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Lizards and snakes (Lepidosauria, Squamata) from the Lajedo de Soledade, Quaternary of Rio Grande do Norte, Brazil

Sílvia Oliveira Lomba [a,*], João Paulo da Costa [b], Kleberson de Oliveira Porpino [c], Hermínio Ismael de Araújo-Júnior [b], Annie Schmaltz Hsiou [a]

[a] Laboratório de Paleontologia e Ribeirão Preto, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Avenida Bandeirantes, 3900, CEP 14040-901, Ribeirão Preto, São Paulo, Brazil

[b] Faculdade de Geologia, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier, 524, 2° Andar, Sala 2032A, Maracanã, Rio de Janeiro, CEP 20550-013, Rio de Janeiro, Brazil

[c] Departamento de Ciências Biológicas, Faculdade de Ciências Exatas e Naturais, Universidade do Estado do Rio Grande do Norte, Rua Professor Antônio Campos, s/n, CEP 59633-010, Mossoró, Rio Grande do Norte, Brazil

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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 Pleistocene megafauna is the Lajedo de Soledade in Apodi, Rio Grande do Norte state. This location is a prominent outcrop of limestone, with approximately 3 km^2 of exposed rock, mainly constituted by the Jandaíra Formation's lower section. Over time, the limestone underwent karstification, forming caves and ravines, many of which are filled with Quaternary sediments. The preserved paleofauna is one of the most diverse for the Quaternary period, including mammals, birds, amphibians, crocodilians, and turtles, which are uncommon in other regional Quaternary deposits. Additionally, fossil remains of squamates were collected but have never been described or adequately identified. Therefore, only fossil mammals have been described until now, and knowledge about the paleoherpetofauna is still scarce. The present study describes fossil Squamata collected at Lajedo de Soledade. Fossils of *Crotalus durissus*, *Epicrates* sp., an embryo of Boidae indet., Viperidae indet., *Tropidurus* sp., and Tupinambinae indet. 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 large lizards currently found in the state. The results of this study are essential for understanding the Quaternary environment of Rio Grande do Norte and for clarifying the past faunal composition of Squamata, which had not been previously described for this locality.

1. Introduction

Generally, Squamata specimens are small and possess fragile skeletal elements compared to other diapsid groups with more robust skeletons, such as crocodiles and dinosaurs. Consequently, studying fossil squamates can be challenging, as these characteristics hinder both fossilization and collection. As a result, their fossil record consists mainly of isolated and fragmented bones (Albino, 2011; Onary et al., 2017). Among lizards, most fossil materials are skull fragments, such as the maxilla and dentary, whereas in snakes, the record is almost exclusively composed of isolated vertebrae (Hsiou, 2010; Onary and Hsiou, 2015). Amphisbaenians have an even scarcer record, represented by skulls and vertebral elements (Camolez and Zaher, 2010).

The Quaternary squamate record of South America primarily consists of extant species (Albino and Brizuela, 2015). It includes representatives of Boidae, Viperidae, Elapidae, and Colubroidea from 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, 2013a, 2013b; Onary et al., 2018). Notably, most fossiliferous sites in Brazil lack precise rock dating. To date, the only

* Corresponding author. Laboratório de Paleontologia e Ribeirão Preto, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Avenida Bandeirantes, 3900, CEP 14040-901, Ribeirão Preto, São Paulo, Brazil.
E-mail addresses: silvialomba06@gmail.com (S.O. Lomba), costa.jp@outlook.com.br (J.P. Costa).

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recognized records of venomous snakes from the Brazilian Cenozoic consist of fragments attributed to the genera *Micrurus* (Elapidae), *Bothrops*, and *Crotalus* (Viperidae) (Camolez and Zaher, 2010; Hsiou et al., 2012; Hsiou and Albino, 2011).

The Quaternary record of lizards is predominantly composed of disarticulated fragments and exhibits significant taxonomic diversity. In South America, excluding Brazil, recorded taxa include Iguanidae, Liolaemidae, Teiidae, Leiosauridae, and Gekkonidae (Rusconi, 1937; Hoffstetter, 1970; Van Devender, 1977; Estes, 1983; Donadío, 1984; De la Fuente, 1999; Albino, 2005). In Brazil, the record is particularly diverse, with fossils attributed to Tropiduridae, Teiidae, Leiosauridae, Polychrotidae, Gekkonidae, and Anguidae. Among these, Teiidae is the

