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Programa de Pós-Graduação em Ciências Biológicas (Zoologia)

MIOLOGIA COMPARADA DE REPRESENTANTES DO GÊNERO *AMPHISBAENA* LINNAEUS, 1758 (SQUAMATA, AMPHISBAENIDAE)

INGRID LIMA E LIMA

Botucatu – SP
2024

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Dissertação apresentada ao Instituto de Biociências, Câmpus de Botucatu, UNESP, para obtenção do título de Mestre no Programa de Pós-graduação em Zoologia.

Orientador: Prof. Dr. Ivan Sergio Nunes da Silva Filho

Co-Orientadora: Profa. Dra. Angele dos Reis Martins

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Palavras-chave: Anatomia; Anfisbênias; Caracteres miológicos; Descrição muscular; Glândulas cefálicas.

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Maria Victória Ramalho da Cunha
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“All that is gold does not glitter,
Not all those who wander are lost;
The old that is strong does not wither,
Deep roots are not reached by the frost.

From the ashes a fire shall be woken,
A light from the shadows shall spring;
Renewed shall be blade that was broken,
The crownless again shall be king.”

— J.R.R. Tolkien

RESUMO

Dentre os Squamata, a subordem Amphisbaenia possui indivíduos que apresentam diversas adaptações para o modo de vida fossorial, atualmente sendo representada por 202 espécies divididos em seis famílias. Apesar do recente aumento no interesse e progresso acerca do grupo, ainda nos deparamos com a falta de diversos tipos de dados. Sendo assim, devido ao número limitado de descrições miológicas conduzidas neste grupo taxonômico, o presente estudo visa fornecer uma descrição da anatomia muscular cefálica de quatro espécies de *Amphisbaena* – *Amphisbaena dubia*, *Amphisbaena darwinii*, *Amphisbaena munoai* e *Amphisbaena microcephala*. Além disso, incorporamos dados de espécies com descrições musculares previamente documentadas na literatura para fornecer uma comparação mais abrangente. Foram descritas variações na musculatura associada ao complexo mandibular e alterações na estrutura dos tendões que sustentam esses músculos. Além disso, foram identificadas variações na forma, origem e inserções do *m. adductor mandibulae externus superficialis*, *medialis* e *profundus*, na disposição das fibras do *m. retractor anguli oris* e do *m. depressor mandibulae*. Ademais, novas percepções sobre o sistema glandular das espécies, com a descrição de uma glândula rictal ainda não registrada para este grupo, juntamente com a criação de 24 de caracteres baseados nessas variações, foram fornecidas. Tais resultados traduzidos em caracteres podem ser utilizados para refinar e aprimorar futuras investigações filogenéticas, esclarecendo a evolução do grupo e suas adaptações morfológicas.

Palavras-chave: anfisbênias, anatomia, caracteres miológicos, descrição muscular, glândulas cefálicas

ABSTRACT

Among Squamata, the suborder Amphisbaenia includes individuals that exhibit various adaptations for fossorial lifestyle, currently represented by 202 species divided into six families. Despite the recent surge in interest and progress concerning the morphology of the group, most studies are mainly focused on their skull and hemipenial shape/morphology, with little data on other morphofunctional complexes such as postcranial data, muscles, cephalic glands and viscera. Herein we aim to describe in detail the cephalic myology of four *Amphisbaena* species – *Amphisbaena dubia*, *Amphisbaena darwinii*, *Amphisbaena munoai* and *Amphisbaena microcephala*. Furthermore, we incorporate data from species with previously documented muscular descriptions available in the literature to provide a broader comparative framework. Variations in the musculature associated with the mandibular complex and alterations in the structure of tendons supporting these muscles were described. Additionally, variations in shape, origin and insertions of the *m. adductor mandibulae externus superficialis, medialis and profundus*, iber arrangement of *m. retractor anguli oris* and *m. depressor mandibulae* were identified. Moreover, novel insights into the glandular system of the species, with the observation of a rictal gland not yet recorded for this group, along with the creation of a set of characters based on these variations, were provided. The obtained results may supply valuable insights and interesting character information to be used in future phylogenetic investigations of the group.

