UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

Description of new fossil Squamata from Lajedo de Soledade, Rio Grande do Norte Quaternary: integrating comparative analyses of extant and fossils using Geometric Morphometrics

Descrição de novos fósseis de Squamata do Lajedo da Soledade, Quaternário do Rio Grande do Norte: integrando análises comparativas entre fósseis e recentes por meio de morfometria geométrica

Sílvia Oliveira Lomba

Dissertação apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da USP, como parte das exigências para a obtenção do título do Mestre em Ciências, Área: Biologia Comparada

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Orientadora: Profª Drª Annie Schmaltz Hsiou

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Profª Drª Annie Schmaltz Hsiou

Dedico à minha família

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> “There is a theory which states that if ever anyone discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarre and inexplicable. There is another theory which states that this has already happened.”
>
> **— Douglas Adams, The Hitchhiker's Guide to the Galaxy**

RESUMO

LOMBA, S.O. Squamata (Lepidosauria) do Lajedo da Soledade, Quaternário do Rio Grande do Norte: integrando análises comparativas entre fósseis e recentes por meio de morfometria geométrica. Dissertação (mestrado) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 2023.

Squamata é um clado muito diverso que consiste em serpentes, lagartos e anfisbenas. O registro fóssil deste grupo é amplo e, no Brasil, se estende do Cretáceo ao Quaternário. Esses registros são compostos, em sua maioria, por materiais fragmentados, o que torna a identificação uma tarefa desafiadora e dependente do acesso a coleções científicas extensas para que sejam identificados de forma apropriada. Nesse contexto, o presente trabalho consiste na identificação de fósseis de escamados coletados no Lajedo de Soledade, no Rio Grande do Norte. As análises foram realizadas por meio de comparações morfológicas minuciosas e de aplicação de morfometria geométrica bidimensional. As análises de morfometria geométrica são cada vez mais usadas na biologia, sendo considerada essencial para estudos morfológicos e filogenéticos. Elas são uma forma quantitativa de se estudar a forma, baseando-se em marcos anatômicos. Com isso, pode-se avaliar variação morfológica e explorar a utilidade desse método na identificação de fósseis. Assim, foi possível dar mais refinamento às atribuições taxonômicas. Foram identificados fósseis de *Crotalus durissus*, *Epicrates*, um embrião de Boidae, Viperidae indeterminados, *Tropidurus* e Teiidae. Era esperado que a diversidade fóssil na área de coleta fosse similar com a fauna atual do local, visto que são materiais relativamente recentes. No entanto, apesar da maioria dos fósseis identificados serem condizentes com espécies atualmente presentes no local, uma vértebra de Teiidae indica a ocorrência pretérita de uma espécie que não está mais presente no Rio Grande do Norte. As análises de morfometria geométrica corroboram as atribuições taxonômicas dos fósseis e se comprova uma ferramenta poderosa na identificação de fósseis. Os resultados do trabalho são fundamentais para que seja possível compreender melhor a composição faunística pretérita de Squamata, que ainda não havia sido descrita para a localidade, e ter mais informações sobre o paleoambiente durante Quaternário do Rio Grande do Norte.

Palavras chave: Squamata; Paleontologia; Quaternário; Anatomia; Morfometria Geométrica

ABSTRACT

LOMBA, S.O. Squamata (Lepidosauria) from Lajedo de Soledade, Rio Grande do Norte Quaternary: integrating comparative analyses of extant and fossils using Geometric Morphometrics. Dissertation (masters) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 2023.

Squamata is a diverse clade consisting of snakes, lizards, and amphisbaenians. The fossil record of this group is extensive and, in Brazil, extends from the Cretaceous to the Quaternary. These records are mainly composed of fragmented materials, which makes identification a challenging task and dependent on access to extensive scientific collections for them to be appropriately identified. The present work involves identifying Squamata fossils collected in Lajedo de Soledade, Rio Grande do Norte. The analyses were carried out through detailed morphological comparisons and the application of two-dimensional geometric morphometry. Geometric morphometry analyses are increasingly used in biology, considered essential for morphological and phylogenetic studies. They are a quantitative way of studying form based on anatomical landmarks. With this, one can assess morphological variation and explore the usefulness of this method in identifying fossils. Thus, it was possible to refine the taxonomic attributions further. Fossils of Crotalus durissus, Epicrates, an embryo of Boidae, indetermined Viperidae, Tropidurus, and Teiidae were identified. The fossil diversity in the collection area would be expected to be similar to the current local fauna since these are relatively recent materials. However, although most of the identified fossils are consistent with species currently present at the site, the Teiidae vertebra indicates the past occurrence of a species that is no longer present in Rio Grande do Norte. Geometric morphometric analyses corroborate the taxonomic attributions of fossils and are proven a powerful tool in fossil identification. The results of this dissertation are essential for a better understanding of the past faunal composition of Squamata, which had not yet been described for the locality, and to have more information about the paleoenvironment during the Quaternary of Rio Grande do Norte.

Key words: Squamata; Paleontology; Quaternary; Anatomy; Geometric Morphometrics

ISNTITUTIONAL ABBREVIATIONS

CHRP: Coleção Herpetológica de Ribeirão Preto, Ribeirão Preto, Brasil

LACM: Natural History Museum of Los Angeles County

MCN.D.: Coleção didática de Herpetologia, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brasil

MCN-PV-DR: Seção de Paleontologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Coleção de Paleontologia de Vertebrado, Coleção Didática de Répteis, Porto Alegre, Brasil

MLS: Museu do Lajedo de Soledade

MZUSP: Museu de Zoologia da Universidade de São Paulo

UF:HERPS: University of Florida, Florida Natural History Museum, Herpetology Collection

UFMT: Coleção da Universidade Federal do Mato Grosso, estado do Mato Grosso, Brasil

ANATOMICAL ABBREVIATIONS

cl: centrum length;

cn: condyle;

coh: condyle height;

cow: condyle width;

ct: cotyle;

cth: cotyle height;

ctw: cotyle width;

di: diapophysis;

h: total height of vertebra;

hip: hypapophysis

hk: hemal keel;

ir: interzygapophyseal ridge;

lf: lateral foramen;

naw: neural arch width;

nc: neural canal;

nch: neural canal height;

ncw: neural canal width;

ns: neural spine;

nsl: neural spine length;

par: parapophysis;

parp: parapophyseal process;

pfo: paracotylar foramen;

po-po: distance between postzygapophyses;

ppz: prezygapophyseal process;

prl: prezygapophysis length;

pr-po: distance between prezygapophyses and postzygapophyses of the same side;

pr-pr: distance between prezygapophyses;

prw: prezygapophysis width;

ptz: postzygapophysis;

pz: prezygapophysis;

sf: subcentral foramen;

sin: sinapophysis

zg: zygantrum;

zh: zygosphene height;

zw: zygosphene width

Summary

1. GENERAL BACKGROUND

The present Master's dissertation comprises two chapters focusing on fossil Squamata from a Quaternary deposit in Rio Grande do Norte. In summary, this study identifies and describes fossil snakes and lizards from Lajedo de Soledade and compares them with current species that are currently present in the fossiliferous locality. Also, the paleoclimate of the region can be discussed based on the occurrence of these animals, that are good environmental markers. On the other hand, identifying these animals can be challenging, since many groups of Squamata have similar skeletons and the fossil record has a fragmentary nature. For this reason, the identification of the fossils using geometric morphometrics is also explored.

1.1.SQUAMATA OPPEL, 1811

Squamata is a Lepidosauria group consisting of lizards, snakes, and amphisbaenians. It is a diverse clade both morphologically and ecologically, with around 11.302 species worldwide, except in the arctic regions (Evans, 2003; Uetz et al., 2022). The monophyly of the group is well accepted, even though the group's internal relations are uncertain (Estes et al., 1988; Gauthier et al., 1988). Some synapomorphies are known, such as presence of scales, paired copulatory organs, and bifurcated tongue (Rieppel, 1988), and characters related to cranial kinetics with the reduced connection of the quadrate-pterygoid (Gauthier et al., 1988).

Traditionally, the early division of Squamata considered two main groups, Lacertilia (lizards and amphisbaenas) and Ophidia (snakes) (Romer, 1956). However, with the advances in cladistic studies of the group, especially over the last 30 years, this division changed, and the group was divided into Iguania (iguanas and chameleons) and Scleroglossa (snakes, amphisbaenians, and remaining lizards) (Estes et al., 1988). Nevertheless, several phylogenetic analyses have shown that Scleroglossa is not a monophyletic group and that Iguania is positioned inside the remaining Squamata, as the sister group of the Anguimorpha (Pyron et al., 2013; Simões et al., 2018). Pyron et al (2013), analyzing only extant species, has retrieved that Serpentes as the sister group of Aguimorpha+Iguania, forming the clade Toxicofera. When adding the fossil record to the analysis, Serpentes is positioned as sister group of Mosasauria, inside the clade Toxicofera (Figure 1) (Reeder et al., 2015; Simões et al., 2018).

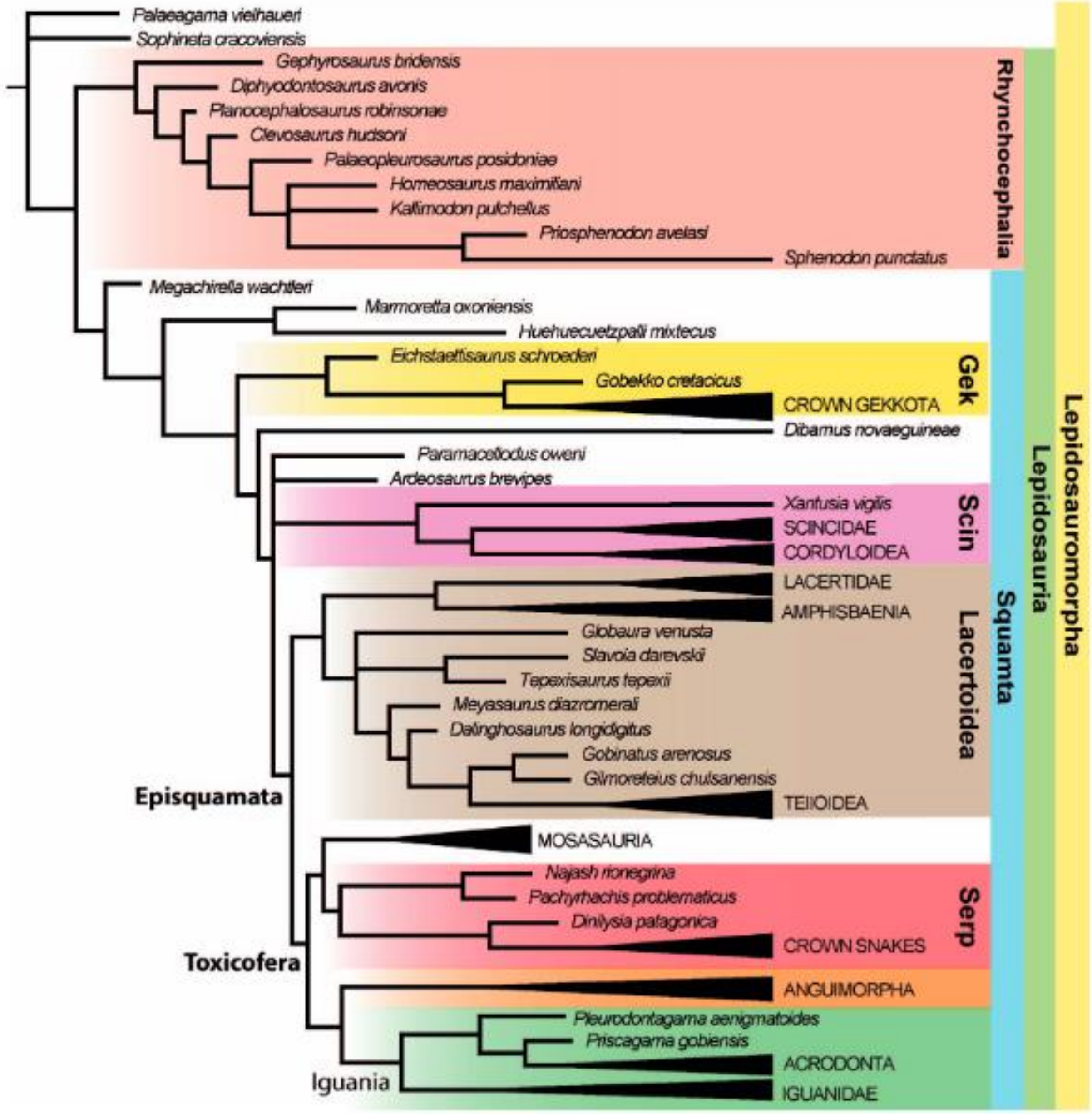

Figure 1: Bayesian phylogeny of the diapsids by Simões et al. (2018) modified by Simões and Pyron, (2021), showing the internal relations in Squamata.

1.2.THE CHALLENGES OF PALEOHERPETOLOGY

The Squamata fossil record encompasses a vast geological time scale. The oldest fossil lizard dates from the Middle Triassic of Italy (Renesto and Posenato, 2003; Simões et al., 2018), while the oldest snake dates from the Lower Cretaceous of England (Caldwell et al., 2015). Despite this remarkable history, the paleontological studies of the squamates have some challenges. Lepidosaurians, as a whole, tend to be small and have fragile bones, which hinders fossilization (Evans, 2003; Onary et al., 2017). For a complete or nearly complete squamate skeleton to be preserved, a combination of depositional factors, like low energy and fine sedimentation are needed, which enables fossilization with minor disarticulation (Evans, 2003; Hsiou, 2010; Onary and Hsiou, 2015). Aside from the taphonomic bias, there is also a collection bias. Usually, small fossils of vertebrates are difficult to find when the excavation is not explicitly exploring them (Villa et al., 2017). Because of these reasons, many fossil Squamata are represented by fragments and isolated bones.

The Cenozoic fossil record of Squamata is highly diverse. However, due to its fragmentary nature, the taxonomic attributions, evolutionary, and morphological studies are complex and time-consuming (Evans, 2003; Camolez and Zaher, 2010; Hsiou, 2010). That is because the knowledge around the skeleton anatomy of many extant Squamata taxa is still lacking, and this information is essential in the identification of these fossils.

Another difficulty faced by paleoherpetologists is the differences in classification methods between neontologists and paleontologists. In paleontology, the material is restricted to the hard parts of the animals, and the species classification is usually limited to the anatomical characteristics of the skeletons. It creates an operational problem since the species classifiers are different (Tschopp et al., 2021). In contrast, neontologists have a more comprehensive range of diagnoses, such as soft tissue and molecular data (Carrasco, 2013). Because of these difficulties in studying fossil Squamata, it is crucial to explore new techniques that might aid in fossil identification.

2. OBJECTIVES

Section 1

The present study aims to do an osteological description of the Squamata from the Lajedo de Soledade, Apodi county, Rio Grande do Norte, northeastern Brazil. The specific goals are:

- Taxonomic analysis of the Squamata specimens deposited in the collection of the Laboratório de Paleontologia of the Faculdade de Geologia, Universidade do Estado do Rio de Janeiro (UERJ, Rio de Janeiro-RJ), contributing to the knowledge about the Squamata Quaternary fauna of Brazil.
- Identify possible characters to promote combinations that indicate specific taxonomic levels.

Section 2

This project aims to make an exploratory analysis to find which tests are more efficient in identifying each fossil taxon. In this way, we expect to contribute to the field, helping future identifications of fossil Squamata in moments in which the macroscopical identification is challenging.

- Throughout of use of geometric morphometrics to obtain more refinement of the taxonomic attributions made by macroscopic analysis.
- Explore the best ways of using the tool to identify different groups of Serpentes.

SECTION 1: IDENTIFICATION AND DESCRIPTION OF NEW FOSSIL SQUAMATA FROM THE LAJEDO DE SOLEDADE, RIO GRANDE DO NORTE, BACIA POTIGUAR

Abstract

Quaternary fossils in Brazil are common in natural tanks, caves and karstic environments. These places are interesting for paleontology because they serve as shelter for many species, may be natural traps, and present sedimentary input by floods that carry skeletal material from the surrounding areas. One karstic environment that has yielded many fossils of Pleistocenic megafauna is the Lajedo de Soledade, in the municipality of Apodi, Rio Grande do Norte. This location is a prominent outcrop of limestone, with approximately 03 Km² of exposed rock, constituted mainly by the inferior section of the Jandaíra Formation. Through the ages, the limestone suffered a process of karstification that formed caves and ravines, where the preserved paleofauna association is one of the most diverse for the Quaternary of Rio Grande do Norte. The mammals collected and identified are from the Megatheriidae, Glyptodontidae, Dasypodidae, Canidae, Felidae, Ursidae, Equidae, Camelidae, Macraucheniidae, Toxodontidae, Cervidae e Gomphotheriidae families. Aside from the mammals, osteoderms of crocodylomorphs and snake vertebrae were also collected, but they were never described or properly identified. Therefore, only fossil mammals have been described until now, and knowledge about the paleoherpetofauna is still scarce. In the present study, we describe fossil Squamata unearthed in Lajedo de Soledade. Fossils of *Crotalus durissus*, *Epicrates*, an embryo of Boidae, Viperidae indet, *Tropidurus*, and Teiidae were identified. These are the first fossil Squamata from the Lajedo to be described and identified. Most of these taxa are present on the extant herpetofauna of Rio Grande do Norte, except for the Teiidae, which does not resemble the current big lizards of the state. The results of this dissertation are essential for understanding the Quaternary environment of Rio Grande do Norte and clarifying the past faunal composition of Squamata, which had not yet been described for the locality.

Key words: Rio Grande do Norte; Ravine; Lajedo de Soledade; *Crotalus*; *Epicrates*; Teiidae

3. INTRODUCTION

3.1.CENOZOIC SOUTH AMERICAN SQUAMATA FOSSIL RECORD

Generally, specimens of Squamata are small and have fragile skeletal elements compared to other groups with mostly more robust skeletons, such as crocodiles and dinosaurs. The study of fossil squamates, therefore, can prove a challenging issue since these characteristics of the group can hamper the fossilization and collection of these fossils. Consequently, the fossil record of these animals is mainly composed of isolated and fragmented bones (Onary et al., 2017). Regarding lizards, most materials are skull fragments, like maxilla and dentary, while in snakes, it is almost exclusively comprised of isolated vertebrae (Hsiou, 2010; Onary and Hsiou, 2015). Amphisbaenians have a much more scarce record, represented by skulls and vertebral elements (Camolez and Zaher, 2010).

Fossils of squamates in South America extend in a vast temporal and geographic distribution, with records from the Cretaceous until the Pleistocene-Holocene. Two (02) snakes have been formally described for the Brazilian Cretaceous, *Boipeba tayasuensis*, a giant Scolecophidia (Fachini et al., 2020), and *Seismophis setentrionalis* (Hsiou et al., 2013a) of uncertain affinities. Two other snakes were reported but never formally described (Bertini and Bonfim-Júnior, 1998; Zaher et al., 2003). In Argentina there is a greater diversity of Cretaceous Serpentes, including some of the most primitive specimens like *Najash rionegrina* and *Dinilysia patagonica* (Smith-Woodward, 1901; Apesteguía and Zaher, 2006; Zaher et al., 2009; Albino and Brizuela, 2015). Also, there is a great diversity of Madtsoiidae and a putative anilioid (Albino, 1986, 1994, 1996a, 2000, 2007, 2011; Martinelli and Forasiepi, 2004; Gómez et al., 2008; Albino and Brizuela, 2014a). In Bolivia, one unnamed Madtsoiidae has been described (Gayet et al., 2001), and in Venezuela there is one marine snake named *Luanophis aquaticus* (Albino et al., 2016).