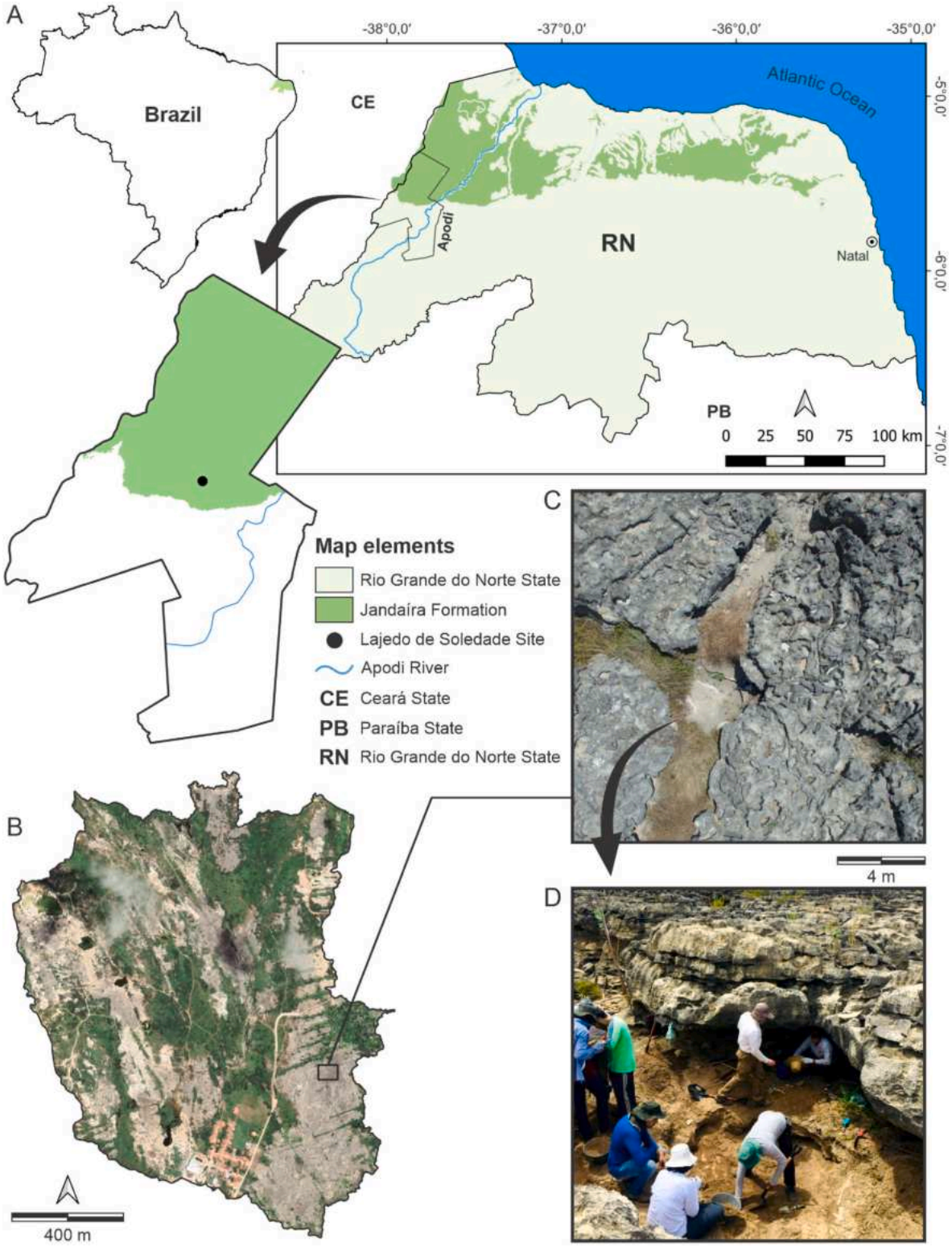

Fig. 1. – Location of Lajedo de Soledade, Apodi/RN. **A**, location map of Lajedo de Soledade; **B**, exposure area of carbonate rocks from the Jandaíra Formation, image obtained from Google Earth; **C**, aerial photo of Ravina das Araras; **D**, excavation area. Modified from Costa et al. (2024).

most prevalent family, with *Tupinambis* exhibiting the highest number of records, especially in Pleistocene deposits (Camolez and Zaher, 2010; Hsiou, 2007; Hsiou et al., 2012, 2016). These fossils have been found in the states of Rio Grande do Sul, Ceará, Minas Gerais, Tocantins, Goiás, Bahia, Acre, Rio de Janeiro, and Mato Grosso.