Keywords: amphisbaenians, anatomy, cephalic glands, muscular descriptions, myological characters

SUMÁRIO

Comparative myology of four species of Amphisbaena (Linnaeus, 1758) (Squamata, Amphisbaenidae) with descriptions on the cephalic glands

Short running title: Comparative myology of four *Amphisbaena* Linnaeus, 1758

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1. INTRODUCTION

The order Squamata encompasses over 12,000 extant species of lizards, snakes, and amphisbaenians (Uetz et al., 2024), and represent the most diverse clade of terrestrial vertebrates worldwide (Simões & Pyron, 2021), occurring in nearly all habitats (Vitt & Caldwell, 2013). Amphisbaenia is a suborder of Squamata, comprised by fossorial animals commonly known as worm-lizards, currently represented by 202 species divided into six families (Uetz et al., 2024). The geographic range of the group includes North America in eastern USA (Rhineuridae); Central America (Cadeidae and Bipedidae); Europe and North Africa (Blanidae); North Africa and Asia (Trogonophidae; Gans, 2005). The family Amphisbaenidae is the most speciose and has a wide distribution in South America, Central America, and Africa (Costa & Garcia, 2019), even though many species exhibit endemic or restricted distributions and remain poorly understood (Gans, 2005; Costa, 2020).

These fossorial Squamata display significant adaptations for subterranean life, including the construction of their own tunnel systems by compressing the soil within the galleries, with horizontal or vertical movements of the head (Gans, 1968). This head-first burrowing behavior is a primary tool for the fossorial lifestyle of Amphisbaenia (Navas et al., 2004), being supported by a suite of morphological features, including cranial adaptations (head shape: rounded, shovel-shaped, spade-shaped, and keel-shaped; Kearney 2003), tegumentary characteristics, and muscular arrangements (Gans, 1986). Round-headed species use a generalized mechanism, while shovel-headed, spade-headed, or keel-headed species employ specialized mechanisms (Gans, 1969; Hohl et al., 2014), this strongly ossified skull enhances resistance to excavation impacts (Gans & Montero, 2008), requiring enduring muscle contractions, especially in dorsal, pectoral and cephalic muscles (Gans, 1968; Navas et al., 2004). Additionally, the tegumentary musculature exhibits a unique configuration, wherein muscles are loosely interconnected with the skin, thereby reducing frictional resistance against the tunnel walls during locomotion (Gans, 1962).

Multiple aspects of amphisbaenian biology remain underexplored, with many species having been described only recently, with their natural history receiving limited attention (Colli et al., 2016). This phenomenon is partly attributed to the fossorial behavior of these animals, which can restrict field observations and complicate specimen collection for laboratory research (Navega-Gonçalves & Benites, 2019; Paiva et al., 2024). Consequently, amphisbaenians remain as the group of Squamata less studied and poorly represented in biological collections (Gans, 1967; Kearney, 2003; Colli et al., 2016), which delays the execution of descriptive or comparative studies (Gans, 2005; Pinna et al., 2014; Roberto et al., 2014). This creates a gap in the knowledge of their morphological, anatomical, functional, and phylogenetic characteristics. Which is concerning, as morphological data, especially those related to myology, have proven effective in studies of functional biology and phylogenetic analyses among vertebrates (O'Reilly et al., 2000; Diaz et al., 2022; Lowie et al., 2023). Addressing this gap can provide more detailed answers regarding the musculature involved in burrowing, the influence of mandibular musculature on food acquisition (Cundall, 1983), and the similarity between amphisbaenians and other highly fossorial squamate species (Daza et al., 2011), among other evolutionary questions concerning this group.

Some studies in recent decades have focused on the myology analysis of reptiles in the order Squamata (Abdala & Moro, 2006; Bhullar, 2009; Martins et al., 2019; Westphal et al., 2019). However, both older and contemporary studies primarily concentrate on snakes and lizards (e.g., Jayne, 1982; Cundall, 1986; De Souza Leite et al., 2021). One extensively investigated factor, for example, is the limb loss in groups exhibiting this characteristic (Greer, 1991; Abdala et al., 2015; Camaiti et al., 2021). These investigations have demonstrated that osteology and myology provide better insights into the evolutionary patterns of limb loss compared to studies solely focused on external characteristics (Camaiti et al., 2021).