Lizards have a more ample record for the Cretaceous of Brazil. Seven (07) species have been described, *Olindalacerta brasiliensis*, *Calanguban alamoi*, *Tijubina pontei*, *Pristiguana brasiliensis*, *Brasiliguana prudensis*, *Gueragama sulamericana*, and *Neokotus sanfranciscanus* (Estes and Price, 1973; Bonfim-Júnior and Marques, 1997; Evans and Yabumoto, 1998; Nava and Martinelli, 2011; Simões et al., 2014, 2015; Candeiro et al., 2018; Bittencourt et al., 2020). In Argentina, on the other hand, only two lizards have been described, a possible Iguanidae and a one Scincomorpha (Apesteguiá et al., 2005; Brizuela and Albino, 2011). Lastly, in Chile, a putative teiid has been described, however its phylogenetic affinities are questioned (Valencia et al., 1990; Albino, 1996a, 2007)

For the Cenozoic, the record can be divided in three distinct moments, Paleogene, Neogene and Quaternary. The Paleogene snake records in Brazil are completely represented by the São José do Itaboraí fauna (Eocene). The record is diverse and composed mainly of isolated vertebrae comprising six (06) genera. These include Madtsoiidae, "Anilidae", and macrostomatan groups, such as extinct Boidae, the extant genus *Corallus*, one Ungaliophiinae, and a single possible Caenophidia (Albino, 1990; Rage, 1998, 2001, 2008; Onary et al., 2017). In Argentina, the Paleogene is represented by two Madtsoiidae and various booids like *Chubutophis grandis* and *Waincophis australis* (Simpson, 1933, 1935; Hoffstetter, 1959; Albino, 1987, 1993, 2011, 2012; Albino and Carlini, 2008). In Bolivia, there is a great diversity of snakes, with one anilioid, one Tropidophidae, one derived macrostomatan, one possible Madtsoiidae, and two booids being described (de Muizon et al., 1983; Rage, 1991; Scanferla et al., 2013). In Peru there has been described the genus *Coniophis* and in Colombia the giant snake *Titanoboa cerrejonensis* has been unearthed (Rage, 1981; Head et al., 2009).

Paleocene fossil lizards have been unearthed in Brazil, Bolivia, and Argentina. In Bolivia, a iguanid has been described by Rage (1991). In Argentina, only the extinct Teiidae *Lumbrearasaurus scagliai,* and two iguanids are known (Donadio, 1985; Albino and Brizuela, 2014b; Brizuela and Albino, 2016). The greater fossil diversity for the Paleocene comes from Brazil, in the fossiliferous locality of São José do Itaboraí. These are 85 fossils fragments representing many lizards lineages, like Scincomorpha, Aguimorpha and Gekkota (Carvalho, 2001).

In the Neogene, the fossil record is much more diverse. The Brazilian Serpentes fossils, are concentrated in the Solimões Formation (late Miocene) and is represented mainly by extant species, like *Eunectes murinus* and *Epicrates* sp., colubroids and a viper, possibly a *Bothrops* sp, (Hsiou and Albino, 2009, 2010, 2011; Onary et al., 2017). However, there are also the extinct genera *Colombophis*, and *Waincophis* (Hsiou and Albino, 2010; Hsiou et al., 2010). In Argentina, *Waincophis* is also present, as well as the other extinct taxon *Gaimanophis,* as well as colubroids, booids, and vipers (Albino, 1992, 1996b, 1996c; Albino and Quintana, 1992; Albino and Montalvo, 2006; Albino and Carlini, 2008; Fernicola and Albino, 2012; Albino et al., 2013). In the Venezuelan

Neogene there is a very diverse fossil record, with reports of the extinct genus *Colombophis,* and extant booids and vipers (Head et al., 2006; Albino and Brizuela, 2014a; Onary et al., 2018). In Colombia, the fossil fauna is similar to that of Venezuela, with *Colombophis*, *Eunectes* and colubroids being reported (Hoffstetter and Rage, 1977; Estes and Báez, 1985; Hecht and LaDuke, 1997; Hsiou et al., 2010). In Ecuador, there is one reported marine snake named *Pterosphenus sheppardi* (Hoffstetter, 1985).

The Neogene lizards are also abundant, especially the records of Teiidae. In Argentina, there is a great record of iguanians and teiids (Brizuela and Albino, 2004, 2008, 2010, 2012; Albino et al., 2006, 2009, 2020; Albino, 2008, 2011; Fernicola and Albino, 2012; Quadros et al., 2018). In Peru, Colombia, Uruguay, Ecuador, and Bolivia there have been described specimens of the extinct teiid *Paradracaena*, as well as other teiids like the genus *Tupinambis* sp. and specimens of iguanids (Estes, 1961; Hoffstetter, 1970; Rage, 1991; Sullivan and Estes, 1997; Pujos et al., 2009). In Brazil, only one specimen of Teiidae have been described, from the extinct genus *Paradracena* (Hsiou et al., 2009).

The more recent records (Quaternary) are mostly of extant species (Albino and Brizuela, 2015). In South America there are records of Boidae, Viperidae, Elapidae, and Colubroidea in Argentina, Colombia, Venezuela, and Brazil (Porta, 1969; Albino and Albino, 1995; Albino, 1999, 2001; Albino et al., 2002; Scanferla and Nenda, 2005; Scanferla et al., 2005, 2009; Scanferla, 2006; Albino and Carlini, 2008; Hsiou and Albino, 2009, 2011; Camolez and Zaher, 2010; Hsiou et al., 2012, 2013b; Onary et al., 2018). It is worth mentioning that, in Brazil, most of these fossiliferous sites lack rock dating data. Up until now, the taxa of venomous snakes recognized for the Brazilian Cenozoic are fragments attributed to the genera *Micrurus* (Elapidae), *Bothrops*, and *Crotalus* (Viperidae) (Camolez and Zaher, 2010; Hsiou and Albino, 2011; Hsiou et al., 2012).

The Quaternary record of lizards is also mainly composed of disarticulated fragments. This record is taxonomically diverse. Aside from Brazil, In South America there are records of Iguanidae, Liolaemidae, Teiidae, Leiosauridae, Gekkonidae (Rusconi, 1937; Hoffstetter, 1970; Van Devender, 1977; Estes, 1983; Donadío, 1984; De la Fuente, 1999; Albino, 2005). In Brazil, the record is also incredibly diverse, with fossils for the Tropiduridae, Teiidae, Leiosauridae, Polychrotidae, Gekkonidae, and Anguidae families, being Teiidae the most prevalent, including the extinct species *Tupinambis uruguaianensis* (Hsiou, 2007; Camolez and Zaher, 2010; Hsiou et al., 2012, 2016). These fossils were found in Rio Grande do Sul, Ceará, Minas Gerais, Tocantins, Goiás, Bahia, Acre, Rio de Janeiro, and Mato Grosso states.

As previously mentioned, many fossils of Squamata are isolated elements. The accurate identification of fossils of this group demands dedication, time, and an extensive osteological collection of living taxa, enabling the evaluation of cranial, intracolumnar, ontogenetic, and intraspecific variation (LaDuke, 1991a; Hsiou, 2017). Therefore, comparative efforts with living specimens of snakes and lizards are essential for more accurate taxonomic and systematic attributions of the analyzed fossils.

When analyzing the fossil record, especially the Quaternary fauna, it is possible to compare the past and present faunistic composition and analyze the variation in the community and environment. It is especially interesting when the analysis uses a fossil assemblage since it exhibits a large taxonomic variety in one place, revealing an expressive temporal faunistic clipping (Evans, 2003). Furthermore, small vertebrates, especially ectothermic animals, are good bioindicators of climate change, due to the ecological associations they establish with the environment (Salles et al., 1999; McMenamin et al., 2008; Böhm et al., 2013).

The Quaternary fossil record in Brazil usually comes from caves and karstic environments, since such places serve as shelter for many species, and are often associated with archeological sites (Onary et al., 2017). Also, they may be natural traps and present sedimentary input by floods that carry skeletal material from the surrounding areas into the cave (Salles et al., 1999). Therefore, these places are a great source of fossil assemblages. In the state of Rio Grande do Norte, around 25 fossiliferous localities are known to bear fossil assemblages (Araújo-Júnior and Porpino, 2011). However, no squamate fossil has been described in the state.

4. MATERIAL AND METHODS

4.1.MATERIAL

4.1.1. **Provenance, geology and paleontology**

The squamate remains come from the Ravina das Araras at the locality Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. The material comprises 81 fossils in several preservation conditions (Supplementary Material I). Lizards (teiid and iguanian specimens) are represented by isolated dentaries and vertebral remains, and snakes (booids and viperids specimens) are represented exclusively by isolated vertebrae. All specimens are stored at the Museu do Lajedo de Soledade (MLS) of Apodi municipality, Rio Grande do Norte, Brazil.

On the overall geological context of the Lajedo Soledade, it is located in Chapada do Apodi, a *cuesta* formation between the states of Ceará and Rio Grande do Norte, northeastern Brazil (Figure 2). The western limits of Chapada do Apodi are bounded by the Jaguaribe and Figueiredo rivers, and the eastern region by the Upanema river. Its' southern boundary is 10 km from the Apodi municipality and extends northwards up to the Atlantic Ocean (Lima Verde, 1976). The Chapada is composed of the Açu Formation (sandstone) and the Jandaira Formation (limestone), as well as some sandstone outcrops of the Barreiras Formation, interpreted as coastal and river Cenozoic deposits, respectively (Angelim, L. A. A. Medeiros, V. C., Nesi, 2006; Pinéo et al., 2020).

The Lajedo de Soledade locality is a prominent outcrop of limestone, with approximately 03 Km² of exposed rock, constituted mainly by the inferior section of the Jandaíra Formation (Potiguar Basin) in Rio Grande do Norte (Bagnoli, 1994; Córdoba et al., 1994). On the flagstone, there are marine fossils and ichnofossils, accounting for when the site was a tidal flat (Porpino et al., 2007). The karstification process influenced the region, which widened rifts and fractures, creating caves and ravines (Córdoba et al., 1994). These ravines have yielded several small and fragmented fossils and are known for its' paleoarcheological potential with many rupestrian paintings. The paleofauna association preserved is one of the most diverse fossil assemblages for the Quaternary of Rio Grande do Norte (Porpino et al., 2004). However, only fossil mammals have been described until now, and knowledge about the paleoherpetofauna is still scarce.

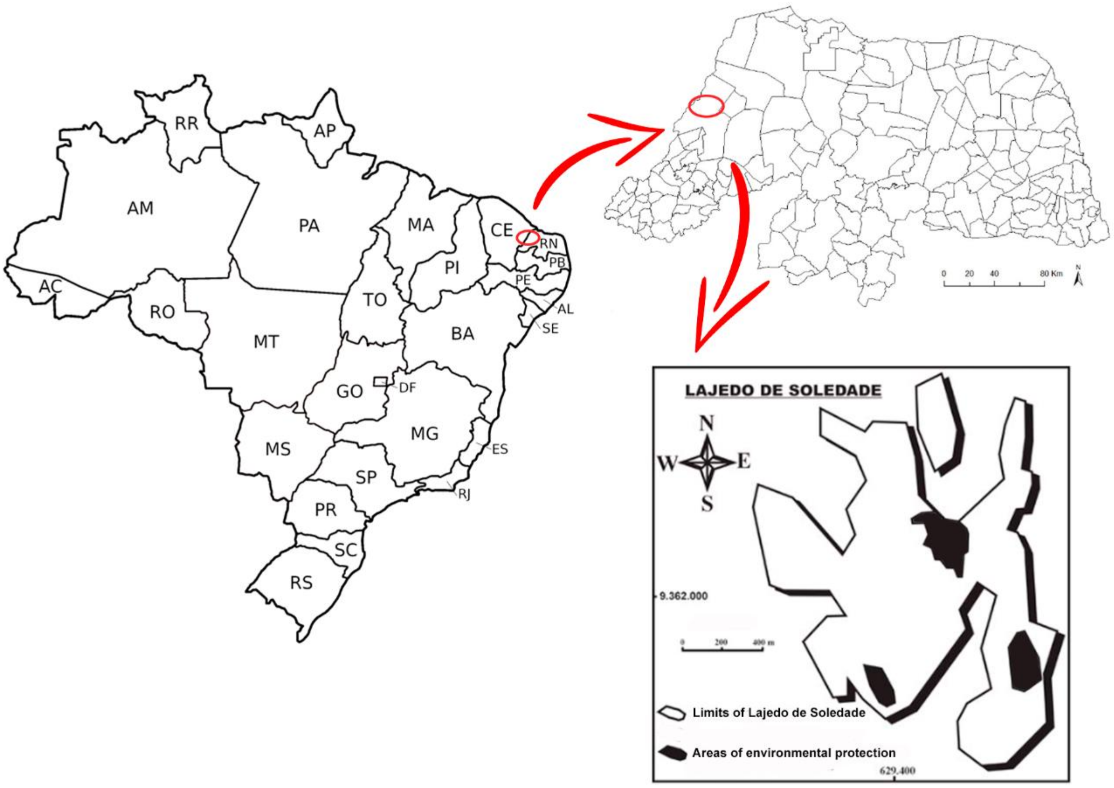

Figure 2: Map of the Lajedo de Soledade and its location in Brazil and in Rio Grande do Norte. Modified from Porpino et al. (2004)

The first work that mentioned fossils from the Lajedo de Soledade was done by Rosado (1957), who reported the presence of Glyptodontidae osteoderms. Later, more surveys also commented on the existence of similar fossil mammals, but without taxonomic and systematic descriptions. Since the '90s, throughout the advance of paleontological studies on the region, many fossils have been collected, identified, and adequately described (Porpino et al., 2007).

The mammals collected and identified are from the Megatheriidae, Glyptodontidae, Dasypodidae, Canidae, Felidae, Ursidae, Equidae, Camelidae, Macraucheniidae, Toxodontidae, Cervidae e Gomphotheriidae families (Santos et al., 2002; Porpino et al., 2004). Aside from the mammals, osteoderms of crocodylomorphs and snake vertebrae were also collected, but they were never described or identified (Porpino et al., 2007).

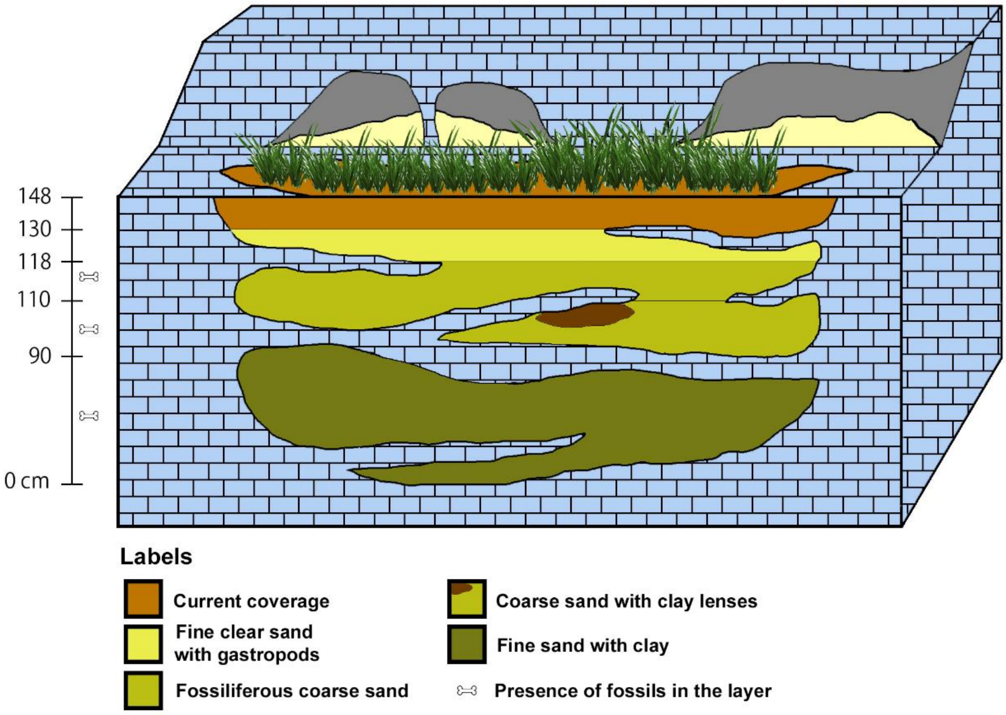

Figure 3: stratigraphyc layers of Ravina das Araras, Lajedo de Soledade. Fossil Squamata analysed in the presente study were unearthed in the level of fossiliferous rough sand and the level of bright fine sand with gastropods. Image made by Gustavo Martins, modified by Sílvia Lomba.

The Pleistocene megafauna retrieved from the location are usually in the fine sand with clay layer, but also in the layers of coarse sand, as shown in Figure 3. The fossil Squamata unearthed on the Lajedo have been collected on the layers of coarse sand and the layer of fine clear sand with gastropods. It is important to point out that the layers have not been dated yet. However, based on the fossil record, the layers in which the megafauna is present is estimated to be late Pleistocene. A more in-depth study regarding the stratigraphy is being done Professor Herminio’s research group. Santos et al. (2002) has pointed out that the sediments and fossils filling the ravines show little sign of transportation and, therefore, where sourced from the near surrounding area.

4.2.METHODS

The material studied herein is housed at the Museu do Lajedo de Soledade Rio Grande do Norte (MLS, Apodi municipality, Brazil). The fossil squamate material was loaned to the Laboratório de Paleontologia de Ribeirão Preto (LPRP, FFCLRP/USP) for the development of the present Master Dissertation through Prof. Dr. Hermínio Ismael de Araújo Júnior (UERJ, Rio de Janeiro, Rio de Janeiro state), who studies the depositional and taphonomic dynamics of the Lajedo de Soledade region. As mentioned above, the squamate remains consist of disarticulated elements collected carefully through excavation and screen-washing at the Lajedo de Soledade by Prof. Hermínio's research group in the last few years.

The study of the material mainly consisted of macroscopic observation, although a stereoscopic microscope was used when necessary. The anatomical study included a comparative analysis carried out of extant specimens through a comparison of the available material deposited at the Coleção Herpetológica de Ribeirão Preto (CHRP) of the Departamento de Biologia of FFCLRP/USP (Ribeirão Preto, São Paulo, Brazil); the Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil); the Florida Natural History Museum, Herpetology Collection (UF:HERPS, Florida, USA) through Morphosourse; the Coleção da Universidade Federal do Mato Grosso (UFMT, Cuiabá, Mato Grosso do Sul, Brazil); the Natural History Museum of Los Angeles County (LACM, Los Angeles, USA) through photographs; and Coleção Didática de Répteis (MCN-PV-DR) and the Coleção Didática de Herpetologia (MCN.D.) of the Museu de Ciências Naturais da Secretaria do Meio Ambiente do Estado do Rio Grande do Sul (SEMARS, Porto Alegre, Rio Grande do Sul, Brazil). The specimens used are listed in the Supplementary Material I.

For the description of the material, the established methodology and anatomical terminology for each of the studied groups were followed. The descriptions followed Auffenberg (1963), Rage (1984), LaDuke (1991a, 1991b), Lee and Scanlon (2002), Albino and Carlini (2008), and Hsiou et al. (2013a) for snakes (Figure 4); and Estes, (1983), Frost, (1992), Veronese and Krause, (1997), and Brizuela and Albino, (2016) for lizards. The systematic attribution follows Pyron et al., (2013), Figueroa et al., (2016), Zaher et al., (2019), Georgalis and Smith, (2020), and Onary et al., (2022).

The quantitative measurements were done following LaDuke (1991a, 1991b) (Figure 5) using a Digimess caliper with 0,02mm precision and a digital 9QS caliper. Images and photos were taken to illustrate the characteristics of each fossil taxon/morphotype and were edited with Adobe Photoshop CC (2021 version). The photos were taken with a digital Canon Rebel T6i camera, with a standard 18-55mm or 100mm macro lens. For smaller specimens, a Leica M205 stereo microscope was used.