In Rio Grande do Norte, around 25 fossiliferous localities are known to contain fossil assemblages (Araújo-Júnior and Porpino, 2011), with only one record documented by Souza-Cunha (1966). Recent collections from the Quaternary deposit of Ravina das Araras, in Lajedo de Soledade, Apodi, Rio Grande do Norte, have resulted in the discovery of vertebrate remains (Costa et al., 2024), including squamate specimens. These materials require a detailed taxonomic study. This work presents a taxonomic analysis of the Squamata specimens collected, contributing to the knowledge of Quaternary squamate fauna in Brazil.

2. Material and methods

2.1. Study area

The squamate remains come from the Ravina das Araras (5°35′546″ S and 37°49′607″ W) at the locality Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil (Fig. 1). The material consists of 17 fossils that are preserved in various conditions. Lizards (teiid specimen) are represented by isolated dentaries and vertebral remains, and snakes (booid and viperid specimens) are represented exclusively by isolated vertebrae. All specimens are stored at the Museu do Lajedo de Soledade (MLS) in the municipality of Apodi, Rio Grande do Norte, Brazil.

The Lajedo de Soledade site is located in the Chapada do Apodi, between the states of Ceará and Rio Grande do Norte, northeastern Brazil. 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 (sandstone) and Jandaíra (limestone) formations, part of the Upper Cretaceous section of the Potiguar Basin and some sandstone outcrops of the Barreiras Formation, interpreted as coastal and river Cenozoic deposits (Angelim et al., 2006; Pinéo et al., 2020).

The Lajedo de Soledade site is a prominent outcrop of limestone, with approximately 03 Km^2 of exposed rock, constituted mainly of the lower section of the Jandaíra Formation in Rio Grande do Norte (Bagnoli, 1994; Córdoba et al., 1994). Marine fossils and ichnofossils are preserved on the flagstone, accounting for when the site was a tidal flat (Porpino et al., 2009). The karstification process significantly influenced the Lajedo area, enlarging fissures and fractures, which led to the development of caves and ravines that were occasionally filled with Quaternary sediments (Córdoba et al., 1994; Porpino et al., 2004; Costa et al., 2024). These karstic environments are notable for yielding numerous small and fragmented fossils and are esteemed for their archaeological potential, particularly due to various rock paintings. The paleofauna preserved at this site represents one of the most diverse fossil assemblages from the Quaternary period in Rio Grande do Norte (Porpino et al., 2004). However, only the fossil mammals from this assemblage have been thoroughly described (Porpino et al., 2004; Costa et al., 2024), and its paleoherpetofauna remains poorly understood.

The excavation area of Ravina das Araras corresponds to a trench approximately 3.0 × 2.7 m in size, which revealed four sedimentary layers, three of which contain fossils (Fig. 2; Costa et al., 2024):

Layer "A": It has a thickness of at least 90 cm, although the actual depth is unknown due to the excavation being halted after reaching the water table. It is composed of medium sand, silt, and clay and contains vertebrate fossils. Layer "B": This layer is about 28 cm thick, consisting of coarse sand, vertebrate fossils, and a clay lens approximately 40 cm wide and 15 cm high. Layer "C": It is around 12 cm thick, composed of fine, light-colored sand, containing gastropod mollusk shells and vertebrate fossils. Layer "D": It is 18 cm thick, corresponds to the current surface layer (soil) and does not contain vertebrate fossils.

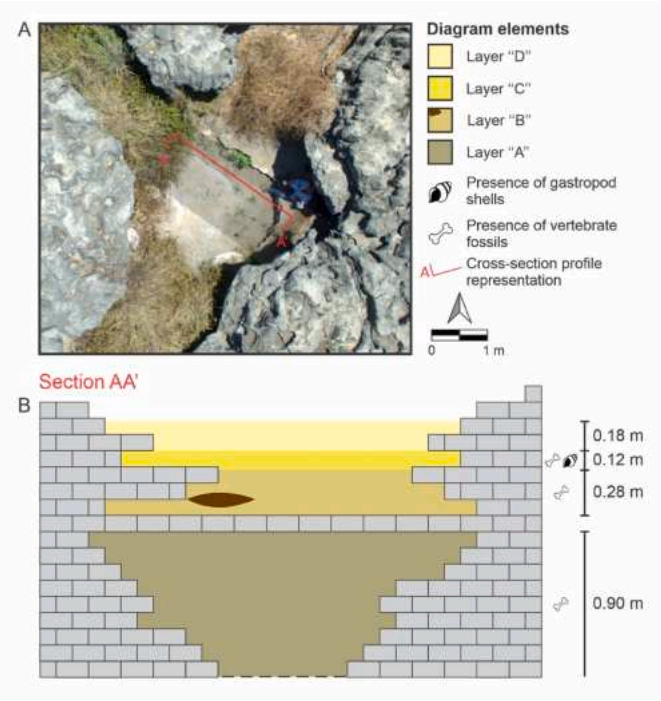

Fig. 2. – Diagram of the sedimentary layers of the Quaternary deposit at Ravina das Araras. **A**, aerial image of Ravina das Araras indicating the cross-sectional profile represented by the diagram; **B**, diagram of the sedimentary layers. Taken from Costa et al. (2024).

