

plot_data <- data.frame(species = data$X,

                        x = data$EV,

                        y = data$OV,

                        fitted = m1$fitted)

ggplot(plot_data, aes(x = x, y = y)) +

```

```
geom_point(color = "black") +  
  
geom_text(aes(label = sapply(species, italic_species)), parse = TRUE, vjust = -1) +  
  
geom_smooth(method = "lm", se = FALSE, color = "red") +  
  
labs(x = "EV", y = "OV", title = "PGLS Analysis: OV ~ EV") +  
  
theme_minimal() +  
  
theme(panel.grid.major = element_blank(),  
  
       panel.grid.minor = element_blank(),  
  
       axis.line = element_line(color = "black"),  
  
       axis.ticks = element_line(color = "black"))  
  
# Modelo PGLS 2: OV x BM  
  
m2 <- pgl(OV ~ BM, cd, lambda = "ML", param.CI = 0.95)  
  
summary(m2)  
  
# ggplot para o Modelo 2  
  
plot_data <- data.frame(species = data$X,  
  
                        x = data$BM,  
  
                        y = data$OV,  
  
                        fitted = m2$fitted)  
  
ggplot(plot_data, aes(x = x, y = y)) +  
  
geom_point(color = "black") +  
  
geom_text(aes(label = sapply(species, italic_species)), parse = TRUE, vjust = -1) +
```

```

geom_smooth(method = "lm", se = FALSE, color = "red") +

labs(x = "BM", y = "OV", title = "PGLS Analysis: OV ~ BM") +

theme_minimal() +

theme(panel.grid.major = element_blank(),

      panel.grid.minor = element_blank(),

      axis.line = element_line(color = "black"),

      axis.ticks = element_line(color = "black"))

# Modelo PGLS 3: EQ x BM

m3 <- pglS(EQ ~ BM, cd, lambda = "ML", param.CI = 0.95)

summary(m3)

# ggplot para o Modelo 3

plot_data <- data.frame(species = data$X,

                        x = data$BM,

                        y = data$EQ,

                        fitted = m3$fitted)

ggplot(plot_data, aes(x = x, y = y)) +

  geom_point(color = "black") +

  geom_text(aes(label = sapply(species, italic_species)), parse = TRUE, vjust = -1) +

  geom_smooth(method = "lm", se = FALSE, color = "red") +

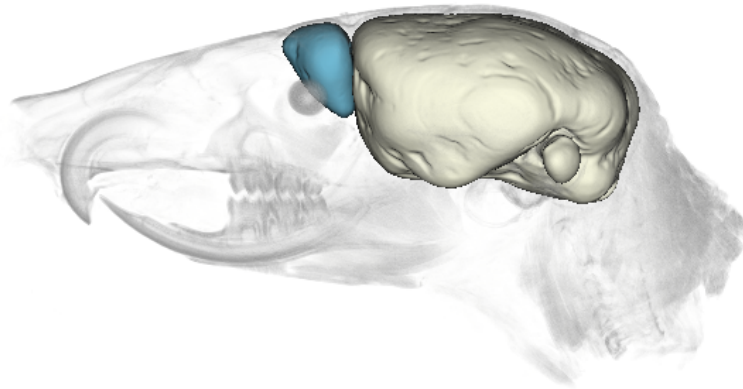
  labs(x = "BM", y = "EQ", title = "PGLS Analysis: EQ ~ BM") +

```

```
theme_minimal() +  
  
theme(panel.grid.major = element_blank(),  
  
      panel.grid.minor = element_blank(),  
  
      axis.line = element_line(color = "black"),  
  
      axis.ticks = element_line(color = "black"))  
  
# Modelo PGLS 4: OV/EV x BM  
  
m4 <- pgl(OV_EV ~ BM, cd, lambda = "ML", param.CI = 0.95)  
  
summary(m4)  
  
# ggplot para o Modelo 4  
  
plot_data <- data.frame(species = data$X,  
  
                        x = data$BM,  
  
                        y = data$OV_EV,  
  
                        fitted = m4$fitted)  
  
ggplot(plot_data, aes(x = x, y = y)) +  
  
  geom_point(color = "black") +  
  
  geom_text(aes(label = sapply(species, italic_species)), parse = TRUE, vjust = -1) +  
  
  geom_smooth(method = "lm", se = FALSE, color = "red") +  
  
  labs(x = "BM", y = "OV/EV", title = "PGLS Analysis: OV/EV ~ BM") +  
  
  theme_minimal() +  
  
  theme(panel.grid.major = element_blank(),
```

```
panel.grid.minor = element_blank(),  
axis.line = element_line(color = "black"),  
axis.ticks = element_line(color = "black"))
```

7.2 Appendix 2 – Lateral view of the endocast of *Oxymycterus quaestor* Thomas, 1903



10 mm

Figure 14 – Lateral view of the endocast within the skull of *Oxymycterus quaestor*.