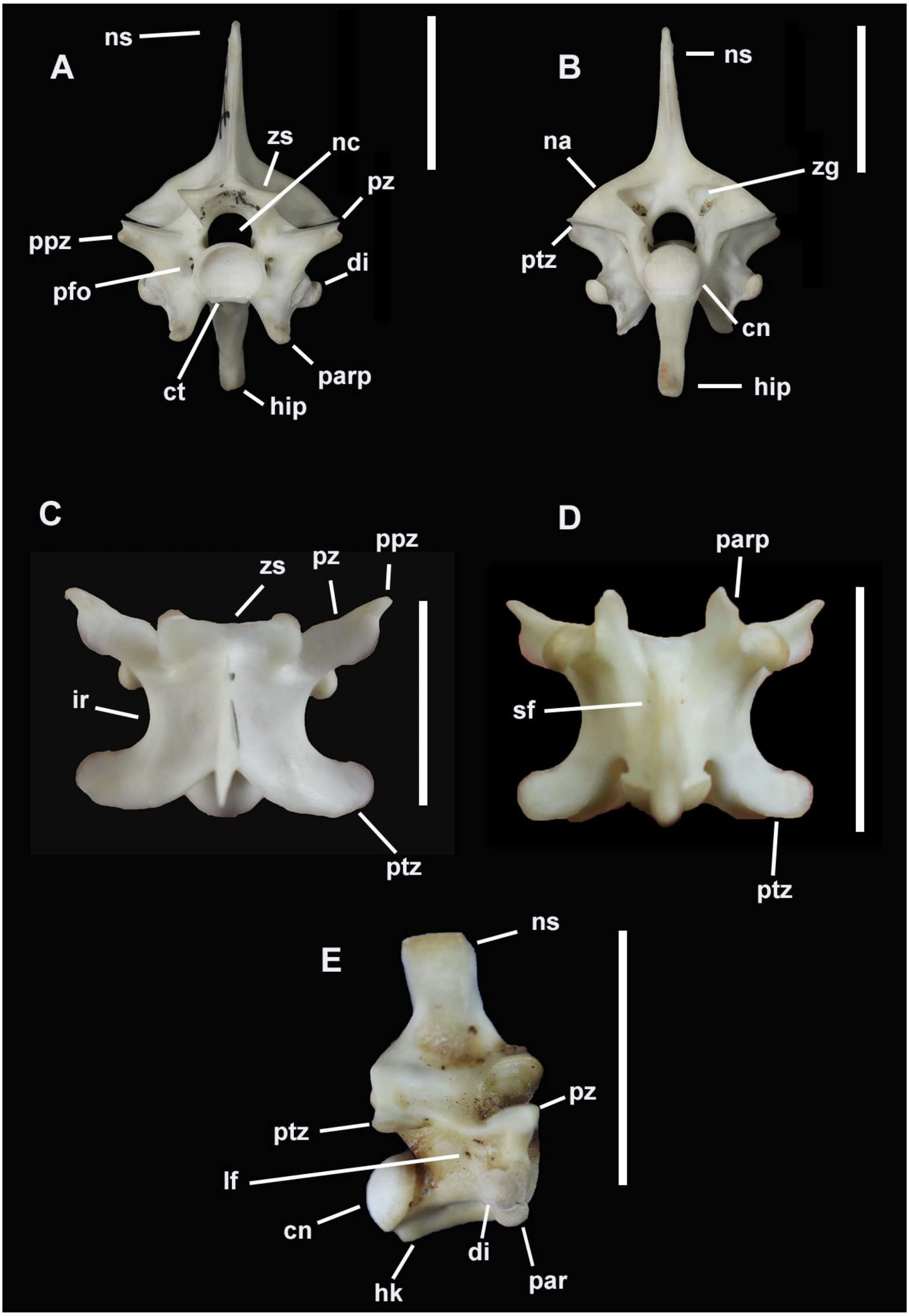

Figure 4: Mid-trunk *Crotalus durissus* (A, B, C, D) and *Epicrates cenchria* (E) vertebrae with anatomical abbreviations used in the present study. Anatomical Abbreviation list is in the beginning of the dissertation. (A) anterior view (B) posterior view, (C) dorsal view, (D) ventral view and (E) lateral view. Scale 1cm

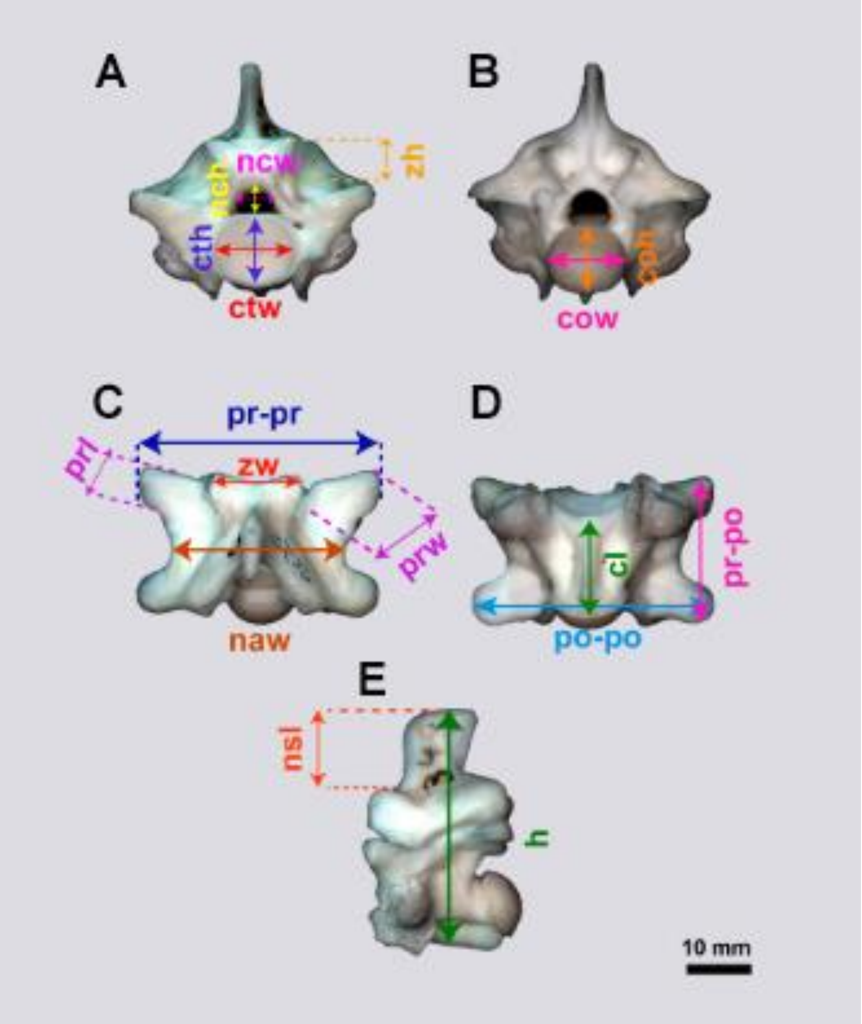

Figure 5: Isolated mid-trunk *Boa constrictor* showing the measurements adopted in the present study. Anatomical Abbreviation list is in the beginning of the dissertation. (A) anterior view (B) posterior view, (C) dorsal view, (D) ventral view and (E) lateral view. Scale 1cm. Modified from Onary et al. (2018)

5. RESULTS

Systematic Paleontology

Squamata Oppel,

Lacertoidea Oppel, 1881

Teiidae Gray, 1827

Undetermined genus and species

(Figure 6)

Referred Material: MLS 483 One incomplete vertebra.

Locality and Horizon: Lajedo de Soledade locality (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene-Holocene (Quaternary) (Porpino et al., 2007). Coarse sand horizon.

Measurements (mm): MLS 483 cl: 10,6; coh: 3,2; cow: 5,3; cth: 3,7; ctw: 5,2; prl: 4,3; prw: 3,5;

Description

The specimen MLS 483 is an incomplete vertebral centrum and comprises the condyle, cotyle, both prezygapophyses, and both sinapophyses (articulations with the ribs). The overall shape of the centrum is triangular, being broader on the anterior portion and narrower on the posterior part, and subcentral foramina are present and very small (pits). The condyle and the cotyle are oval, being wider than tall. The neural canal has a discrete crest in the middle. The right prezygapophyseal articular facet is oval. The right sinapophysis has abnormal bone growth, which probably is indicative of some kind of paleopathology.

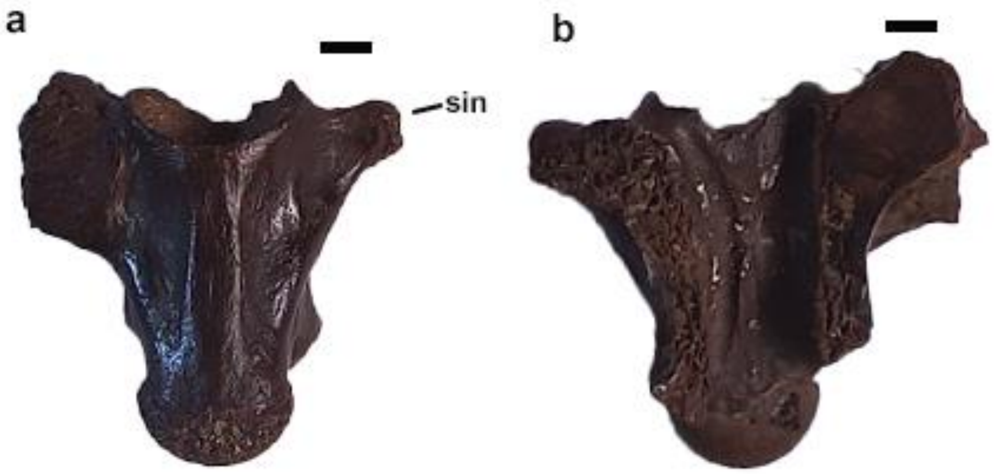

Figure 6: Teiidae trunk vertebra. (a) ventral view, (b) dorsal view. Scale 2mm

Toxicofera Vidal & Hedges, 2005

Iguania Cope, 1864

Tropiduridae Bell, 1843

Tropidurus Wied-Neuwied, 1825

***Tropidurus* sp.**

(Figure 7)

Remarks: The genus is widely distributed in all of South America, predominantly in areas of open vegetation and more arid climates (Carvalho et al., 2013). These animals are also present in patches of savannah in the Amazon Forest. Despite this, their presence in humid habitats is limited. Currently, 22 species of *Tropidurus* are recognized in Brazil, despite some unresolved groupings (Costa et al., 2021; Moclán et al., 2023). In Rio Grande do Norte, two species are currently recognized, *T. hispidus* and *T. semitaeniatus* (Carvalho, 2013; Costa et al., 2021)

Referred Material: MLS 486 well preserved left dentary

Locality and Horizon: Lajedo de Soledade locality (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene-Holocene (Quaternary) (Porpino et al., 2007). Gastropod’s horizon.

Description

The MLS 486 is a well-preserved delicate left dentary with 16 preserved teeth. The remaining thirteen teeth are tricuspidate, with two accessory cusps around the central cusp, one anterior and one posterior. The three more apical teeth are unicuspidated. The dentition is pleurodont. The Meckel canal is closed, remaining only a small foramen in the anterior portion of the dentary, near the mandibular symphysis. The posterior portion of the dentary is preserved. Its' dorsal margin is flat, for the articulation with the coronoid.

In labial view, eight mental foramina are visible. In lingual view, on the posterior portion, there is a notch that extends until the antepenultimate tooth where the splenial articulates with the dentary (Camolez and Zaher, 2010; Hsiou et al., 2012). The alveolar shelf is weakly eroded (*sensu* Frost, 1992), which is a characteristic that is absent in the outgroups. The subdental shelf is shallow. The mandibular symphysis region is internally oriented in dorsal view, while in the lingual view, it is dorsally oriented.

Figure 7: *Tropidurus* left dentary. (a) lingual view, (b) labial view. Scale 2mm

Identification and comparison of lizard specimens

Due to the incompleteness of preservation of MLS 483 it is almost impossible to identify the species. However, based on its great vertebral size, it can be attributed to a large lizard. The extant biggest lizards of Brazil are *Iguana*, *Salvator*, *Tupinambis*, *Crocodilurus*, and *Dracaena*. On Rio Grande do Norte, the two large lizards present are *Iguana iguana* and *Salvator merianae*.

It is possible to know that the fossil is not *Iguana iguana* since this taxon has bigger subcentral foramina anteriorly positioned on the vertebral centrum. On MLS 483, these foramina are small (pits) and on the medial portion of the vertebral centrum. In addition, in the *I. iguana* comparison specimens it was observed foramens in the neural canal, which are not present in MLS 483. Also, for an *I. iguana* vertebra of this length, the condyle and the cotyle are smaller than the ones in MLS 483. However, the vertebra is also different than those of *Salvator merianae,* which are wider in the anterior portion, MLS 483 is slimmer.

Aside from *Iguana,* the remaining big lizard taxa in Brazil belong to the Teiidae family and, therefore, the more likely family of the fossil. Also, the following characteristics are shared between MLS 483 and Teiidae: large size, no prezygapophyseal process, triangular vertebral centrum, oval cotyle and condyle (ctw>cth, cdw>cdh), and marked precondylar constriction (Brizuela and Albino, 2016). With this information, MLS 483 is probably another species of *Tupinambis* different from *Salvator merianae*. Unfortunately, during the present study only specimens of *S. merianae* were available. For more precise identification, more comparison specimens are needed.

In regards to MLS 486, the present fossil was attributed to the *Tropidurus* genus but not a species. It can be attributed to *Tropidurus* by the pleurodont dentition, the closed Meckel canal, and the weakly eroded alveolar shelf (Frost, 1992; Hsiou et al., 2012). Currently, two species are recognized for Rio Grande do Norte. These are *T. semitaeniatus* and *T. hispidus* (Carvalho, 2013; Costa et al., 2021). However, studies comparing the cranial anatomy of different *Tropidurus* species retrieved no character to differentiate between species (Adorni, 2018). Therefore, MLS 486 was attributed to the genus *Tropidurus,* undetermined species.

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Constrictores Oppel, 1811 *sensu* Georgalis & Smith 2020

Booidea Gray, 1825 *sensu* Pyron, Reynolds & Burbink 2013

Boidae Gray, 1825

Epicrates Wangler, 1830

***Epicrates* sp.**

(Figure 8)

Remarks. The most recent list of Brazilian reptiles recognizes four species of *Epicrates*, *E. assisi*, *E. crassus*, *E. cenchria*, and *E. maurus* (Costa and Bérnils, 2018; Costa et al., 2021). The genus is reported for all of the Brazilian states, except Santa Catarina, though this is probably due to a sampling bias (Costa and Bérnils, 2018; Costa et al., 2021). For the state of Rio Grande do Norte, only one *Epicrates* species is recognized, *E. assisi*. This species is also reported for the Chapada do Apodi by Lima Verde (1976).

Referred Material: MLS 485 eroded anterior trunk vertebra; MLS 492 one complete mid-trunk/posterior trunk vertebra, MLS 493 one almost complete mid-trunk/posterior trunk vertebra, MLS 494 one complete mid-trunk/posterior trunk vertebra, MLS 495 one almost complete mid-trunk/posterior trunk vertebra, MLS 496 one almost complete mid-trunk/posterior trunk vertebra, MLS 497 one complete mid-trunk/posterior trunk vertebra, MLS 498 one complete mid-trunk/posterior trunk vertebra, MLS 499 one almost complete mid-trunk/posterior trunk vertebra.

Locality and Horizon: Lajedo de Soledade locality (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene-Holocene (Quaternary) (Porpino et al., 2007). MLS 485, MLS 492, MLS 493, MLS 494, MLS 495, MLS 496, and MLS 497 are from the coarse sand horizon, MLS 498 and MLS 499 are from the gastropod's horizon.

Measurements (mm): MLS 485 cl: 4,7; coh: 2,7; cow: 2,8; cth: 2,5; ctw: 2,7; naw: 6,9; nch: 2,3; ncw: 2,3; po-po: 9,6; pr-pr: 9,5; pr-po: 6,5; prl: 2,7; prw: 1,9; zh: 1,2; zw: 4,3; **MLS 492** cl: 4,5; coh: 2,6; cow: 2,9; cth: 2,2; ctw: 2,8; h: 8,2; naw: 5; nch: 1,8; ncw: 1,8; nsh: 2,9; po-po: 7,7; pr-pr: 7,7; pr-po: 5,4; prl: 2,1; prw: 1,5; zh: 0,6; zw: 3,5; **MLS 493** cl: 4,2; coh: 2,7; cow: 2,9; cth: 2,2; ctw: 2,7; h: 8,3; naw: 5,1; nch: 1,8; ncw: 1,8; nsh: 2,7; po-po: 7,6; pr-pr: 8; pr-po: 5,3; prl: 2,2; prw: 1,5; zh: 0,7; zw: 3,6; **MLS 494** cl: 4,5; coh: 2,5; cow: 2,9; cth: 2; ctw: 2,7; h: 8,4; naw: 5,1; nch: 1,9; ncw: 1,8; nsh: 3,2; po-po: 7,9; pr-pr: 8,2; pr-po: 5,5; prl: 2,5; prw: 1,5; zh: 0,7; zw: 3,5; **MLS 495** cl: 4,2; coh: 2,3; cow:

2,7; cth: 2,1; ctw: 2,7; naw: 4,9; nch: 1,6; ncw: 1,7; pr-pr: 7,6; pr-po: 5,1; prl: 2,1; prw: 1,6; zh: 0,6; zw: 3,2; **MLS 496** cl: 5,6; coh: 3,1; cow: 3,4; cth: 2,7; ctw: 3,4; h: 9,6; naw: 6,3; nch: 1,9; ncw: 2,2; nsh: 2,8; po-po: 9,4; pr-pr: 10,3; pr-po: 6,6; prl: 2,9; prw: 2,2; zh: 0,9; zw: 4,4; **MLS 497** cl: 5,5; coh: 3,1; cow: 3,5; cth: 2,7; ctw: 3,2; h: 9,8; naw: 6,5; nch: 1,9; ncw: 2,2; nsh: 3,2; po-po: 9,8; pr-pr: 10,5; pr-po: 6,7; prl: 2,9; prw: 2,1; zh: 0,9; zw: 4,3; **MLS 498** cl: 5,6; coh: 3,4; cow: 3,6; cth: 2,6; ctw: 3,2; h: 10,1; naw: 6,8; nch: 2,2; ncw: 2,7; nsh: 3,9; po-po: 10; pr-pr: 10,1; pr-po: 6,8; prl: 3,1; prw: 2,1; zh: 1; zw: 4,9; **MLS 499** cl: 4,3; coh: 2,5; cow: 2,8; cth: 2,1; ctw: 2,7; naw: 4,8; nch: 1,7; ncw: 1,6; po-po: 7,4; pr-pr: 7,9; pr-po: 5,3; prl: 2,5; prw: 1,6; zh: 0,6; zw: 3,2;

Description

These vertebrae are relatively small. In anterior view, the prezygapophyses are slightly inclined diagonally concerning the horizontal plane, showing a small prezygapophyseal process. The cotyle is wider than tall (ctw>cth), having a slight oval shape. The zygosphene is robust, around 1mm thick, and wider than the cotyle (zw>ctw). The zygosphene roof is straight in MLS 485, MLS 496, MLS 497, and MLS 498 while this structure is elevated in MLS 492, MLS 493, MLS 494, MLS 495, and MLS 499. The paracotylar fossae are deep, and the foramina are usually absent, except for MLS 492 and MLS 496 that have a single small foramen (pit) on the left side of the cotyle. The neural spine is tall (LaDuke, 1991b) and corresponds to less than half of the total height of the vertebra in all specimens in which this structure is preserved (nsh<h). The neural canal has a trifoliate aspect and is narrower than the cotyle (ncw<ctw).