During the excavation, three limestone slabs were identified, interspersed with the sedimentary layers;only the third was a continuous slab. The first slab, ranging from 1 to 10 cm thick, was found between layers "D" and "C". The second was positioned between layers "C" and "B," with a thickness of about 18 cm. The third, approximately 10 cm thick, separated layer "A" from the other layers, apparently lacking stratigraphic correlation (no vertical connection) with the different layers.

2.2. Taxonomic description

The study of the material mainly consisted of macroscopic observation, although a stereoscopic microscope was used when necessary. The anatomical research included a comparative analysis of the specimens using available material deposited at the following collections and institutions: Coleção Herpetológica de Ribeirão Preto (CHRP) of the Departamento de Biologia of FFCLRP/USP (Ribeirão Preto, São Paulo, Brazil); Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil); Florida Museum of Natural History, Herpetology Collection (UF: HERPS, Florida, USA) through Morphosourse; Coleção da Universidade Federal do Mato Grosso (UFMT, Cuiabá, Mato Grosso, Brazil); Natural History Museum of Los Angeles County (LACM, Los Angeles, USA) through photographs; and Coleção Didática de Répteis (MCN-PV-DR) and Coleção Didática de Herpetologia (MCN.D.) of 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 Supplementary Material I.

The established methodology and anatomical terminology for each studied group were followed to describe the material. The descriptions follow Auffenberg (1963), Rage (1984), LaDuke (1991a, 1991b), Lee and Scanlon (2002), Albino and Carlini (2008), and Hsiou et al. (2013a) for snakes (Fig. 3); and Estes (1983), Frost (1992), Veronese and Krause (1997), and Brizuela and Albino (2016) for lizards. The systematic