Although there are descriptive myology studies on amphisbaenians, they are scarce and mostly outdated (Renous, 1977; Bonin, 1965), leaving a wide-open niche for studies. For example, earlier studies described part of the jaw adductor musculature of *Amphisbaena alba* Linnaeus, 1758 (Lakjer, 1926), and some observations and descriptions were added for the same species, as well for *Amphisbaena microcephala* Wagler, 1824 and *Trogonophis wiegmanni* Kaup, 1830 (Haas et al., 1973). Later, Rieppel (1979) partially described the jaw adductor musculature of *A. alba* and *Amphisbaena fuliginosa* Linnaeus 1758. More recently, we have descriptions of muscles located around the neck-trunk region for *A. alba* (Tsuihiji et al., 2012) and descriptions of pectoral muscles through diceCT visualization for five species of Amphisbaenia (Westphal et al., 2019). This indicates that the descriptions for this group are sporadic and further investigations are needed for better correlations between the homologies of this muscular system.

The cranial muscles of amphisbaenians are of special interest due to the complete loss of the upper temporal arch (jugal) and the closure of the cranial box, modifications similar to those seen in snakes (Haas et al., 1973). This cranial structure, associated with powerful temporal musculature, also facilitates food capture and crushing (Gans, 1969). Therefore, descriptive myology studies allow correlating these and other specializations with the different muscular characteristics of these species (Gans & Montero, 2008), providing important data on the functional morphology of amphisbaenians. Furthermore, we must not overlook the knowledge regarding their cephalic glands, as information about their macro and microstructure remain unknow (Foureaux et al., 2010), the conception and integration of these internal characters for a phylogenetic analysis has proven valuable for other Squamata groups (Abdala et al., 2009), yet it has not been applied to amphisbaenians.

Among the South American worm-lizards, we highlight four species, *Amphisbaena dubia* (Müller, 1924), *Amphisbaena darwinii* (Duméril & Bribon, 1839), *Amphisbaena munoai* (Klappenbach, 1960) and *Amphisbaena microcephala* (Wagler, 1824). *A. dubia* is endemic from Brazil (Evers et al., 2006), but its population density is unknown, and its phylogenetic placement remains unaddressed in extant evolutionary studies (Mott & Vieites, 2009; Gauthier et al., 2012; Pyron et al., 2013). *A. munoai* and *A. darwinii* are found under stones in rocky outcrops in the Uruguay and southern Brazil (Perez & Borges-Martins, 2019). All those three share the round-headed pattern, differing only in size (Gans & Montero, 2008). Conversely, *A. microcephala* is shovel-headed, and has a widespread distribution (Hohl et al., 2017), occurring in different regions of South America (Ribeiro et al., 2011).

The diversity, precise identification of species and their boundaries, remain unresolved in many *Amphisbaena* groups (Perez & Borges-Martins, 2019), being crucial to employ diverse datasets, including myological descriptions, to advance knowledge of the group's evolutionary history. For that reason, herein, we described the cranial myology and its variations in these four species of amphisbaenians. This research involves comparing these anatomical features and discuss with respective cranial shapes, alongside a review of existing literature. Beyond that, we also described the cephalic glands observed and propose a list of myological characters.

5. CONCLUSIONS

Our study offers a broad description of the cephalic myology and glandular information for four species of *Amphisbaena*, showing the variation between then and among different head shapes representatives here available. The species with rounded heads (*A. darwinii*, *A. dubia* and *A. munoai*) showed more similarity among themselves than the species with shovel-shaped heads (*A. microcephala*). Especially the species *A. darwinii* and *A. munoai*, which are phylogenetically close (Graboski et al., 2022) and exhibited a nearly identical set of muscles.

We identified a novel rictal or supralabial accessory gland in the shovel-headed *A. microcephala*, that is absent in the other three species. This highlights the importance of investigating the glandular characteristics within other cranial types of Amphisbaenia (e.g., spaded-headed and keel-headed) present in other species, in order to search for patterns associated with different ecological lifestyles and their phylogenetic relationships.

While our study lays the groundwork for understanding these morphological traits, it is necessary to test the formulated characters within a broader phylogenetic framework, since new phylogenies investigating various sources of characters, such as osteology and myology, which are rare in in Amphisbaenia to date (Navas et al., 2004; Rieppel, 1979; Westphal et al., 2019), should be conducted. This integrative approach will be crucial for advancing our understanding of the evolution of this group.

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