In dorsal view, the neural arch is wider than long (po-po>pr-po). The anterior edge of the zygosphene has anteriorly projected articular facets and a median lobe typically crenated (*sensu* Auffenberg, 1963). The prezygapophyses are laterally oriented, longer than wide (prl>prw), except in MLS 485 in which the prezygapophyses are strongly anteriorly oriented, being wider than long (prl<prw), which differentiates this specimen from the remaining. The prezygapophyseal processes are very short in all vertebrae. The interzygapophyseal ridge is well-marked between the prezygapophysis and the postzygapophysis. There is a deep notch on the posterior portion of the neural arch between the postzygapophysis (the posterodorsal notch), which makes the condyle visible.

In posterior view, the neural arch is depressed, with a slightly arched aspect. The postzygapophyses are slightly inclined upward. This slope is subtler than in the prezygapophyses. The zygantrum is large and with paired zygantral foramina. Lateral to the zygantrum, there are small pits of varied quantities in all specimens. The condyle is wider than tall (cow>coh).

In lateral view, the vertebrae are anteroposteriorly short. The neural spine is tall (*sensu* LaDuke, 1991b) and is slightly inclined backwards in the specimens in which this structure is preserved. The condyle is slightly inclined dorsally. The hemal keel has a gentle salience near the condyle. In MLS 485, there is a broken hypapophysis. Despite it not being preserved, it is possible to observe it is posteriorly projected. The parapophysis and the diapophysis have a clear separation, with the diapophyses dorsoposteriorly and the parapophyses anteroventrally. The lateral foramina are present, being one small foramen on each side of the vertebrae.

In ventral view, the vertebral centrum is short and triangular. The postzygapophyses articular facets are triangular in MLS 485 and also elongated on the remaining specimens. The sub-central foramina are present, in varying numbers. The hemal keel is well-developed and thin in 492, MLS 493, MLS 494, MLS 495, MLS 496, MLS 497, MLS 498, and MLS 499. It originates in the cotyle and extends posteriorly until the condyle, where there is a small protuberance. In specimen MLS 485 there is a broken hypapophysis.

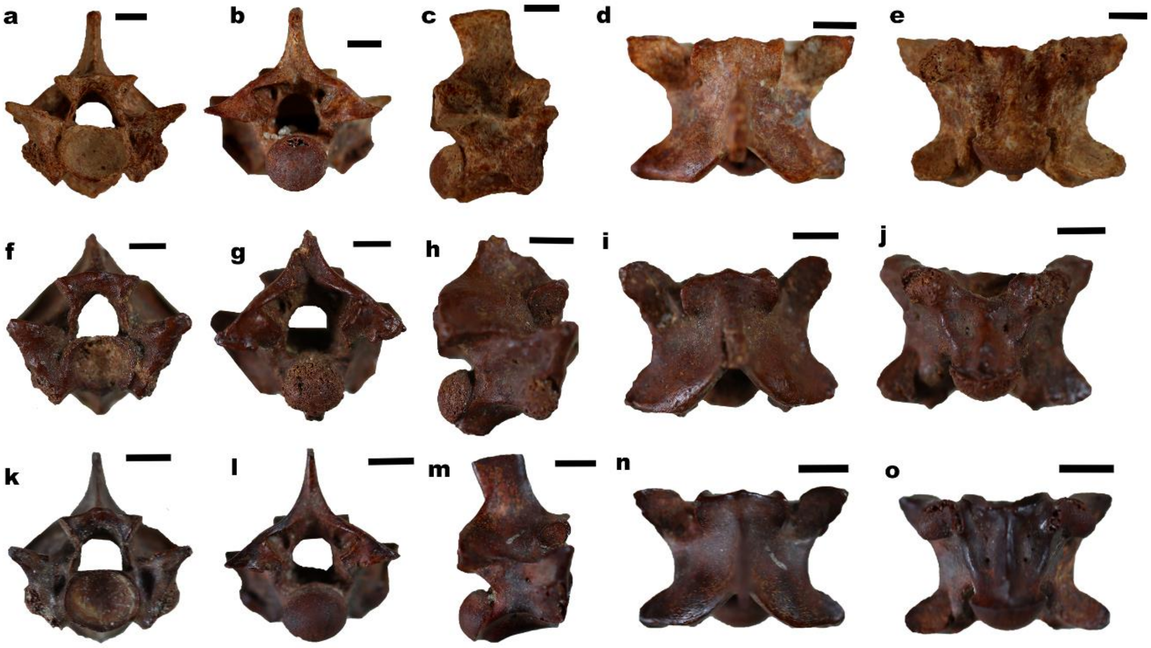

Figure 8: *Epicrates* vertebrae. (a, f, k) anterior view, (b, g, l) posterior view, (c, h, m) lateral view, (d, I, n) dorsal view, (e, j, o) ventral view. Scale 2mm

Boidae

Undetermined genus and species

(Figure 9)

Referred Material: MLS 484 One mid-trunk/posterior vertebra of an embryo.

Locality and Horizon: Lajedo de Soledade locality (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene-Holocene (Quaternary) (Porpino et al., 2007). Coarse sand horizon.

Measurements (mm): MLS 484 cl: 3,6; coh: 1,8; cow: 1,5; cth: 1,7; ctw: 2,4; h: 6,4; naw: 5,1; nch: 2,4; ncw: 2,5; po-po: 6,3; pr-pr: 6,4; pr-po: 4,9; prl: 1,6; prw: 0,9; zh: 0,5; zw: 3,1;

Description

The MLS 484 is a small abraded trunk vertebra. In anterior view, the zygosphene is very thin and with an elevated roof. The zygosphene is not entirely developed, having very discrete articular facets. The prezygapophyses are short and parallel to the horizontal plane. The neural canal is huge compared to the total size of the vertebra and has no internal crests, but it is narrower than the zygosphene (cnw<zw). The cotyle is wider than tall (ctw>cth). The paracotylar fossae are shallow, and there are no paracotylar foramina. The parapophyses are not present.

In dorsal view, the neural arch is short anteroposteriorly (po-po>pr-po). The anterior edge of the zygosphene appears to be straight, with the articular facets slightly anteriorly projected, but the left side of the zygosphene is broken. The interzygapophyseal constriction is discrete. The prezygapophyses are either worn out or underdeveloped, but it is possible to observe that they are anteriorly oriented and lack the prezygapophyseal prosses. Most of the posterior portion of the neural arch is absent, with only the postzygapophyses region present.

In posterior view, the neural arch is incomplete, making it impossible to confirm its shape. The zygantrum is not developed. The condyle is worn out, with only the internal part of this structure being preserved. The condyle is small, smaller than the neural canal (cnw>cow), and round. From its’ ventral edge emerges a small process.

In lateral view, the vertebra is anteroposteriorly short. The zygosphene is discrete. The zygosphenal articular facets are not developed. The paradiapophyses are either completely worn out or underdeveloped. It is possible to see a discrete hemal keel with a little projection on the posterior portion. The lateral foramina are absent.

In ventral view, the vertebral centrum is triangular, being wider on the anterior portion, and narrower on the posterior portion. The hemal keel is developed, however discrete and thin, with a small ventral projection near the cotyle. The subcentral fossae are absent, and the subcentral foramina are present, having one on each side of the hemal keel.

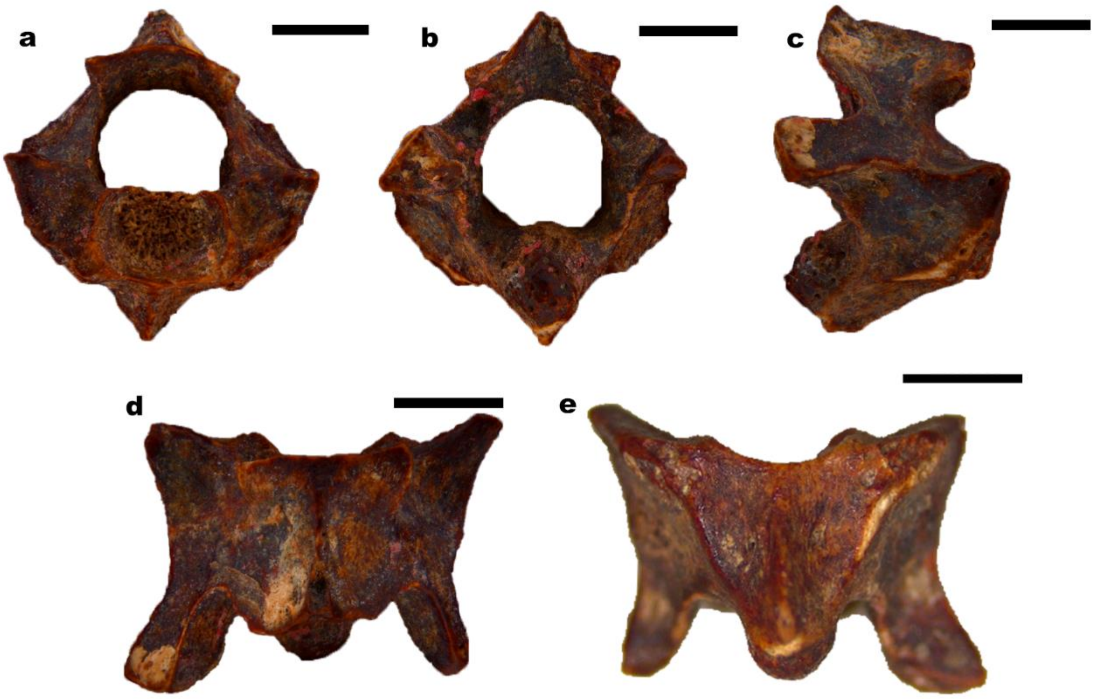

Figure 9: MLS 484. a) anterior view, (b) posterior view, (c) lateral view, (d) dorsal view, (e) ventral view. Scale 2mm.

Identification and comparisons of Boidae specimens

The specimens MLS 485, MLS 492, MLS 493, MLS 494, MLS 495, MLS 496, MLS 497, MLS 498, and MLS 499 can be attributed to the Boidae due to the following combination of vertebral characteristics: laterally wide and anteroposteriorly short vertebrae, vaulted neural arch that is wider than the vertebral centrum, short prezygapophyseal process, wide and thick zygosphene, well-developed neural spine, presence of a posterodorsal notch, and sub-central foramina present (Rage, 2001; Lee and Scanlon, 2002; Szyndlar and Rage, 2003; Hsiou and Albino, 2009; Hsiou et al., 2013b). These fossils can be distinguished from *Boa* and *Eunectes* by their small size, less vaulted neural arch, and different zygosphene morphology, which is thinner and crenated on all specimens (Hsiou and Albino, 2010; Onary et al., 2018). *Eunectes* has a thicker zygosphene with a prominent median tubercle (Hsiou and Albino, 2009). *Boa* also has a thicker zygosphene, but with a concave morphology in dorsal view (Albino and Carlini, 2008; Onary-Alves et al., 2017; Onary and Hsiou, 2018).

The fossils can be distinguished from *Corallus*. *Corallus* has low neural spine and prezygapophyses parallel to the horizontal plane, while the fossils have the dorsoventrally high neural spine and inclined prezygapophyses (Camolez and Zaher, 2010; Teixeira, 2013; Onary et al., 2018). In addition, they can be attributed to the genus *Epicrates* due to the aforementioned characteristic and by the following features: small vertebrae showing a wide, and anteroposteriorly short and robust neural arch, a triangular vertebral centrum, tall neural spine, thick and crenated zygosphene, oval and anterolaterally oriented zygosphenal articular facets, presence of small parazygantral foramina (pits), and irregular presence of paracotylar foramina (Teixeira, 2013; Onary and Hsiou, 2018).

It could be argued that the morphological variation between specimens is due to ontogenetic or intracolumnar variation. That could be the case, however, this variation was not observed in the available comparison material. Another explanation could be interspecific variation. To properly understand these differences, more extant specimens of more species are needed. Currently, only one species of *Epicrates* is recorded for Rio Grande do Norte, which is *Epicrates assisi*. However, no specimen of this species was available for comparison. Also, no post-cranial character has been identified to distinguish the species of *Epicrates*. Therefore, all specimens are attributed to the genus *Epicrates*.

It is possible to identify the MLS 484 as a booid due to the vertebra being laterally wide and anteroposteriorly short and the presence of subcentral foramina (Rage, 2001; Lee and Scanlon, 2002; Hsiou and Albino, 2009; Hsiou et al., 2013b). Furthermore, the vertebra can be attributed to an embryo due to the great size of the neural canal and underdeveloped zygosphene and zygantrum, which are formed in more final stages of embryonic development (Winchester and Bellairs, 1977; Xing et al., 2018). More precise identification is problematic since this specimen is an embryo, and all known diagnostic characters are for adults. Due to the lack of knowledge on the ontogeny of the Brazilian booids, it is more prudent to identify it at the family level. Until now, this is the first record of a snake fossil embryos for Brazil.

Caenophidia Hoffstetter, 1939

Colubroides Zaher et al., 2009

Colubriformes Günther, 1864

Endoglyptodonta Zaher et al., 2009

Viperidae Bonaparte, 1840

Crotalinae Gray, 1825

Crotalus Linnaeus, 1758

Crotalus durissus Linaeus, 1758

(Figure 10)

Remarks: The *Crotalus* genus is represented in Brazil by a single species, *C. durissus*, which is widely distributed in the country. Its area extends from the northeastern region to the southern region, as well as the states of Goiás and Mato Grosso. In the northern region, the distribution is disjointed since this species is not present in areas of dense vegetation, such as the interior of the Amazon Forest, being able to be present in areas of thinner vegetation (Wüster et al., 2005). In the northern region, *Crotalus* has been reported to the states of Tocantins, Roraima, Amapá, Rondônia, and Pará (Marajó Island) (Costa et al., 2021). This species is characteristic of open vegetation and more arid climates (Campbell and Lamar, 1989; Colli et al., 2002).

Material: MLS 479 One anterior trunk vertebra with broken neural spine and hypapophisis MLS 480 One mid-trunk/posterior trunk vertebra with broken neural spine, hypapophysis, right prezygapophyseal and parapophyseal processes.

Locality and Horizon: Lajedo de Soledade locality (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene-Holocene (Quaternary) (Porpino et al., 2007). Coarse sand horizon.

Measurements (mm): MLS 479 cl: 5,9; coh: 2,7; cow: 3,1; cth: 2,7; ctw: 2,9; naw: 4,8; nch: 2,2; ncw: 2,2; po-po: 8,8; pr-pr: 9,1; pr-po: 7,1; prl: 2,5; prw: 2,1; zh: 0,7; zw: 4,5; **MLS 480** cl: 7,9; coh: 4,1; cow: 4,1; cth: 3,7; ctw: 4,2; naw: 7,8; nch: 2,4; ncw: 2,4; po-po: 13,5; pr-pr: 13,6; pr-po: 9,7; prl: 4; prw: 2,3; zh: 1; zw: 6,1;

Description

The specimens MLS 479 and 480 share an anteroventrally developed parapophyseal process, which is the only vertebral synapomorphy proposed for Viperidae

(Zaher, 1999). The neural spine and hypapophysis are broken in both vertebrae. In anterior view, the prezygapophyses are lightly oblique in relation to the horizontal plane. The zygosphene is thin with an elevated roof. It is wider than the neural canal (zw>ncw). The cotyle is slightly wider than tall (ctw>cth). The floor of the neural canal is narrower than the cotyle (ncw<ctw). The paracotylar foramina are present in both vertebrae. The parapophyseal processes are well-developed and anteroventrally oriented, with no lateralization.

In dorsal view, the neural arches are laterally wider than anteroposteriorly long (po-po>pr-po). The anterior edge of the zygosphene of MLS 479 is straight, while the zygosphene of MLS 480 has a concave "V" shaped anterior edge. The prezygapophyses are anterolaterally oriented in MLS 479 and laterally oriented in MLS 480. In both specimens, the prezygapophyses are longer than wide (prl>prw). The anterior vertebra has short prezygapophyseal processes, while the mid-trunk/posterior vertebra has medium-length prezygapophyseal processes (*sensu* LaDuke, 1991), only the left prezygapophyseal process is preserved. The interzygapophyseal ridge is well-marked and curved between the pre and postzygapophysis in both specimens. The posterodorsal notch, between the postzygapophyses, is deep and makes the condyle visible.

In posterior view, the postzygapophyses are horizontal concerning the horizontal plan. The neural arch is triangular, more arched on the anterior vertebra (MLS 479). The zygantrum is wide, and the zygantral foramina are present. Lateral to the zygantrum, there are small pits of varied quantities. The condyle is round (cdw ~ cdh).

In lateral view, the neural spine is broken. The hypapophysis is well developed in both specimens. However, this structure is broken, therefore, it is not possible to know its' length or if it surpasses the condyle. The parapophysis and the diapophysis have a clear separation, with the diapophyses dorsoposteriorly and the parapophyses anteroventrally oriented. In the anteroventral region of the parapophyses there is a long parapophyseal process. In the specimens MLS 480, only the left parapophyseal process is preserved. The lateral foramina are present, being one small foramen on each side of the vertebrae. The condyle is slightly inclined dorsally.

In ventral view, the centrum is longer than the width of the neural arch on MLS 479 (cl>naw) and on MLS 480 the centrum is as long as the width of the neural arch (cl~naw).

The subcentral fossae are deep and the foramina are present. The fossae are only present on the anterior portion of the vertebral body.

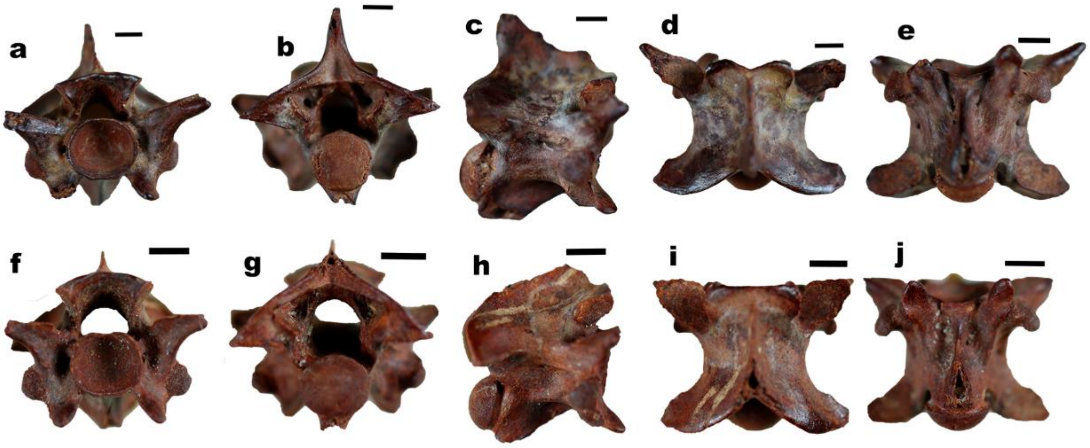

Figure 10: *Crotalus durissus* vertebrae. (a) mid-trunk/posterior trunk in anterior view, (b) mid-trunk/posterior trunk in posterior view, (c) mid-trunk/posterior trunk in lateral view, (d) mid-trunk/posterior trunk in dorsal view, (e) mid-trunk/posterior trunk in ventral view, (f) anterior trunk in anterior view, (g) anterior trunk in posterior view, (h) anterior trunk in lateral view, (i) anterior trunk in dorsal view, (j) anterior trunk in ventral view. Scale 2mm.

Viperidae

Undetermined genus and species

(Figure 11)

Material: MLS 481 one vertebral centrum with right prezygapophysis and paradiapophysis, MLS 482 one vertebral centrum with right prezygapophysis and paradiapophysis.