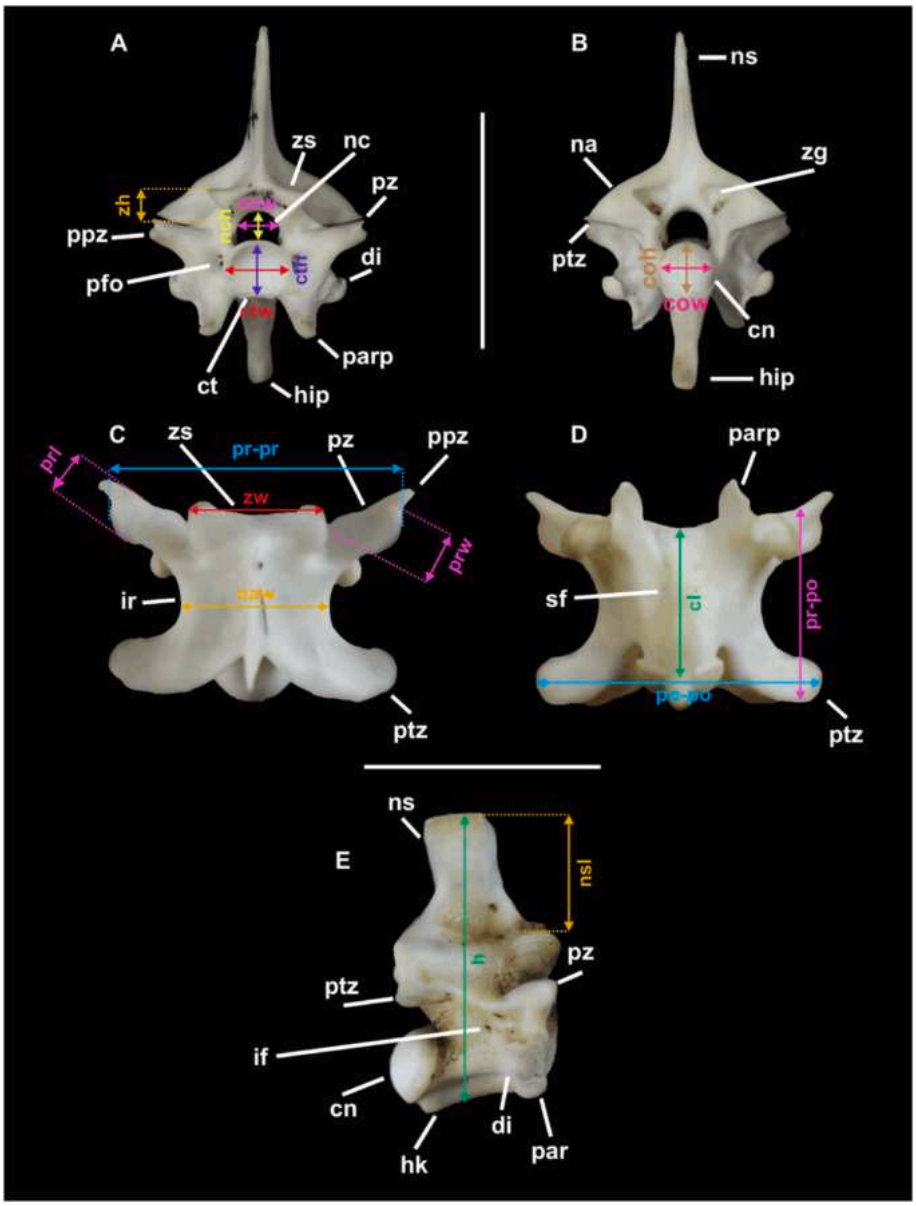

Fig. 3. – Mid-trunk vertebrae of *Crotalus durissus* (CHRP2077; A–D) and *Epicrates cenchria* (MCN-PV-DR 0002; E), with anatomical abbreviations. **A**, anterior view; **B**, posterior view; **C**, dorsal view; **D**, ventral view; **E**, lateral view. cl, centrum length; cn, condyle; coh, condyle height; 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. Scale bars = 10 mm.

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 taken following LaDuke (1991a, 1991b; Fig. 3), using a Digimess caliper with 0.02 mm 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 images were taken with a digital Canon Rebel T6i camera, with a standard 18–55 mm or 100 mm macro lens. For smaller specimens, a Leica M205 stereo microscope was used.

3. Results and discussion

3.1. Systematic paleontology

Squamata Oppel, 1881.
Lacertoidea Oppel, 1881.
Teiidae Gray, 1827.
Tupinambinae Bonaparte, 1831
Tupinambinae indet.
(Fig. 4A–C).

Material: MLS 483, an incomplete and isolated trunk vertebra. MLS 854, right maxila.

Locality and Horizon: Layers B (MLS 483) and C (MLS 854), Ravina das Araras, Lajedo de Soledade locality (Jandaíra Formation, Potiguar

Fig. 4. – Fossil tetrapod Squamata from the Lajedo de Soledade site. **A**, MLS 483, trunk vertebrae of Tupinambinae indet. in ventral view; **B–C**, MLS 854, fragment of right maxilla of Tupinambinae indet. in labial (B) and occlusal (C) views; **D–E**, MLS 486, left dentary of *Tropidurus* sp. in lingual (D) and labial (E) views. Scale bars = 10 mm.

Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene–Holocene (Quaternary) (Porpino et al., 2009; Costa et al., 2024).

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, prezygapophyses, and 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 arch exhibits a poorly developed median crest. The right prezygapophyseal articular facet is oval. The right sinapophysis has an abnormal bone growth, which is probably indicative of some kind of paleopathology.

The specimen MLS 854 is an incomplete right maxilla. Only the posterior portion of the bone is preserved. The posterior region of the fossil is thinner in the articulation area with the jugal and lacrimal.

In labial view, the external wall is smooth, with no ornamentation. Labial foramina are not visible. The dentition is subpleurodont and heterodont. The posteriormost tooth is slightly smaller than the others. All preserved teeth are molariform.

In lingual view, the replacement pits directly above each tooth are visible. The supradental ridge is well developed and easily visible. The superior alveolar foramen is not visible due to the poor preservation of the fossil and encrusted sediments.

Remarks: Due to the incomplete 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 largest extant lizards of Brazil are *Iguana* Laurenti, 1768, *Salvator* Duméril and Bibron, 1839, *Tupinambis* Daudin, 1802, *Crocodilurus* Spix, 1825, and *Dracaena* Daudin, 1801. Currently, in Rio Grande do Norte, the two large lizards present are *Iguana iguana* (Linnaeus, 1758) and *Salvator merianae* Duméril and Bibron, 1839 (Costa et al., 2021).

It is reasonable to assume that the fossil is not an *I. iguana* as this species has a bigger subcentral foramen 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, foramina are present in the neural canal in MLS 483. Also, for an *I. iguana* vertebra of this length, the condyle and the cotyle are smaller than those in MLS 483. However, the vertebra also differs from those of *S. merianae*, which are wider in the anterior portion, while MLS 483 is slimmer.

In addition to the iguana, the main lizard taxa present in Brazil belong to the family Teiidae, making them the most likely candidates for the fossil identification. 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). Considering these features, MLS 483 is probably another species of *Tupinambis* or *Salvator* distinct from *S. merianae*. Unfortunately, only specimens of *S. merianae* were available during the present study for comparison. For more precise identification, more comparison specimens are needed. Due to limitations, the specimen was only identified at the subfamily level. For the maxilla, based on the molariform dentition, it is possible to identify this specimen as Tupinambinae (*sensu* Pyron et al., 2013) as this is characteristic of the genera *Dracaena* and *Tupinambis/Salvator* (Presch, 1974) (Camolez and Zaher, 2010; Estes, 1983). The teeth do not show signs of expansion on their top, suggesting it is not a specimen of *Dracaena* (Presch, 1974).

Toxicofera Vidal and Hedges, 2005.

Iguania Cope, 1864.

Tropiduridae Bell, 1843.

Tropidurus Wied-Neuwied, 1824.

Tropidurus sp.

(Fig. 4D–E).

Material: MLS 486, left dentary.

Locality and Horizon: Layer B, Ravina das Araras, Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene–Holocene (Quaternary) (Porpino et al., 2009; Costa et al., 2024).

Description: 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 most apical teeth are unicuspidated. The dentition is pleurodont. The Meckel canal is closed, and only a tiny foramen remains 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 the labial view, eight mental foramina are visible. In the lingual view, on the posterior portion, a notch extends up to 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), a characteristic absent in the outgroups. The subdental shelf is shallow. The mandibular symphysis region is internally oriented in the dorsal view, while in the lingual view, it is dorsally oriented.

Remarks: The genus is widely distributed throughout 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: *Tropidurus hispidus* (Spix, 1825) and *Tropidurus semitaeniatus* (Spix, 1825; Carvalho, 2013; Costa et al., 2021).

Regarding MLS 486, 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). However, studies comparing the cranial anatomy of different *Tropidurus* species did not identify any characters that differentiate between species (Adorni, 2018). Therefore, a specific assignment is not feasible for MLS 486.

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923.
Constrictores Oppel, 1811 *sensu* Georgalis and Smith (2020).
Booidea Gray, 1825 *sensu* Pyron, Reynolds and Burbink 2013
Boidae Gray, 1825.
Epicrates Wangler, 1830.
Epicrates sp.
(Fig. 5).

Material: MLS 485, anterior trunk vertebra; MLS 492, MLS 493, MLS 494, MLS 495, MLS 496, MLS 497, MLS 498, and MLS 499, mid-trunk/posterior trunk vertebrae.

Locality and Horizon: Layers B (MLS 485, MLS 492, MLS 493, MLS 494, MLS 495, and MLS 496) and C (MLS 498 and MLS 499), Ravina das Araras, Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene–Holocene (Quaternary) (Porpino et al., 2009; Costa et al., 2024).

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 1 mm thick, and broader 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, which 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 others. The prezygapophyseal processes are very short in all vertebrae. The interzygapophyseal ridge is well marked between the prezygapophysis and the postzygapophysis. A deep notch on the posterior portion of the neural arch between the postzygapophysis (the posterodorsal notch) makes the condyle visible.

In the posterior view, the neural arch is depressed, with a slightly arched aspect. The postzygapophyses are slightly inclined upward. This slope is less pronounced than in the prezygapophyses. The zygantrum is large and has 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 slightly inclined backward in the specimens where 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. Although it is not preserved,

Fig. 5. – Fossil vertebrae of *Epicrates* sp. from the Lajedo de Soledade site. **A**, MLS 485 anterior trunk vertebra; **B–C**, MLS 496 (B) and MLS 492 (C) mid-trunk/posterior trunk vertebrae; anterior, posterior, lateral, dorsal, and ventral views. Scale bar = 10 mm.

its projection can be observed posteriorly. The parapophysis and the diapophysis have a clear separation, with the diapophyses positioned dorsoposteriorly and the parapophyses anteroventrally. The lateral foramina are present, with one small foramen on each side of the vertebrae.

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

Remarks:

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 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* Linnaeus, 1758 and *Eunectes* Wagler, 1830 by their small size, less vaulted neural arch, and different zygosphene morphology, which is thinner and crenate on all specimens (Hsiou and Albino, 2010; Onary et al., 2018). *Eunectes* have 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* Daudin (1803). *Corallus* has a low neural spine and prezygapophyses parallel to the horizontal plane, while the fossils have a 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* based on the previously mentioned traits and the following features: small vertebrae with a robust neural arch that is broad and anteroposteriorly short, 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. However, the available comparison material did not present this variation. Another explanation could be interspecific variation. Additional extant specimens of other species are needed to understand these differences properly. Currently, only one species of *Epicrates* is recorded for Rio Grande do Norte, *Epicrates assisi*. However, no specimen of this species was available for comparison. Also, no postcranial character has been identified to distinguish the species of *Epicrates*. Therefore, all specimens are attributed to the genus *Epicrates*.