Locality and Horizon: Lajedo de Soledade locality (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene-Holocene (Quaternary) (Porpino et al., 2007). Sand with oxide horizon

Measurements (mm): MLS 481 cl: 7,1; coh: 3,9; cow: 4,1; prl: 4; prw: 2,3; **MLS 482** cl: 7,6; coh: 4; cow: 3,8; prl: 4; prw: 2,1;

Description

Both vertebrae show clear signs of abrasion, which wore out half of both vertebrae. The MLS 481 and MLS 482 show only the left prezygapophyses, the vertebral centrum, the left paradiapophysis, and a piece of the hypapophysis being preserved in each vertebra.

The vertebrae have laterally oriented prezygapophyses, and the prezygapophyseal process is of medium length (*sensu* LaDuke, 1991) and with a pointed extremity in both vertebrae. The cotyle is broken, which hampers the identification of its' shape, but following the condyle's shape, it is probably closest to a round shape. The paracotylar, lateral, and sub-central foramina are present in both vertebrae. The paradiapophyses are divided in diapophysis and parapophysis. A well-developed and anteroventrally orientated process emerges from the parapophysis, which enables the identification of this fossil as a Viperidae.

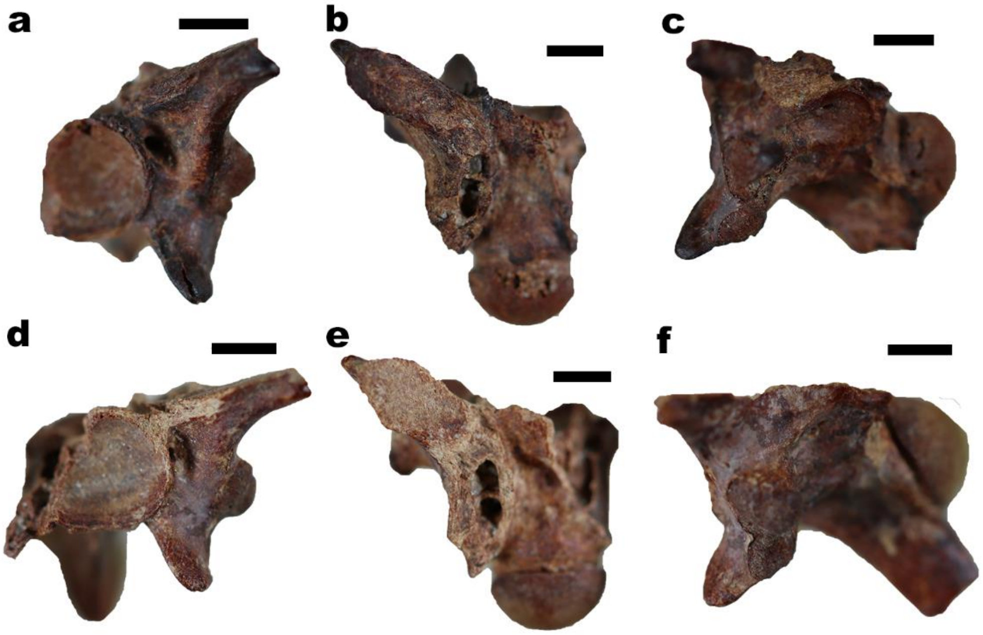

Figure 11: Viperidae mid-trunk/ posterior trunk vertebrae. (a)(d) anterior view, (b)(e) dorsal view, (c)(f) lateral view. Scale 2mm

Identification and comparisons of Viperidae specimens

MLS 479, MLS 480, MLS 481, and MLS 482 can be identified as a Viperidae based on the well-developed parapophyseal process (Zaher, 1999). Currently, there are three species of Viperidae in Rio Grande do Norte. These are *Bothrops erythromelas*, *Bothrops* *leucurus*, and *Crotalus durissus*. *Bothrops* tends to have shorter neural spine, more oblique pre and postzygapophyses, shorter and lateralized parapophyseal processes, and short prezygapophyseal process (Camolez and Zaher, 2010; Hsiou and Albino, 2011; Lomba, 2020). *Crotalus* on the other hand usually has a taller neural spine, less oblique pre and postzygapophyses, longer and not lateralized parapophyseal processes, and longer prezygapophyseal process. Also, *Crotalus* may have a concave “V” shaped zygosphene, but this morphology is highly variable (Lomba, 2020). *Lachesis* vertebrae also have different morphology to those of *Crotalus* and *Bothrops*. *Lachesis* has a smaller and lateralized parapophyseal process, small prezygapophyseal processes, and straight anterior edge of the zygosphene in dorsal view while in anterior view the zygosphenal articular facets have a dorsal projection, creating a concave morphology.

MLS 480 can be confidently identified as *Crotalus durissus* based on the combination of the following vertebral characteristics: anteroventrally well-developed parapophyseal processes elevated zygosphene with a "V" shaped anterior edge, almost horizontal prezygapophyses and medium prezygapophyseal process (Camolez and Zaher, 2010; Lomba, 2020). Even though MLS 479 does not have a medium prezygapophyseal process (*sensu* LaDuke, 1991) and has a straight anterior edge of the zygosphene, it is still possible to confidently attribute it to *Crotalus durissus* due to the non-lateralization of the parapophyseal processes and the almost horizontal prezygapophyses. The differences between the two vertebrae are attributed to the vertebral shape variation along the spine, which is observable on the comparative material. MLS 479 is from a more anterior position on the vertebral column, while MLS 480 is from a more posterior position.

Concerning MLS 481 and 482, by observing the prezygapophyseal and the parapophyseal processes, these fossils are more similar to *Crotalus* than to *Bothrops* since the prezygapophyseal process is of medium length (*sensu* LaDuke, 1991) and the parapophyseal process has little lateralization. However, the abrasion affected other structures of interest for taxonomic attributions, such as the zygosphene and the neural spine. Therefore, a genus taxonomic attribution may be imprudent.

6. DISCUSSION

The Brazilian fossil record of Squamates is extensive and relatively well known, despite the fragmented nature of the fossils. However, much of the available fossils are concentrated more in southward regions (Estes and Price, 1973; Albino, 1990; Rage, 1998, 2001, 2008; Camolez and Zaher, 2010; Nava and Martinelli, 2011; Simões et al., 2015; Candeiro et al., 2018; Bittencourt et al., 2020; Fachini et al., 2020). Despite the knowledge of many fossiliferous sites, our understanding of the northeastern fossil squamates is still insufficient. The known squamates fossils from the Brazilian northeast were unearthed in Maranhão, Ceará, and Bahia (Bonfim-Júnior and Marques, 1997; Evans and Yabumoto, 1998; Camolez and Zaher, 2010; Hsiou et al., 2012, 2013a; Simões et al., 2014). Therefore, these are the first fossil squamates described for the state of Rio Grande do Norte and for the Lajedo de Soledade, adding to the paleontological knowledge of the region. It is noteworthy that is also the first description of a fossil snake embryo for Brazil.

Brazilian vipers as a whole are difficult to differentiate. There are some known differences between *Crotalus* and *Bothrops* but until this moment no comparisons with *Bothrocophias* have been made (Camolez and Zaher, 2010; Hsiou and Albino, 2011). One *Lachesis* specimen was analyzed in this study through photographs, which is the first available description of *Lachesis* vertebrae, but more vertebrae should be analyzed in the future to better understand the vertebral morphology and intracolumnar variation of this genus and improve the identification of fossil specimens. Also, many species are somewhat cryptic, being defined by either molecular data or soft tissue characters (Dal Vechio et al., 2021; Barbo et al., 2022). In spite of these problems, the fossils MLS 479 and MLS 480 described in the present study could be confidently identified as *Crotalus durissus* after thorough comparison with extant specimens, based on the characteristics described in the results section.

The genus *Tropidurus* has a similar problem, having many cryptic groups and even the extant species differentiations are not resolved (Domingos et al., 2017; Moclán et al., 2023). The present study could identify the fossil MLS 486 as *Tropidurus* based on the comparison with extant specimens, and on the combination of pleurodont dentition, closed Meckel canal, and weakly eroded alveolar shelf (Frost, 1992; Hsiou et al., 2012). However, it is not possible to give a confident identification in the species level. For these reasons, more thorough anatomical studies must be performed in extant Squamata to better understand the fossil record.

Crotalus durissus and *Tropidurus* spp. are widespread taxa in Brazil; however, their paleontological record in the Brazilian Late Pleistocene-Holocene is relatively scarce when compared to the current species distribution, with fossils described for Ceará, Minas Gerais, and Bahia (Camolez and Zaher, 2010; Hsiou et al., 2012). These species are characteristic of areas with open vegetation and are not present in dense forests, this being a critical factor in understanding the process of colonization by these species (Wüster et al., 2005; Carvalho et al., 2013).

The presence of the Teiidae vertebra (MLS 483) is very interesting for the Lajedo de Soledade locality. Nowadays, the only large living lizards in Rio Grande do Norte are *Salvator merianae* and *Iguana iguana* (Costa et al., 2021). This vertebra is different from those of both taxa, indicating the presence of another big lizard species that have previously lived in the Lajedo de Soledade region. This suggests that the species distribution patterns in Brazil have changed since the Late Pleistocene/Early Holocene. However, posterior studies with more comparison specimens and species are needed for more taxonomic precision and to better understand the regions' Squamata fauna.

The taxa described here are mostly compatible with faunal assessments made for the Chapada do Apodi and for the Rio Grande do Norte (Lima Verde, 1976; Costa et al., 2021). As said previously, *Crotalus durissus* and *Tropidurus* are characteristic of dryer areas with open vegetation, much like the current vegetation of Lajedo de Soledade, which is hyperxerophile (Porpino et al., 2004). The presence of *Epicrates* in the region may seem contradictory to these climactic characteristics since the genus is semi-arboreal and is reported to shed its skin in water puddles. However, the Lajedo de Soledade, like many karstic areas in the Caatinga, is a humid refuge, which is corroborated by a large number of anuran vertebrae in this assemblage, even a Siluriform pectoral spine.

Based on the megafauna fossil assemblage, Porpino et al. (2004) and Mabesoone et al., (1990) have suggested a colder climate, although semi-arid, and a combination of savannah and more closed vegetation during the late Pleistocene. The Holocene paleoclimate of the Chapada do Apodi has been investigated by Utida et al. (2020). The study shows many events of climate change happened during the Holocene. These studies evidenced that between 11 and 5 thousand years ago was the most humid moment of the

Holocene, followed by a period of dryness from 5000 to 3000 years ago. The species identified here are compatible with both the climatic inferences for the Late Pleistocene and 5000-3000 years ago. However, when taking into account the association of the fossil Squamata with megafauna in the coarse sand layer, 5000 to 3000 years ago is too recent. Thus, to further understand these climactic details in the Lajedo de Soledade, the different sedimentary layers of the ravines need to be dated.

The Lajedo de Soledade has proven itself an interesting location for paleontology. The mammal fossil fauna is relatively well known; however, the other taxa are still poorly understood. The present study shows that this locality provides extremely interesting fossil Squamata. More excavations should be done in the Lajedo, which appears to be an interesting place to shed light on the biogeography of some taxa and changing rates of diversity. The presence of a fossil taxon that does not occur in the present location reveals this locality's potential to elucidate Brazilian paleontological history further.

SECTION 2: GEOMETRIC MORPHOMETRIC ANALYSIS WITH FOSSIL VIPERIDAE AND BOIDAE, AN EXPLORATORY ANALYSIS

Abstract

The shape is the geometric information after the object's rotation, scale, and position is withdrawawn. There is a limitation in traditional morphometrics, in which the measurements are intrinsically related to size. In this way, Geometric Morphometrics is a powerful tool for accessing morphological variation. This type of analysis separates shape and size variables, superimposing the analyzed objects in the same scale and position. Furthermore, Principal Components Analysis (PCA) effectively visualizes shape variation in datasets of big dimensionality. This analysis transforms the variables in non-correlated orthogonal axis (PCs), in which the first PCs are aligned in the direction of maximal variance. Another interesting analysis that can be performed is Random Forest. The Random Forest is a Machine Learning technique of classification and regression based on the aggregation of a large number of decision trees. In this study, we explored the identification of fossil Serpentes using Geometric Morphometric tools. The results showed that vertebrae of different Boidae can be easily separated using PCA; therefore, the fossils were adequately identified using this method. Viperidae vertebrae had a different pattern. They were not easily separated using PCA, so a different approach was needed. The Random Forest analysis effectively classified the fossil vertebrae of Viperidae, but it was not wholly reliable. These results elucidate important information regarding Geometric Morphometric methods in fossil identification and can lead to other studies with a similar hypothesis.

Key words: Geometric Morphometrics; vertebrae; Machine Learning; Principal Components Analysis; Boidae; Viperidae

7. INTRODUCTION

The Quaternary fossils Squamata pose a challenge for paleontologists because their bones are usually fragile, leading to a fossil record composed of isolated and fragmentary material (Hsiou, 2010; Onary and Hsiou, 2015; Onary et al., 2017). Another difficulty in studying these fossils is that many extant groups have similar skeletons, such as snakes of the Viperidae family. Therefore, the need arises for more accurate ways to study these bones qualitatively and quantitatively, which can be geometric morphometrics.

Morphometrics is the quantitative study of form, which is composed of shape and size (Richtsmeier et al., 2002). According to Kendall (1977), what we understand by shape is the geometric information remaining after the withdrawal of the object's rotation, scale, and position. The shape of organisms is, perhaps, the most ancient and fundamental theme of studies in many biology subjects (Adams et al., 2004; Zelditch et al., 2004). When investigating shape, it is usually described by comparisons with known shapes. However, this type of description can be subjective and non-applicable for groups with subtle variations that are not easily perceptible (Jackson and Claybourn, 2018). Fortunately, technological advances and new methods have allowed for less subjective ways to analyze shapes, which can be essential for smaller and fragmented materials.

The traditional type of morphometrics is investigated using linear morphometrics (i.e., linear measurements). However, these measurements usually contain little information about shape and are highly correlated with size (Zelditch et al., 2004; Parés-Casanova et al., 2020). This is unsurprising since shape and size are not biologically independent, but there have been efforts to independently analyze the two which can shed light on important information regarding specimens identification (Richtsmeier et al., 2002; Zelditch et al., 2004; Parés-Casanova et al., 2020). Here is when geometric morphometrics (GM) comes in. GM is a quantitative way to talk about shape. It is a powerful tool to assess the morphological variation, even when the differences are subtle. Therefore, it enables easier visualization of complex shape variation (Zelditch et al., 2004; Webster and Sheets, 2010). Moreover, this method allows for a better separation of shape and size variables since it analyses the relative coordinates of landmarks instead of linear measurements. For these reasons, it is being recognized as a powerful instrument to study objects that show subtle variation.

Landmark-based geometric morphometrics analyses the spatial coordinates of anatomic points. These points need to be biological correspondents in every object;

generally, they are homologous (Zelditch et al., 2004; Machado, 2010). When choosing landmarks, it is important to consider which anatomical points are relevant to the study (Zelditch et al. 2004). According to Bookstein (1997), there are three types of landmarks: (1) juxtaposition of tissues, the precise point where structures join; (2) extremities of structures, points of maximum curvature or maximum invagination; (3) extreme points, points of greater distances in relation to another point. In addition, if curves and contours of structures are essential to the study, semilandmarks can also be used (Webster and Sheets, 2010). With this, it is possible to translate biological spatial information to numerical data that can be compared and statically discriminated (Jackson and Claybourn, 2018).

Several methods of geometric morphometric analysis were already implemented to identify fossil specimens according to the materials' specifications (Marramà and Kriwet 2017, Courtenay et al. 2019, Leshno Afriat et al. 2021). This tool has proven helpful in comparing different species, being considered indispensable for morphological and phylogenetic research in recent years (Lawing and Polly, 2010; Palci and Lee, 2019). Studies of a great diversity of organisms stand out, such as insects (Jeratthitikul, 2013), fossil invertebrates (Jackson and Claybourn, 2018; Torres-Silva et al., 2019), rodents (Cardini and O'Higgis, 2004; Cordeiro-Estrela et al., 2008), fish (Clabaut et al., 2007; Kerschbaumer and Sturmbauer, 2011), fossil vertebrates (Hubbe, 2008; Vivar Martíinez, 2014; Marramà and Kriwet, 2017) and even trace fossils (Rodrigues and Santos, 2004; Cardonatto and Melchor, 2018).

7.1.PRINCIPAL COMPONENTS ANALYSIS

Many techniques have been used to access morphological variation in living and fossil taxa and in the identification of fossils. One of those tests is the Principal Components Analysis (PCA). PCA is an exploratory analysis widely used to better visualize the morphological variation among individuals. That is due to its function of transforming a large set of variables into a smaller one, which still contains the majority of the information (Jollife and Cadima, 2016; Holland, 2019).

This analysis transforms the variables in non-correlated orthogonal axes, the Principal Components (PCs), in which the first PC is aligned in the direction of maximal variance (Webster and Sheets, 2010; Janžekovič and Novak, 2012). For this to happen, first, the data is normalized, which is done by Procrustes Superimposition in geometric morphometrics. In this superimposition, the mean shape of the analyzed objects is calculated. Then all objects are superimposed, so all have the same direction, size, and orientation, remaining only the shape information (Zelditch et al., 2004). Then, the eigenvalues and eigenvectors are calculated, related to the covariation matrix. The eigenvector represents the direction, while the eigenvalues represent the scale (Monteiro and dos Reis, 1999; Burden and Faires, 2010). It is essential to calculate the PCs because they represent the direction of the axes with the most variance.

The Principal Components are new variables made up of the old variables. These new variables are uncorrelated. When the PCs are created, most variation is condensed in the first PCs, especially the first and the second ones. The dimensionality of the data is reduced since most of the variation is concentrated in a small number of variables. Therefore, the first PC is the axis in which the data presents the most variance, and the second PC is an uncorrelated axis with the second most variance. With this, the result is a visualization of the shape variation of the analyzed data.

7.2.MACHINE LEARNING BY RANDOM FOREST

Machine learning (ML) is an area of artificial intelligence (AI) that aims to create algorithms capable of learning. This term was invented by Samuel (1959) in a paper on machine learning using the game of checkers. He described this technique as “the field of study that allows computers to learn without being explicitly programmed” (apud El Naqa and Murphy, 2015). There are two types of ML, supervised and unsupervised learning. The difference between the two is the type of data used for training, the first uses data with known output, while the former uses data with unknown output (Alafandy et al., 2022). One of the many ways to run Machine Learning algorithms is Random Forest.

Random Forest (RF) is a classification and regression method based on the aggregation of many decision trees first proposed by Breiman (2001). This method has two primary uses (1) to create a prediction model and (2) to evaluate which variables are more valuable to make these predictions (Boulesteix et al., 2012). RF has features that make it very useful, like dealing with high-dimension data and not requiring a specific model.

Decision trees are maps of possible outcomes in a series of related choices. The RF algorithms create each decision tree based on a random subset of data with known predictors and responses. Moreover, the subset not used for making the tree is used to measure the error and internally validate the tree. The many random trees combined to form a “forest”. The majority voting makes the final decision of the Random Forest algorithm of all decision trees. This method has appeal in many areas since it can handle high dimensional data, with a strong correlation between predictors, and requires little tuning (Boulesteix et al., 2012; Hediger et al., 2022). It has been used in several areas, such as engineering (Gong et al., 2018), medicine (Hu, 2010), genetics (Calle et al., 2011), and even ecology (Cutler et al., 2007).

8. MATERIAL AND METHODS

8.1.MATERIAL

The material studied herein is housed at the Museu do Lajedo de Soledade Rio Grande do Norte (MLS, Apodi municipality, Brazil). The fossil squamate material was loaned to the Laboratório de Paleontologia de Ribeirão Preto (LPRP, FFCLRP/USP) for the development of the present Master Dissertation through Prof. Dr. Hermínio Ismael de Araújo Júnior (UERJ, Rio de Janeiro, Rio de Janeiro state). The material consists of vertebrae previously identified as *Crotalus durissus* and *Epicrates*, collected in the Ravina das Araras in Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte, northeastern Brazil. The studied Squamata are probably from the Late Pleistocene/early Holocene (around 11000 years ago), suggested by its association with Pleistocenic megafauna, however the different sedimentary horizons are yet to be dated. The fossil material is discriminated in Table 1.