The most recent list of Brazilian reptiles recognizes four species of *Epicrates*: *E. assisi* Machado, 1945, *E. crassus* Cope, 1862, *E. cenchria* (Linnaeus, 1758), and *E. maurus* Gray, 1849; Costa and Bérnils (2018); Costa et al. (2021). The genus is reported for all 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* (Guedes et al., 2023). This species is also reported for the Chapada do Apodi by Lima Verde (1976).

Boidae indet.

(Fig. 6).

Referred Material: MLS 484, mid-trunk/posterior vertebra.

Locality and Horizon: Layer B, Ravina das Araras, Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene–Holocene (Quaternary) (Porpino et al., 2009; Costa et al., 2024).

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 the anterior view, the zygosphene is very thin and has an elevated roof. The zygosphene is not entirely developed, having very poorly developed 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 poorly developed. The prezygapophyses are either worn out or underdeveloped, but it is possible to observe that they are anteriorly oriented and lack the prezygapophyseal processes. Most of the posterior portion of the neural arch is absent, with only the postzygapophyseal region present.

In posterior view, the neural arch is incomplete, making it impossible to confirm its shape. The zygantrum is undeveloped. The condyle is worn, 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 a small process emerges.

In lateral view, the vertebra is anteroposteriorly short. The zygosphene is poorly developed. The zygosphenal articular facets are undeveloped. The paradiapophyses are either completely worn or underdeveloped. It is possible to see a poorly developed hemal keel with a little projection on the posterior portion. The lateral foramina are absent.

In ventral view, the vertebral centrum is triangular, wider on the anterior portion, and narrower on the posterior portion. The hemal keel is developed, with a small ventral projection near the cotyle. The

Fig. 6. – Fossil vertebrae of Boidae indet. from the Lajedo de Soledade site. **A**, MLS 484, mid-trunk/posterior vertebra; anterior, posterior, lateral, dorsal, and ventral views. Scale bar = 5 mm.

subcentral fossae are absent, and the subcentral foramina are present, with one on each side of the hemal keel.

Remarks: 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 the final stages of embryonic development (Winchester and Bellaïrs, 1977; Xing et al., 2018). More precise identification is problematic, as this specimen is an embryo, and all known diagnostic characters are based on adult individuals. 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 snake fossil embryos for Brazil.

Viperidae Bonaparte, 1840

Crotalinae Gray, 1825.

Crotalus Linnaeus, 1758

Crotalus durissus Linaeus, 1758

(Fig. 7).

Material: MLS 479, anterior trunk vertebra; MLS 480, mid-trunk/posterior trunk vertebra.

Locality and Horizon: Layer B, Ravina das Araras, Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene–Holocene (Quaternary) (Porpino et al., 2009; Costa et al., 2024).

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 for Viperidae (Zaher, 1999). The neural spine and hypapophysis are broken in both vertebrae. In the anterior view, the prezygapophyses are lightly oblique with respect 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 neural canal floor 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, 1991a,b). 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, it is damaged, making it impossible to determine its length or whether 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.

Remarks: The genus *Crotalus* Linnaeus, 1758 is widely distributed and represented in Brazil by a single species, *C. durissus* Linnaeus. Its occurrence area extends from the northeastern to the southern regions of Brazil and also the states of Goiás and Mato Grosso. In the northern region, the distribution of this species is fragmented, as it is absent in densely vegetated areas like the interior of the Amazon Forest; however, it can be found in areas with 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).

MLS 479, MLS 480, MLS 481, and MLS 482 can be identified as 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* Amaral, 1923, *Bothrops leucurus* Wagler, 1824, and *Crotalus durissus*. *Bothrops* tend to have shorter neural spines, more oblique pre- and postzygapophyses, shorter and lateralized parapophyseal processes, and short prezygapophyseal processes (Camolez and Zaher, 2010; Hsiou and Albino, 2011; Lomba et al., 2024). Conversely, *Crotalus* usually has taller neural spines, less oblique pre and

Fig. 7. – Fossil vertebrae of *Crotalus durissus* from the Lajedo de Soledade site. **A**, MLS 480 mid-trunk/posterior trunk vertebra; **B**, MLS 479 anterior trunk vertebra; anterior, posterior, lateral, dorsal, and ventral views. Scale bar = 10 mm.