Collection number	ID
MLS 479	*Crotalus durissus* anterior vertebra
MLS 480	*Crotalus durissus* mid-trunk/posterior trunk vertebra
MLS 485	*Epicrates* anterior trunk vertebra
MLS 492	*Epicrates* mid-trunk/posterior trunk vertebra
MLS 493	*Epicrates* mid-trunk/posterior trunk vertebra
MLS 494	*Epicrates* mid-trunk/posterior trunk vertebra
ML2 495	*Epicrates* mid-trunk/posterior trunk vertebra
MLS 496	*Epicrates* mid-trunk/posterior trunk vertebra
MLS 497	*Epicrates* mid-trunk/posterior trunk vertebra
MLS 498	*Epicrates* mid-trunk/posterior trunk vertebra
MLS 499	*Epicrates* mid-trunk/posterior trunk vertebra

Table 1: Specimens used in the geometric morphometrics analysis

Extant specimens were used for comparison. The Squamata specimens used belong to the Coleção Herpetológica de Ribeirão Preto (CHRP) of the Departamento de Biologia of FFCLRP/USP (Ribeirão Preto, São Paulo, Brazil); the Coleção da Universidade Federal do Mato Grosso (UFMT, Cuiabá, Mato Grosso do Sul, Brazil); and Coleção Didática de Répteis (MCN-PV-DR) of the Museu de Ciências Naturais da Secretaria do

Meio Ambiente do Estado do Rio Grande do Sul (SEMARS, Porto Alegre, Rio Grande do Sul, Brazil). The specimens are listed in the Supplementary Material II.

8.2.METHODS

The first sample vertebrae were separated from each extant specimen to perform the analysis. One vertebra was sampled from every ten vertebrae until the last trunk vertebra. For the Boidae specimens, all vertebrae with a hypapophysis were considered anterior trunk vertebrae, and the remaining were considered mid-trunk/posterior trunk vertebrae. For the Viperidae specimens, it is more difficult since all trunk vertebrae have hypapophysis. In this case, the first five (05) sampled vertebrae (10th, 20th, 30th, 40th, and 50th) were considered anterior trunk vertebrae, and the remaining were considered mid-trunk/posterior trunk vertebrae.

Secondly, images of all specimens were taken in anterior, lateral, posterior, and dorsal views using a digital Canon Rebel T6i camera with a standard 18-55mm or a 100mm macro lens. For smaller specimens, a Leica M205 stereo microscope was used. These pictures were converted into TPS files using tpsUtil (Rohlf, 2021a). Then, the landmarks were selected using tpsDig (Rohlf, 2021b). The TPS files with the landmarks were then uploaded into the R software (R Development Core Team 2022), in which the Generalized Procrustes Analysis was performed, and the tests were conducted.

8.2.1. Principal Components Analysis

For the fossils previously identified as Boidae, only a PCA was made using the geomorph package (Adams and Otárola-Castillo, 2013). It is because the PCA separated well the two analyzed genera: *Corallus* and *Epicrates*. Also, the machine learning test incorrectly identified the vertebrae when a test using only the extant specimens was made. It might be due to the small sample size since only three (03) specimens of extant *Corallus* and two (02) *Epicrates* were used. Therefore, only the PCA was performed for these fossils.

For these specimens, 24 landmarks were selected for anterior view, 20 for dorsal view, 15 for lateral view, and 21 for posterior view, as shown in Figure 12. The tests were performed twice, with only the extant specimens and one adding the fossils.

First, the IDs of the specimens were deleted from the dataset. That is because when the analysis is done with the IDs, the data is merged. Then, a Generalized Procrustes Superimposition was performed using the gpagen function. A data frame was made using the geomorph.data.frame function, now adding the IDs of the specimens. An ANOVA and a pairwise comparison were performed using the procD.lm and pairwise functions, respectively. ANOVA was tested to verify significant differences between the two extant genera. The Principal Components Analysis was made using the gm.prcomp function. The detailed R script is in the Supplementary Material II.

PCA without the fossils was made to confirm that a PCA would separate the *Epicrates* from the *Corallus* vertebrae. Then, if the two groups showed clear separation, the fossils were added to the analysis. Not all fossils were used in all analyses. The fossils used depended on the state of preservation, avoiding the use of missing landmarks. The fossils that were used in each analysis are explicit on the graphs in the Results section.

8.2.2. Random Forest

With the fossils previously identified as Viperidae, Machine Learning by Random Forest was analyzed to refine the taxonomic attribution and explore methods that may help fossil identification.

Extant Brazilian species of *Crotalus* and *Bothrops* were used to compare with the fossils. Firstly, landmarks were selected on the fossils since they had broken structures. With this, missing landmarks that could affect the results were avoided. 22 landmarks were established in anterior view, 20 in dorsal view, 14 in lateral view, and 19 in posterior view, as shown in Figure 13. The same landmarks for the fossils were selected on the TPS files of the comparison specimens. The detailed specimens list is in the Supplementary Material II.

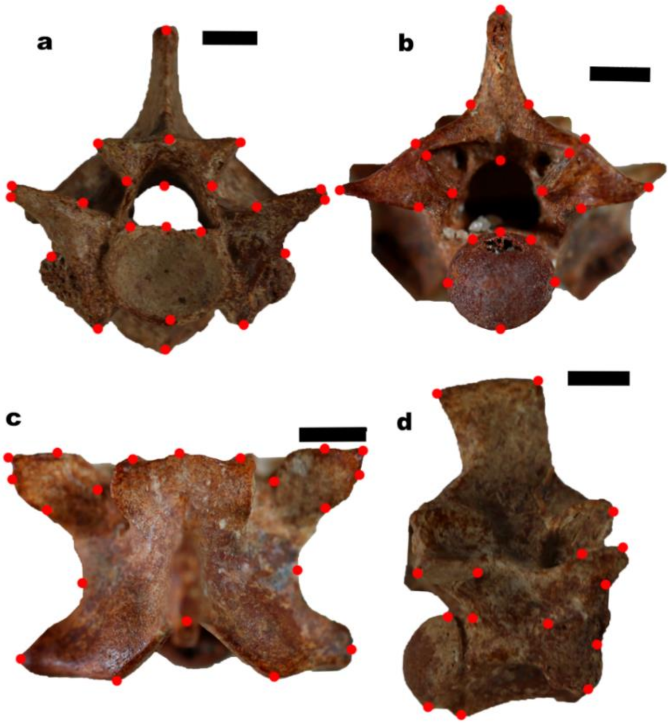

Figure 12: Landmarks used for the analysis of the Boidae fossils. a: Landmarks in anterior view; b: Landmarks in posterior view; c: Landmarks in dorsal view; d: Landmarks in lateral view. Scale 2mm.

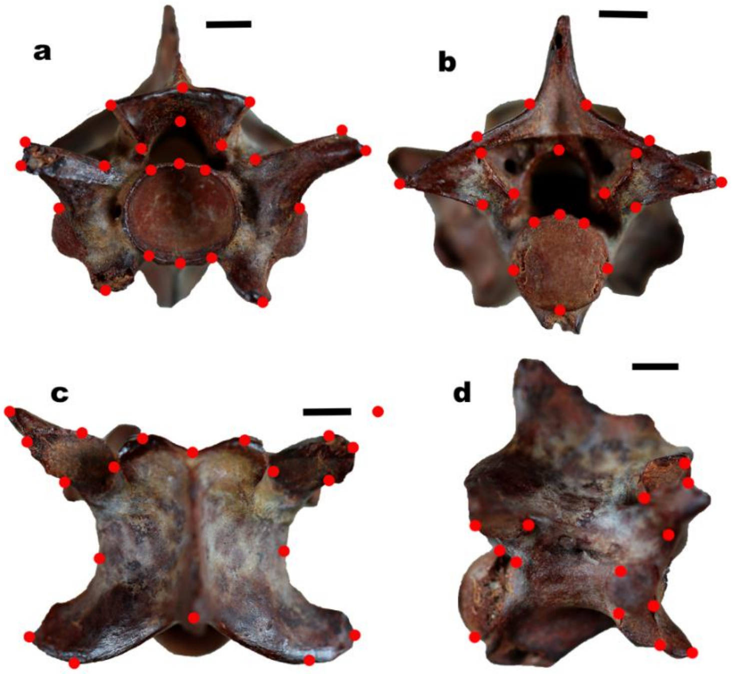

Figure 13: Landmarks used for the analysis of the Viper fossils. a: Landmarks in anterior view; b: Landmarks in posterior view; c: Landmarks in dorsal view; d: Landmarks in lateral view. Scale 2mm.

Before the machine learning analysis, ANOVA tests using only the extant specimens were made to ensure the selected landmarks revealed differences between the used genera.

First, the TPS files were uploaded into R separately, one TPS file for the anterior trunk vertebrae and one for the mid-trunk/posterior trunk vertebrae. The fossils were already in the files based on their previously identified trunk region. Then, a Generalized Procrustes Superimposition was performed using the gpagen function. Next, the PCA was performed using the gm.prcomp function, and a dataframe was generated with the data.frame function. Then, the dataframes of the anterior trunk and the mid-trunk/posterior trunk vertebrae were binded using bind.rows. The genera and the trunk region were saved as factors using the as.factor function.

Following, the training and validation datasets were divided. 70% of the specimens went to the training dataset, and the remaining 30% went to the validation. Both fossils were in the validation dataset. With this, a model was created using the randomForest function. The predictions for the fossils were made by using the predict function and applying the developed model to the validation dataset. One thousand (1000) decision trees were used. The importance of each variable was observed utilizing the importance function. The detailed R script is in the Supplementary Material II.

9. RESULTS

9.1. PRINCIPAL COMPONENTS ANALYSIS

The Principal Components Analysis (PCA) separated the genera well; therefore, adding the fossils to the analysis was sufficient to identify them.

In anterior view, the PCA separated well *Corallus* and *Epicrates* on PC2, with *Epicrates* falling in the positive PCs and *Corallus* falling in the negative PCs. The differences lie in the prezygapophyses and the neural spine. The prezygapophyses are parallel to the horizontal plane, and the neural spine is shorter in *Corallus*, while in *Epicrates*, the prezygapophyses are oblique, and the neural spine is taller (Fig.14 A). PC1 shows the intracolumnar variation, with the anterior vertebrae falling in the positive PCs and mid-trunk/posterior vertebrae falling within the negative PCs. When the fossils were added, they fell within the *Epicrates* genus and the mid-trunk/posterior vertebrae (Fig.14 B), corroborating the macroscopic identification.

In posterior view, the PCA separated well *Corallus* and *Epicrates* on PC2 (Fig.15 B). PC1 shows the intracolumnar variation, with the anterior vertebrae falling in the positive PCs and mid-trunk/posterior vertebrae falling within the negative PCs. The PC2 shows the divergence between the two genera, with *Epicrates* falling in the positive PCs and *Corallus* falling in the negative PCs. It shows that the differences lie mainly in the postzygapophyses, parallel to the horizontal plane in *Corallus* and oblique to the horizontal plane in *Epicrates*. The neural spine is also different, slightly taller in *Epicrates* than in *Corallus*. When the fossils were added, they fell within the *Epicrates* genus (Fig.15 B), corroborating the macroscopical identification and the PCA in the anterior view.

In the dorsal view, *Corallus* and *Epicrates* show a clear separation (Fig.16 A). However, this division is not clear in either PC1 or PC2 alone. The separation is diagonal. It shows that there is a correlation between PC1 and PC2. *Corallus* tends to have narrower (pz-pz) and longer (pr-pz) vertebrae since all vertebrae are either on the positive PCs or around 0 PC1. In contrast, *Epicrates* is concentrated on the negative PCs of PC1, with only some vertebrae around the 0 PC1. The PC2 shows where the interzygapophyseal constriction is on the vertebra. In *Epicrates*, this constriction is more anterior, while *Corallus* tends to be more posterior. This morphological variation was not noticed in the macroscopical analysis. When the fossils are added to the PCA, they fall closer to the *Epicrates* morphospace (Fig.16 B).

In lateral view, the division between the two genera is also diagonal, though the inclination is more discrete (Fig.17 A). The PC1 shows mostly the variation between the genera, while the PC2 shows mostly the intracolumnar variation. This analysis shows differences between the genera are on the neural spine, and the length of the neural arch and that these differences are more pronounced on the trunk vertebrae. In regards to the fossil identification, they are closer to the *Epicrates* group but not unambiguously within *Epicrates* (Fig.17 B), which indicates this view is not ideal for this type of analysis.

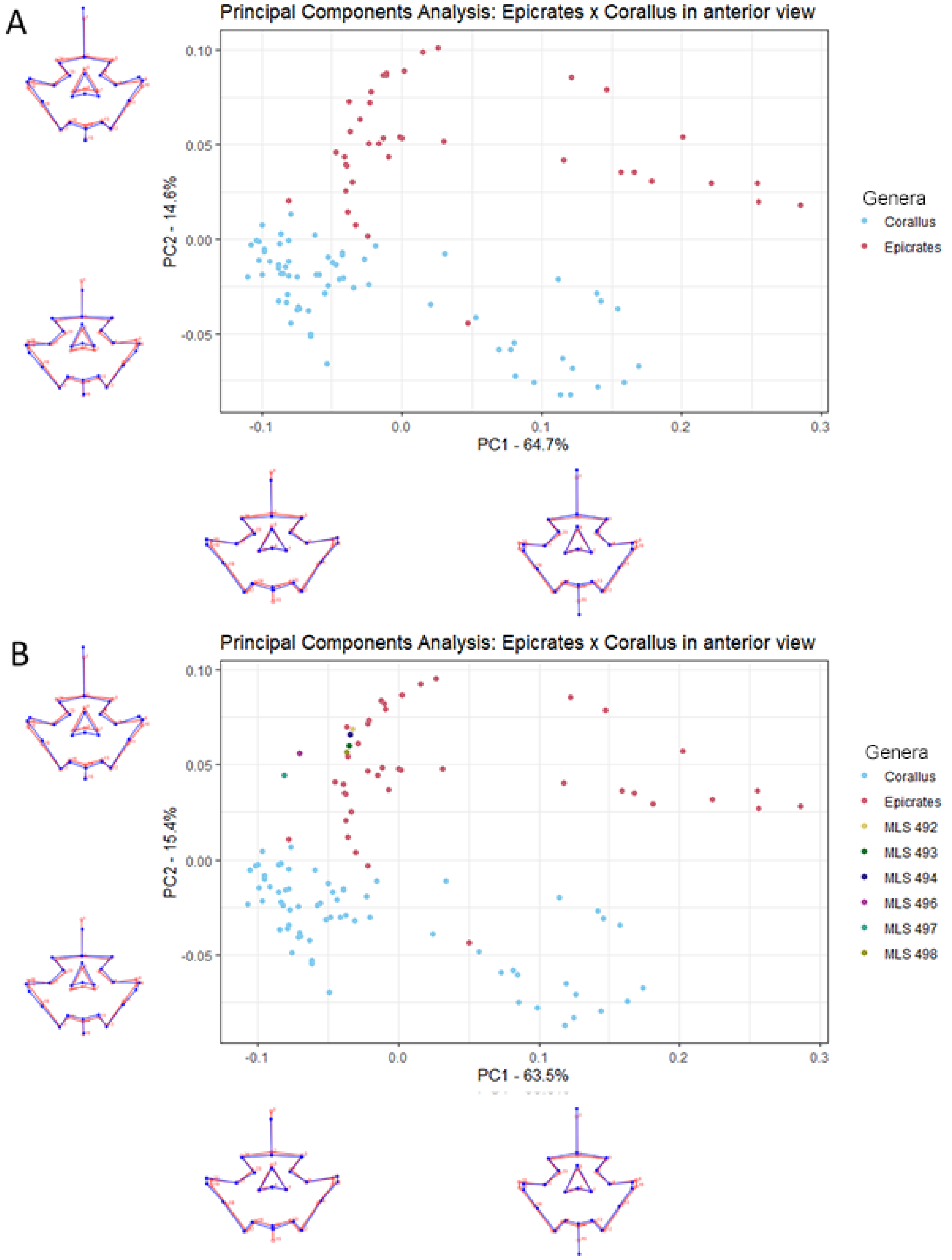

Figure 14: Principal Components Analysis (PCA) of Boidae vertebrae in anterior view. The PCA using only extant specimens are in A, and the fossils are added in B

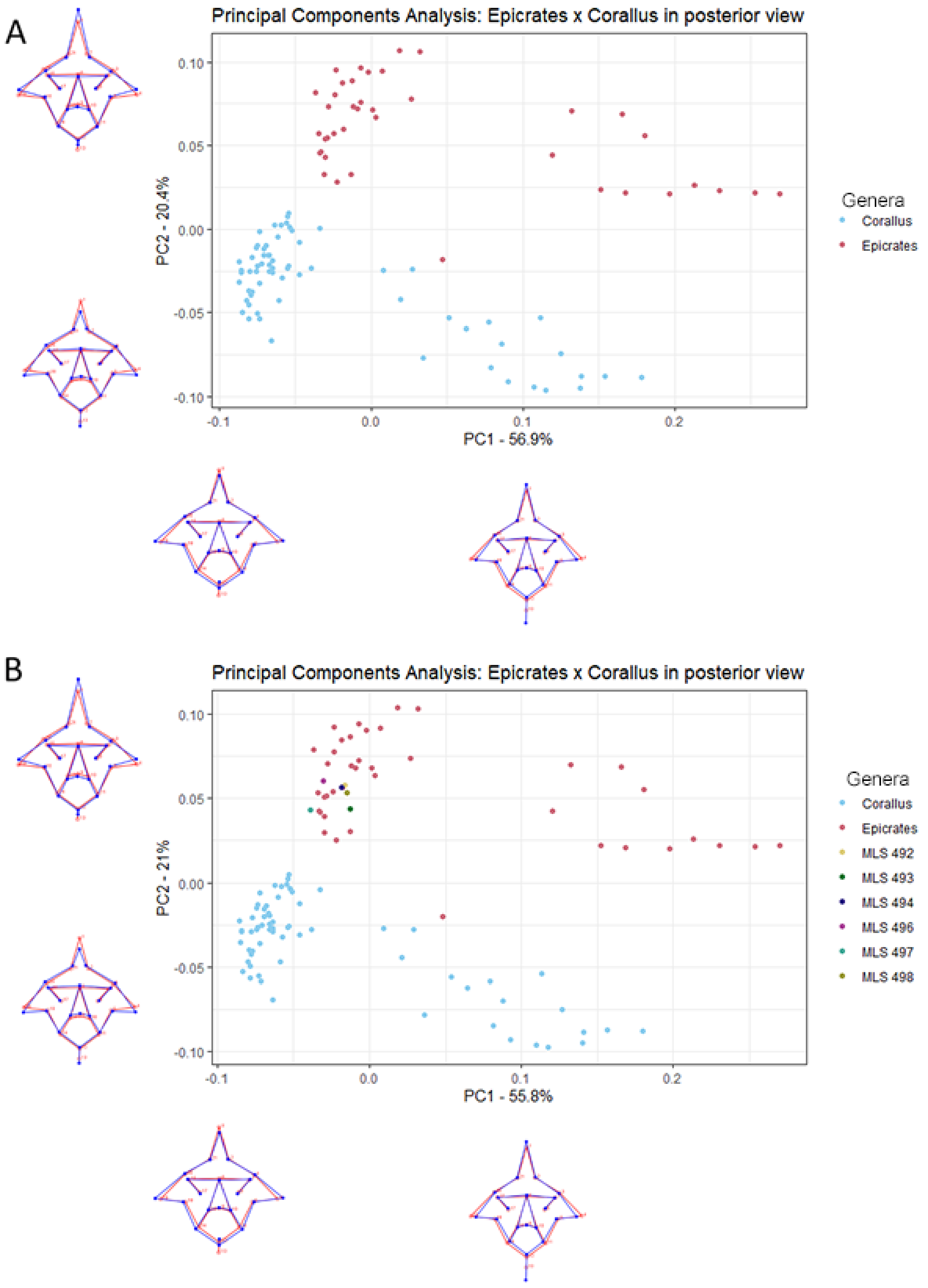

Figure 15: Principal Components Analysis (PCA) of Boidae vertebrae in posterior view. The PCA using only extant specimens are in A, and the fossils are added in B

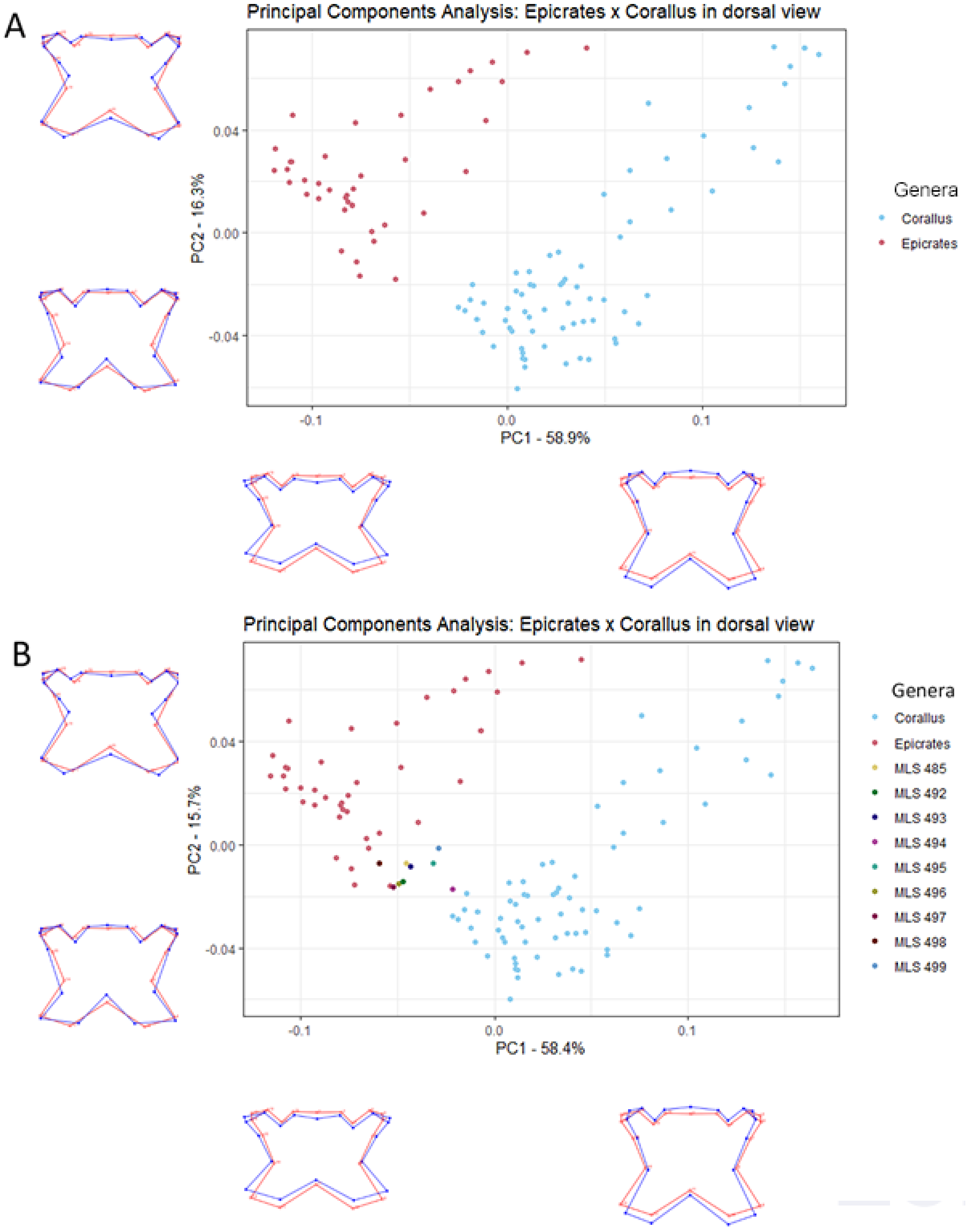

Figure 16: Principal Components Analysis (PCA) of Boidae vertebrae in dorsal view. The PCA using only extant specimens are in A, and the fossils are added in B

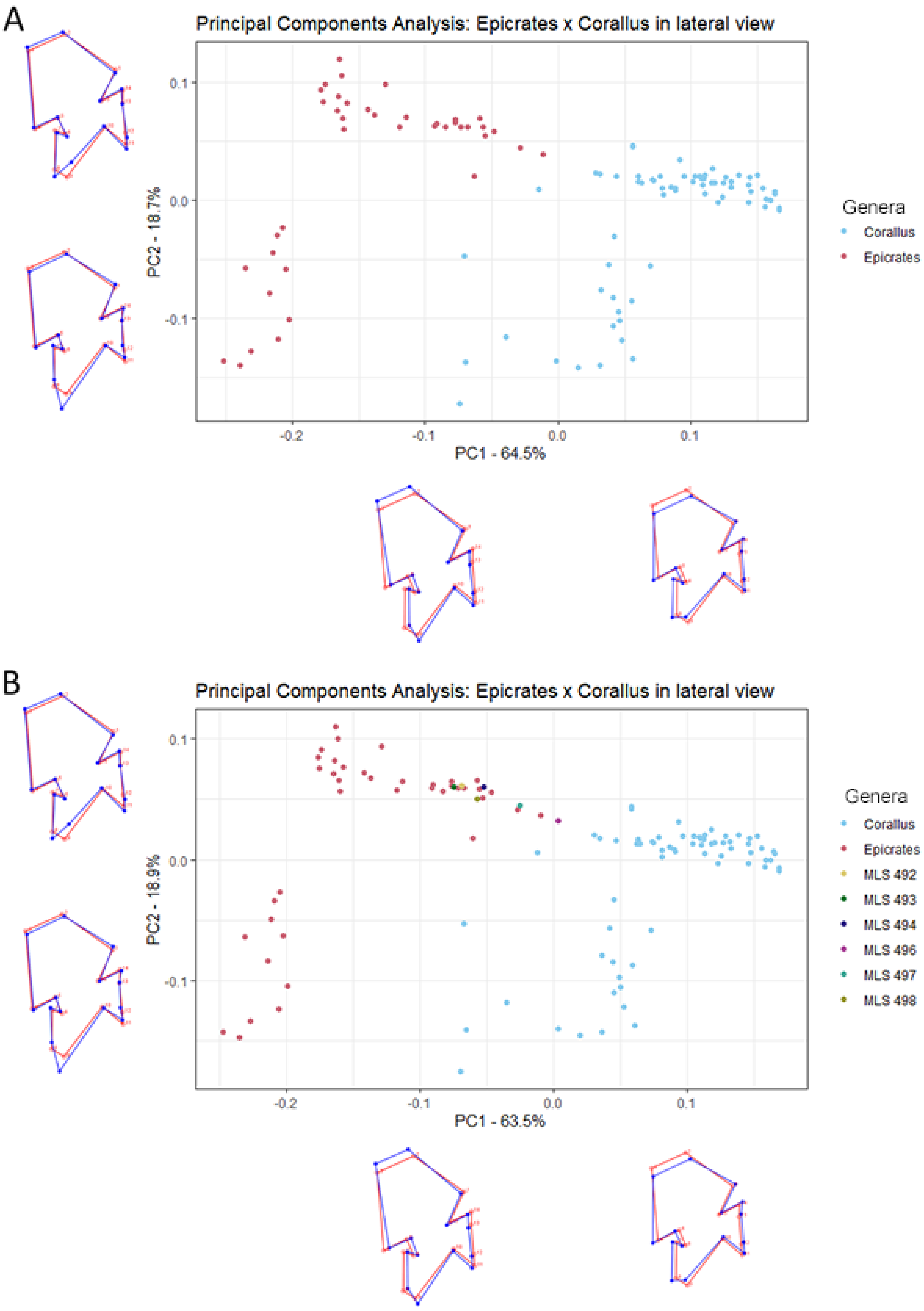

Figure 17: Principal Components Analysis (PCA) of Boidae vertebrae in lateral view. The PCA using only extant specimens are in A, and the fossils are added in B

9.2.RANDOM FOREST

First, the ANOVA tests showed that the selected landmarks represented significant variation between *Crotalus* and *Bothrops* specimens in all views (Supplementary Material II). Then, in the machine learning analyses, the practice dataset in all four views were 100% classified correctly. The out-of-bag (OOB) error rate was 0%.

In the validation dataset, the fossils were identified as *Crotalus durissus* when analyzed in anterior, dorsal, and lateral views, corroborating the macroscopic identification. However, in posterior view, the anterior trunk fossil vertebra (MLS 479) was identified as *Bothrops,* while the mid-trunk/posterior trunk fossil vertebra (MLS 480) was identified as *Crotalus*. It might sound strange, but it is probably because the main structures used for differentiation between the genera are not visible in posterior view.

In all views, the Mean Decrease Gini of the PC2 is more significant than the PC1. Lomba, (2020) showed that the PC1 is more related to the intracolumnar variation in Viperidae when the entire vertebral column is analyzed (Figure 18). Therefore, it makes sense that PC2 is more important to genus identification.

We also tested the algorithm by doing the analysis using only extant specimens of the known genus, substituting the correct ID with either “fossilP” (for anterior trunk vertebrae) or “fossilG” (for mid-trunk/posterior trunk vertebrae). These tests were performed twice for each view, one using *Bothrops* vertebrae as the fossils and one using *Crotalus* vertebrae as the unknown specimen. These tests showed a more accurate classification when the *Crotalus* vertebrae were used as the fossils, correctly identified in all regions and views except in the posterior view. When *Bothrops* vertebrae were used, only in anterior view both the anterior trunk and mid-trunk/posterior trunk were correctly identified. The anterior vertebra was correctly identified in dorsal and posterior views, but the mid-trunk/posterior trunk vertebra was misidentified. In lateral view, the opposite happened.

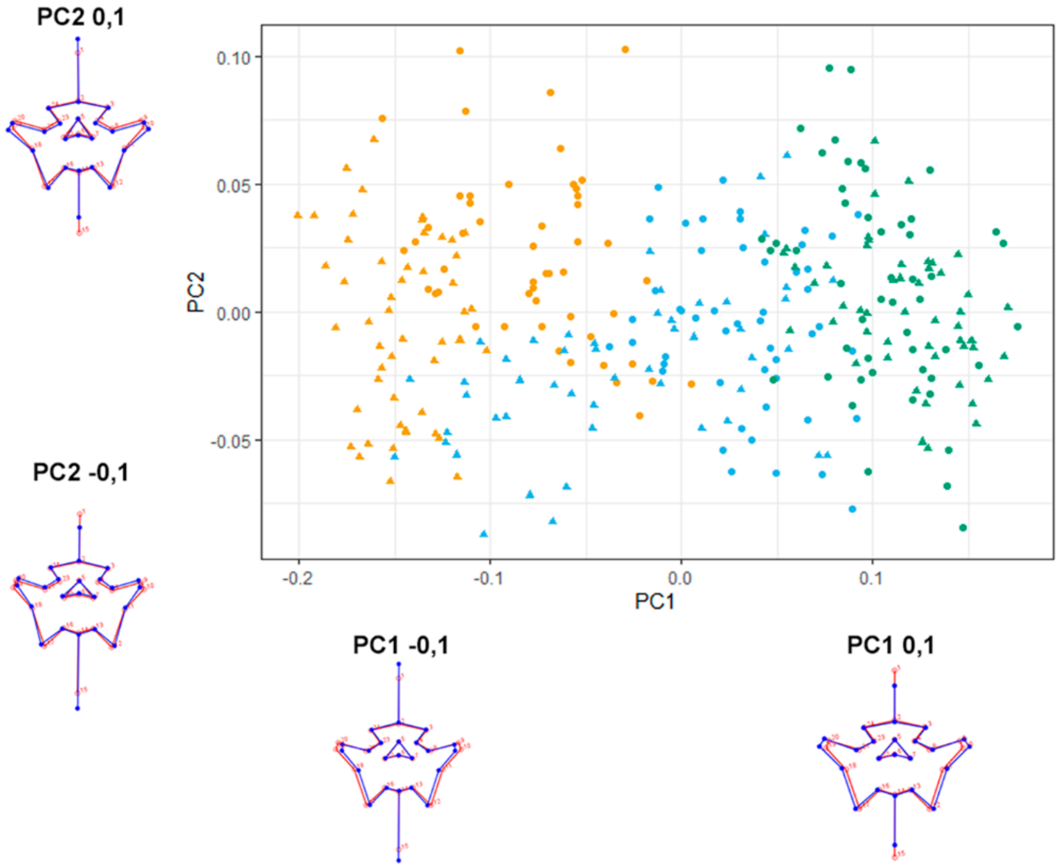

Figure 18: Principal Components Analysis of *Bothrops* and *Crotalus* in anterior view. In yellow are the anterior trunk vertebrae, in light blue are the mid-trunk vertebrae, and in green are the posterior trunk vertebrae. The circles are *Bothrops*, and the triangles are *Crotalus*. Modified from Lomba (2020).

10. DISCUSSION

With these results, it is possible to notice that there is no universal method when using Geometric Morphometric; different situations require distinct methods of analysis to be used, which depend on a multitude of factors, such as taxonomic group and what comparison specimens are available. The Viperidae, for example, are not separated from the PCA (Lomba, 2020), but booids are distinguishable in this analysis. On the other hand, Boidae was not correctly identified using the Random Forest, perhaps due to the small sample of extant specimens.

The Principal Components Analysis has proven to be an interesting method for identifying fossil Boidae. Even though all PCA analyses separated the two genera, the anterior and posterior views are the ones in which the fossils are more clearly classified. It is reasonable since the inclination of the pre and post-zygapophysis is one characteristic that differentiates the two genera (Teixeira, 2013; Onary et al., 2018). It has also proven to be an interesting analysis to access intracolumnar variation. The PCAs showed that the intracolumnar variation is more significant on the anterior trunk vertebrae, and the mid-trunk/posterior trunk vertebrae usually have a more constant shape. Also, this analysis evidenced that anterior trunk vertebrae and mid-trunk/posterior trunk vertebrae have the same proportionate length in the neural spine. It would be extremely interesting to add *Eunectes* and *Boa* to this analysis and have a more integral view of Brazilian Boidae.

Principal Components Analysis has been widely used to visualize variations of shape (de Souza, 2016; Palci et al., 2016; Marramà and Kriwet, 2017). It has been implemented in paleontological studies of diverse taxa, even though it is not always the most effective method (Gray et al., 2017; Marramà and Kriwet, 2017). In snakes, it has been implemented mostly on skulls (Palci et al., 2016; Da Silva et al., 2018). When the object of study is the vertebral column, it is usually done with extant species (Sarris et al., 2012; Lomba, 2020). The use of this technique for snake fossil vertebrae identification had never been explored before.

The Random Forrest has proven to be an effective method for classifying these Viperidae fossils; however, it is not effective on all occasions. The way the vertebral regions were divided in the present study will probably not be ideal for every situation. It will depend on how well the vertebral region of the studied fossil can be determined. MLS 479 could be easily classified as an anterior trunk vertebra in this context. However, MLS

480 was harder to identify as either mid-trunk or posterior trunk. Therefore, both regions were combined into the same category.

It was noticeable that, despite the 0% OOB error, there is some classification error in the algorithm. The Random Forest has more accuracy when the vertebra of an unknown genus is a *Crotalus* vertebra. Also, the anterior view seems to be the best for this type of analysis since all vertebrae were correctly identified in the tests implemented in this work. This evidences how similar the vertebrae of *Crotalus* and *Bothrops* are. Also, this corroborates personal observations made when comparing extant specimens, and the *Crotalus* vertebrae seem to have more prominent characteristics that are easier to identify.

Machine Learning is an ever-growing field. Its applications in various areas are widely explored (Daescu and Leavey, 2021; Ivanichenko et al., 2021; Mehta and Anand, 2022; Minowa et al., 2022; Nelson, 2023). The applications are likely to be used more and more in the following years. In paleontology, however, this methodology is still in its early stages (Moclán et al., 2023), highlighting the contributions of this work to the field. Similar to the case of the PCA, this analysis had never been used to identify snake fossil vertebrae before.

There is still much more to be explored with GM with extant and fossil specimens. Especially in paleoherpetology, there is still a lot to be tried. For example, 3D analysis of the vertebrae could be very interesting since some vertebral structures that could be of interest are not easily and repeatably marked in 2D analysis. Also, this method would combine all views, improving accuracy.

These results can bring interesting implications to Paleontology. It doesn’t make the paleontologist's job obsolete since it is still necessary to identify the vertebrae's trunk region and to which big taxonomic group it belongs. Furthermore, no analysis should be trusted blindly since some error is always possible. The results obtained in the present study have shown themselves to be trustworthy most of the time, but that might not be the case for every situation. In this context, these types of analysis can aid paleontologists in the identification of fossils that are more ambiguous, being helpful to strengthen analyses in this area. Therefore, this new facet of Paleontology should be continuously explored. Many different methodologies can be applied to better understand the morphology of extant species, the fossil record, and the anatomical variations of other groups.

GENERAL CONCLUSIONS

The present study represents the first description of fossil Squamata for the state of Rio Grande do Norte. Here, two different methods were used to identify said fossils. We used both classical osteological description and bidimensional Geometric Morphometrics (GM). A reliable GM method to identify fossil Boidae was performed. Also, a method to identify fossil Viperidae was developed, and even though it is not 100% reliable, it is helpful in the identification of these snakes. It is the first step toward a more accurate method. This is also the first time *Lachesis* vertebrae have been used for comparison, even though briefly.

When using classical osteological description, the Boidae fossils could be somewhat easily identified as *Epicrates*. It may be due to this family's smaller species diversity compared to other Brazilian snakes. Also, the Boidae genera tend to have vertebrae that are easier to differentiate and have been extensively studied (Hsiou and Albino, 2009, 2010; Hsiou et al., 2012, 2013b; Teixeira, 2013; Onary and Hsiou, 2018; Onary et al., 2018). This is evidenced in the Principal Components Analysis, which simply disposes of the studied objects (in this case, the vertebrae) in the axis of more significant variation, not considering the groups. This analysis showed a clear separation between the extant specimens of *Corallus* and *Epicrates*, with almost no superimposition areas.

With the Viperidae, the situation is different. The vertebrae of the vipers are much more similar when comparing the genera. To correctly identify fossil vipers, extensive knowledge of the vertebral anatomy of the group is needed. Lomba (2020) show that the vertebral morphology of *Bothrops* and *Crotalus* is similar. Using qualitative methods, it is possible to differentiate the two genera utilizing a combination of characteristics that are sometimes difficult to spot. When using GM, things get more complicated. The PCA does not help separate *Bothrops* and *Crotalus*, but it is helpful to see the intracolumnar variation. Therefore, a different method is needed. The Machine Learning analysis with Random Forest is more efficient in identifying if a vertebra belongs to *Crotalus* or *Bothrops*. Still, more investigation should be made (e.g., 3D Geometric Morphometrics) to find an even more accurate method. A combination of qualitative and Machine Learning analysis seems to be the most promising way to identify these fossils accurately.

Fossils of *Tropidurus* can be confidently identified as the genus. However, it is yet impossible to locate the species. Soft tissue or molecular data are used for species identification in extant *Tropidurus*, and even the neontologic identification is not well resolved (Moclán et al., 2023). Also, the only study analyzing the skull of these lizards did not retrieve any diagnostic characters (Adorni, 2018). Therefore, the lack of diagnostic features on these animals' skeletons makes it impossible to identify the dentary species. Different analyses should be done with extant specimens to differentiate the species, even the cryptic ones.

The Teiidae vertebra requires more comparative analyses as well. The present study points towards a species that is no longer present in Rio Grande do Norte, however, it is not possible to say which species due to the lack of comparison material. In the future, it will be important to properly identify this specimen, comparing it to other Teiidae aside from *Salvator merianae*. With this, more data about past species distributions will be available and shed light in the biogeography of Brazilian Squamata.

Due to the lack of osteological studies and the increasing number of cryptic species retrieved using new analysis (Domingos et al., 2017; Wagner et al., 2018; Melville et al., 2019), the proper identification of fossil Squamata tends to be complicated. Because of these differences in characters used in the identification of fossils and extant species, only with an accurate analysis on the skeleton of these extant animals, the duly identification of fossil taxa is possible. With this in mind, Geometric Morphometrics might be an interesting approach when studying extant and fossil Squamata, and maybe useful to resolve some identification issues.

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SUPPLEMENTARY MATERIAL I

STUDIED FOSSIL MATERIAL

MLS 479: Crotalus durissus anterior vertebra

MLS 480: Crotalus durissus mid-trunk/posterior trunk vertebra

MLS 481: Viperidae vertebra

MLS 482: Viperidae vertebra

MLS 483: Teiidae trunk vertebra

MLS 484: Vertebra of Boidae embryo

MLS 485: Epicrates anterior vertebra

MLS 486: Tropidurus left dentary

MLS 487: Siluriorme pectoral fin

MLS 488: Boidae mid-trunk/posterior trunk vertebra

MLS 489: Anura vertebra

MLS 490: Anura vertebra

MLS 491: Anura vertebra

MLS 492: Epicrates mid-trunk/posterior trunk vertebra

MLS 493: Epicrates mid-trunk/posterior trunk vertebra

MLS 494: Epicrates mid-trunk/posterior trunk vertebra

MLS 495: Epicrates mid-trunk/posterior trunk vertebra

MLS 496: Epicrates mid-trunk/posterior trunk vertebra

MLS 497: Epicrates mid-trunk/posterior trunk vertebra

MLS 498: Epicrates mid-trunk/posterior trunk vertebra

MLS 499: Epicrates mid-trunk/posterior trunk vertebra

MLS 500: Anura vertebra

MLS 501: Colubroide mid-trunk/posterior trunk vertebra

MLS 502: Colubroide mid-trunk/posterior trunk vertebra

MLS 503: “Lizard” trunk vertebra

MLS 504: Boidae mid-trunk/posterior trunk vertebra, vertebral centrum

MLS 505: Colubroide mid-trunk/posterior trunk vertebra

MLS 506: Colubroide mid-trunk/posterior trunk vertebra

MLS 507: Colubroide mid-trunk/posterior trunk vertebra

MLS 508: Colubroide mid-trunk/posterior trunk vertebra

MLS 509: “Lizard” caudal vertebra

MLS 510: “Lizard” caudal vertebra

MLS 511: Colubroide mid-trunk/posterior trunk vertebra

MLS 512: Colubroide mid-trunk/posterior trunk vertebra

MLS 513: Colubroide mid-trunk/posterior trunk vertebra

MLS 514: Colubroide mid-trunk/posterior trunk vertebra

MLS 515: Colubroide mid-trunk/posterior trunk vertebra

MLS 516: Colubroide mid-trunk/posterior trunk vertebra

MLS 517: “Lizard” caudal vertebra

MLS 518: Colubroide mid-trunk/posterior trunk vertebra

MLS 519: Colubroide mid-trunk/posterior trunk vertebra

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MLS 527: Colubroide mid-trunk/posterior trunk vertebra

MLS 528: Colubroide mid-trunk/posterior trunk vertebra

MLS 529: Colubroide mid-trunk/posterior trunk vertebra

MLS 530: Anura vertebra

MLS 531: Sacral vertebra of Anura

MLS 532: Anura vertebra

MLS 533: Anura vertebra

MLS 534: Anura vertebra

MLS 535: Anura vertebra

MLS 536: Anura vertebra

MLS 537: Anura vertebra

MLS 538: Lizard trunk vertebra

MLS 539: Anura vertebra

MLS 540: Anura vertebra

MLS 541: Anura vertebra

MLS 542: Anura vertebra

MLS 543: Anura vertebra

MLS 544: Anura vertebra

MLS 545: Anura vertebra

MLS 546: Anura vertebra

MLS 547: Anura vertebra

MLS 548: Anura vertebra

MLS 549: Anura vertebra

MLS 550: Anura vertebra

MLS 551: Anura vertebra

MLS 552: Anura vertebra

MLS 553: Anura vertebra

MLS 554: Anura vertebra

MLS 555: Anura vertebra

MLS 556: Anura vertebra

MLS 557: Anura vertebra

MLS 558: Anura vertebra

MLS 559: Anura vertebra

COMPARATIVE MATERIAL

Collection number	Species
MZUSP 2295	*Ameiva ameiva*
MZUSP 34973	*Ameiva ameiva*
MZUSP 90288	*Ameiva ameiva*
MZUSP 91998	*Ameiva ameiva*
MZUSP 92004	*Ameiva ameiva*
MZUSP 92029	*Ameiva ameiva*
CHRP 3469	*Apostolepis dimidiata*
CHRP 3472	*Boa constrictor*
MCN.D. 333	*Boa constrictor*
MCN.D. 335	*Boa constrictor*
MCN.D. 343	*Boa constrictor*
MCN.D. 344	*Boa constrictor*
MCN.D. 347	*Boa constrictor*
MCN.D. 351	*Boa constrictor*
CHRP2070	*Bothrops alternatus*
CHRP2071	*Bothrops alternatus*
CHRP2072	*Bothrops alternatus*
CHRP2073	*Bothrops alternatus*
CHRP2082	*Bothrops alternatus*
CHRP2069	*Bothrops jararaca*
CHRP2081	*Bothrops jararaca*
MZUSP 14002	*Bothrops jararacussu*
MZUSP 14007	*Bothrops jararacussu*
CHRP1803	*Bothrops moojeni*
CHRP2068	*Bothrops moojeni*
CHRP2078	*Bothrops moojeni*
CHRP2079	*Bothrops moojeni*
CHRP2080	*Bothrops moojeni*
UFMT 05362	*Corallus batesi*
MCN-PV-DR 0001	*Corallus hortulanus*
UFMT 02398	*Corallus hortulanus*
CHRP1800	*Crotalus durissus*
CHRP1801	*Crotalus durissus*
CHRP1802	*Crotalus durissus*
CHRP2065	*Crotalus durissus*
CHRP2066	*Crotalus durissus*
CHRP2067	*Crotalus durissus*
CHRP2074	*Crotalus durissus*
CHRP2075	*Crotalus durissus*
CHRP2076	*Crotalus durissus*
CHRP2077	*Crotalus durissus*
CHRP 3470	*Dipsas ventrimaculata*
MCN-PV-DR 0002	*Epicrates cenchria*

MCN-PV-DR 0003	*Epicrates crassus*
CHRP 3464	*Erythrolamprus aesculapii*
MCN.D 306	*Eunectes murinus*
MCN.D 342	*Eunectes murinus*
MCN.D. 316	*Eunectes murinus*
UF:HERPS:181922	*Iguana iguana*
-	*Iguana iguana*
LACM 164543	*Lachesis muta*
CHRP 3471	*Micrurus frontalis*
CHRP 3465	*Oxyrhopus guibei*
CHRP 3466	*Oxyrhopus guibei*
CHRP 3467	*Phalotris mertensi*
CHRP 3468	*Phalotris mertensi*
CHRP 3473	*Salvator merinae*
CHRP 3474	*Salvator merinae*
CHRP 3475	*Salvator merinae*
CHRP 1128	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1129	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1132	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1133	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1138	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1591	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1592	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1593	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1594	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 1595	*Tropidurus catalanensis*+"torquatos restingas"
CHRP 255	*Tropidurus hispidus*
CHRP 256	*Tropidurus hispidus*
CHRP 259	*Tropidurus hispidus*
CHRP 262	*Tropidurus hispidus*
CHRP 263	*Tropidurus hispidus*
CHRP 1346	*Tropidurus imbituba*
CHRP 1351	*Tropidurus imbituba*
CHRP 1353	*Tropidurus imbituba*
CHRP 1355	*Tropidurus imbituba*
CHRP 1357	*Tropidurus imbituba*
CHRP 1618	*Tropidurus imbituba*
CHRP 1619	*Tropidurus imbituba*
CHRP 1620	*Tropidurus imbituba*
CHRP 1621	*Tropidurus imbituba*
CHRP 1622	*Tropidurus imbituba*
CHRP 1139	*Tropidurus torquatus* stricto sensu
CHRP 1140	*Tropidurus torquatus* stricto sensu
CHRP 1144	*Tropidurus torquatus* stricto sensu
CHRP 1145	*Tropidurus torquatus* stricto sensu
CHRP 1146	*Tropidurus torquatus* stricto sensu

CHRP 1624	*Tropidurus torquatus* stricto sensu
CHRP 1625	*Tropidurus torquatus* stricto sensu
CHRP 1626	*Tropidurus torquatus* stricto sensu
CHRP 1627	*Tropidurus torquatus* stricto sensu
CHRP1623	*Tropidurus torquatus* stricto sensu

SUPPLEMENTARY MATERIAL II

EXTANT SPECIMENS USED IN THE GEOMETRIC MORPHOMETRICS ANALYSIS

CHRP 2070	*Bothrops alternatus*
CHRP 2071	*Bothrops alternatus*
CHRP 2072	*Bothrops alternatus*
CHRP 2073	*Bothrops alternatus*
CHRP 2082	*Bothrops alternatus*
CHRP 1803	*Bothrops moojeni*
CHRP 2068	*Bothrops moojeni*
CHRP 2078	*Bothrops moojeni*
CHRP 2079	*Bothrops moojeni*
CHRP 2080	*Bothrops moojeni*
UFMT 05362	*Corallus batesi*
MCN-PV-DR 0001	*Corallus hortulanus*
UFMT 02398	*Corallus hortulanus*
CHRP 1800	*Crotalus durissus*
CHRP 1801	*Crotalus durissus*
CHRP 1802	*Crotalus durissus*
CHRP 2065	*Crotalus durissus*
CHRP 2066	*Crotalus durissus*
CHRP 2067	*Crotalus durissus*
CHRP 2074	*Crotalus durissus*
CHRP 2075	*Crotalus durissus*
CHRP 2076	*Crotalus durissus*
CHRP 2077	*Crotalus durissus*
MCN-PV-DR 0002	*Epicrates cenchria*
MCN-PV-DR 0003	*Epicrates crassus*

ANOVA VALUES

	d	UCL (95%)	z	Pr>d
Corallus:Epicrates	0.09944209	0.03857549	3.578155	0.001

Table 2. ANOVA values of living *Corallus* and *Epicrates* in anterior view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

	d	UCL (95%)	z	Pr>d
Corallus:Epicrates	0.1158161	0.02889238	4.573185	0.001

Table 3: ANOVA values of extant *Corallus* and *Epicrates* in dorsal view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

	d	UCL (95%)	z	Pr>d
Corallus:Epicrates	0.2283899	0.05456258	4.492548	0.001

Table 4: ANOVA values of extant *Corallus* and *Epicrates* in lateral view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

	d	UCL (95%)	z	Pr>d
Corallus:Epicrates	0.1167954	0.0395478	4.20801	0.001

Table 5: ANOVA values of extant *Corallus* and *Epicrates* in posterior view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

	d	UCL (95%)	z	Pr>d
Bothrops:Crotalus	0.03658959	0.01482052	4.487836	0.001

Table 6: ANOVA values of extant *Bothrops* and *Crotalus* in anterior view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

	d	UCL (95%)	z	Pr>d
Bothrops:Crotalus	0.0444734	0.01279529	4.838372	0.001

Table 7: ANOVA values of extant *Bothrops* and *Crotalus* in dorsal view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

	d	UCL (95%)	z	Pr>d
Bothrops:Crotalus	0.05715187	0.01610204	5.129584	0.001

Table 8: ANOVA values of extant *Bothrops* and *Crotalus* in lateral view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

	d	UCL (95%)	z	Pr>d
Bothrops:Crotalus	0.03742105	0.0144359	4.379068	0.001

Table 9: ANOVA values of extant *Bothrops* and *Crotalus* in posterior view. d: distance between means; UCL: upper confidence limits; z: size effect; Pr>d: significance level hypothesis test

GINI VALUES

	Mean Decrease Gini
PC1	34.199975
PC2	54.615034
Position	2.298678

Table 10: Random Forest of anterior view

	Mean Decrease Gini
PC1	40.451147
PC2	42.597682
Position	3.829652

Table 11: Random Forest of dorsal view

	Mean Decrease Gini
PC1	46.29528
PC2	72.22622
Position	2.44989

Table 12: Random Forest of lateral view

	Mean Decrease Gini
PC1	41.759393
PC2	43.289024
Position	4.150258

Table 13: Random Forest of posterior view

R SCRIPTS

Principal Components Analysis

```
####Importing from library
library(geomorph)
library(ggplot2)
library(car)
library(viridisLite)
library(viridis)

####Importing datset
#IMPORTANT: Landmarks must be bidimensional and in *.TPS format

dados <- readland.tps("total.TPS", specID = "ID", negNA = T)
dimnames(dados)[[3]] #Checa os nomes de IDs
dim(dados) #Checa a dimensão do array criado para receber os dados de landmark

#PROCRUSTES SUPERIMPOSITION (GPA)

species = as.factor(dimnames(dados)[[3]]) #Saves the genus identification in the original database
dados2 <- unname(dados) #creates a new dataset without the names of the genus
gpa <- gpagen(dados2) #does superimposition
#x11();plotAllSpecimens(gpa$coords) #Plota o resultado da superimposicao

#Procustes ANOVA

gdf <- geomorph.data.frame(gpa, species = species) #Generates a dataframe with Procrustes values and genera for the analysis

#MANOVA for Goodall's F test or Procruste ANOVA
```

```
fit1 <- procD.lm(coords ~ species, effect.type = "Rsq", data = gdf) #randomize raw values
summary(fit1)
#plot(fit1)
gp <- interaction(gdf$species)
pw <- pairwise(fit1, groups = gp)
summary(pw, test.type = "dist", confidence = 0.95, stat.table = T)

####### PCA ########

#Doing the analysis
pca <- gm.prcomp(gpa$coords)
pc1 <- pca$x[,1]
pc1 <- as.data.frame(pc1)
pc1$especie <-   rownames(pca$x)

#Ploting the percentages of contribution of each PC
pvar <- (pca$sdev^2)
pvar.per <-round(pvar/sum(pvar)*100, 1)
names(pvar.per) <- seq(1:length(pvar))
barplot(pvar.per, xlab= "Componentes Principais", ylab = "% Variação")
#Ploting the PCA

#Generating the dataframe for the ggplot graph
pca.data <- data.frame(Sample = rownames(pca$x),
        X = pca$x[,1],
        Y = pca$x[,2])
#Colorblind friendly colors for the plot
cbp1 <- c("#E69F00", "#56B4E9", "#009E73", "#000000",
         "#D55E00", "#0072B2", "#F0E442", "#CC79A7")
```

```
#Plotting the graph
ggplot(data = pca.data, aes(x = X, y = Y, label = Sample))+
        geom_point(aes(colour = gdf$species))+
        xlab(paste("PC1 - ", pvar.per[1], "%", sep = ""))+
        ylab(paste("PC2 - ", pvar.per[2], "%", sep = ""))+
        theme_bw()+
        scale_colour_manual(values=cbp1)+
        ggtitle("Principal Components Analysis: Epicrates x Corallus in X view")
```

Machine Learning Random Forest

```
library(geomorph)
library(ggplot2)
library(cowplot)
library(randomForest)
library(dplyr)
library(caret)

dados_anterior <- readland.tps("anteriores_vistaposterior.TPS",
                               specID = "ID",negNA = T)
dados_medias <- readland.tps("mediaseposteriores_vistaposterior.TPS",
                               specID = "ID",negNA = T)

######## Checking the data

dimnames(dados_anterior)[[3]] #Checks the names of IDs
dim(dados_anterior) #Checks the dimensions of the array created to recieve the landmark data
```

```
#IMPORTANT: The initial array must have 3 dimensions, presenting 3 values,
#being p = landmarks, k = dimensions, n = number of specimens

########  Estimating missing data (there can’t be any)


#Missing data usually appear as NAs, but just to be sure
any(is.na(dados_anterior))
any(is.na(dados_medias))

### In case there is missing data
#dados <- estimate.missing(dados)

########  Procrustes Superimposition (GPA)

gpa_anteior <- gpagen(dados_anterior)
gpa_medias <- gpagen(dados_medias)

########  PCA

pca_anterior <- gm.prcomp(gpa_anteior$coords)
pca_medias <- gm.prcomp(gpa_medias$coords)

# Generating dataframe with PCs and genus
anterior <- rep('anterior', times = length(pca_anterior$x[,1]))
pca_data_anterior <- data.frame(Genero = rownames(pca_anterior$x),
                                PC1 = pca_anterior$x[,1],
                                PC2 = pca_anterior$x[,2],
                                Posicao = anterior)
```

```
medias <- rep('medias', times = length(pca_medias$x[,1]))
pca_data_medias <- data.frame(Genero = rownames(pca_medias$x),
                              PC1 = pca_medias$x[,1],
                              PC2 = pca_medias$x[,2],
                              Posicao = medias)

str(pca_data_anterior)
str(pca_data_medias)

pca_data <- bind_rows(pca_data_anterior, pca_data_medias)

str(pca_data)
pca_data$Genero <- as.factor(pca_data$Genero)
pca_data$Posicao <- as.factor(pca_data$Posicao)
levels(pca_data$Genero)

########  Random Forests

# Dividing the dataset in practice and validation
fossil <- filter(pca_data, Genero == 'fossilG' | Genero == 'fossilP' )
fossil$Genero[which(fossil$Genero == 'fossilG')] <- NA
fossil$Genero[which(fossil$Genero == 'fossilP')] <- NA
fossil <- droplevels(fossil)
pca_data2 <- dplyr::filter(pca_data, Genero != 'fossilG' & Genero != 'fossilP')
pca_data2 <- droplevels(pca_data2)
levels(pca_data2$Genero)
indice <- createDataPartition(y = pca_data2$Genero, p = 0.7, list=FALSE)
data_treino <- pca_data2[indice,]
data_validacao <- pca_data2[-indice,]
```

```
data_validacao <- bind_rows(data_validacao, fossil)
levels(data_treino$Genero)
model <- randomForest(Genero ~ ., data = data_treino, ntree=1000, proximity = TRUE)
model

# Generating error plot
oob.error.data <- data.frame(
  Trees=rep(1:nrow(model$err.rate), times=3),
  Type=rep(c("OOB", "Bothrops", "Crotalus"), each=nrow(model$err.rate)),
  Error=c(model$err.rate[,"OOB"],
                  model$err.rate[,"Bothrops"],
                  model$err.rate[,"Crotalus"]))

ggplot(data=oob.error.data, aes(x=Trees, y=Error)) +
  geom_line(aes(color=Type))

oob.values <- vector(length = 3)
for(i in 1:3) {
temp.model <- randomForest(Genero ~ ., data = data_treino, mtry=i, ntree=1000)
oob.values[i] <- temp.model$err.rate[nrow(temp.model$err.rate),1]
}

oob.values
min(oob.values)
which(oob.values == min(oob.values))

##Doing the validation with the remaining 30%
validacao <- predict(model, data_validacao, type = 'Class')
validacao
```

```
table(validacao, data_validacao$Genero)


#Seing the importance of each PC

importance(model)

varImpPlot(model, sort=TRUE, n.var=min(30, nrow(model$importance)),

        type=NULL, class=NULL, scale=TRUE,
main=deparse(substitute(Variables)))
```