postzygapophyses, longer and not lateralized parapophyseal processes, and longer prezygapophyseal processes. Also, *Crotalus* may have a concave "V" shaped zygosphene, but this morphology is highly variable (Lomba et al., 2024). *Lachesis* vertebrae also have a different morphology from that of *Crotalus* and *Bothrops*. *Lachesis* has a smaller and lateralized parapophyseal process, small prezygapophyseal processes, and a straight anterior edge of the zygosphene in the dorsal view. In contrast, in the 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 et al., 2024). Even though MLS 479 does not have a medium prezygapophyseal process (*sensu* LaDuke, 1991a,b) 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 variation in vertebral shape along the spine, which is observable in the comparative material. MLS 479 is from a more anterior position on the vertebral column, while MLS 480 is from a more posterior position.

Viperidae indet.

(Fig. 8).

Material: MLS 481 and MLS 482, vertebral centrum.

Locality and Horizon: Layer B, Ravina das Araras, Lajedo de Soledade (Jandaíra Formation, Potiguar Basin), Rio Grande do Norte state, northeastern Brazil. Late Pleistocene–Holocene (Quaternary) (Porpino et al., 2009; Costa et al., 2024).

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 has worn 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, 1991a,b) 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 into diapophysis and parapophysis. A well-developed and anteroventrally orientated process emerges from the parapophysis, which enables the identification of this fossil as a Viperidae.

Remarks: Concerning MLS 481 and MLS 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, 1991a,b) and the parapophyseal process has little lateralization. However, the abrasion impacted other important structures for taxonomic attribution, such as the zygosphene and the neural spine. Therefore, any generic attribution would be unreliable.

3.2. Biostratigraphic aspects

The biostratigraphic aspects of Ravina das Araras, considering the layers fully described in the Material and methods section, are summarized below and illustrated in Fig. 9:

Layer "A," the deepest of the fossil-bearing units, is composed of medium sand, silt, and clay, and does not contain any records of Squamata.

Layer "B," the intermediate fossil-bearing unit composed of coarse sand, includes occurrences of *Crotalus durissus*, *Epicrates* sp., *Tropidurus* sp., Tupinambinae indet., Boidae indet., and Viperidae indet.

Layer "C," the most superficial of the fossil-bearing units, is composed of fine, light-colored sand containing gastropod mollusk shells, and features records of *Epicrates* sp. and Tupinambinae indet.

3.3. Paleoenvironmental implications

The Brazilian fossil record of Squamates is extensive and relatively well known despite the fragmented nature of the fossils. However, most of the available fossils are concentrated in the southern 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). Our understanding of the northeastern fossil squamates is still insufficient despite the knowledge of many fossiliferous sites. The known squamate fossils from the region were discovered in Maranhão, Ceará, and Bahia states

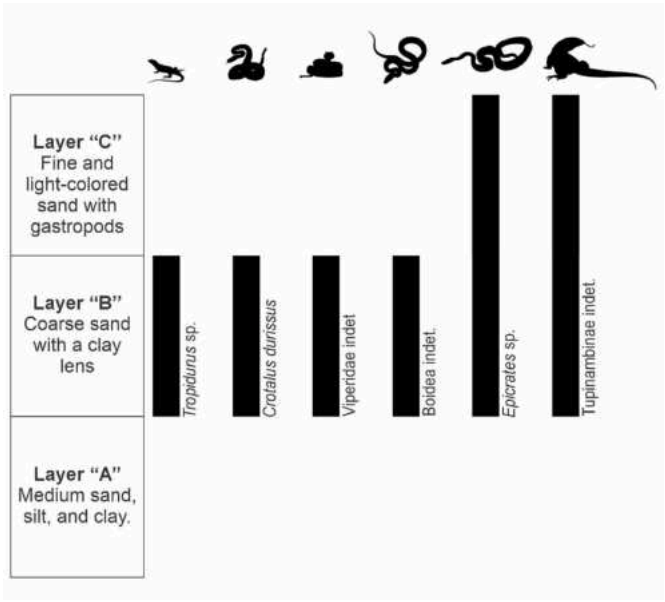

Fig. 9. – Distribution of taxa by layer.

Fig. 8. – Fossil vertebrae of Viperidae indet. from the Lajedo de Soledade site. **A–B**, MLS 482 in anterior (A) and dorsal (B) views; **C–D**, MLS 481 in anterior (C) and dorsal (D) views. Sacale bar = 10 mm.

(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 Lajedo de Soledade, adding to the paleontological knowledge of the region. Notably, this is also the first description of a fossil snake embryo from Brazil.

Crotalus durissus and *Tropidurus* spp. are living widespread taxa of Brazil; however, their Late Pleistocene-Holocene record is comparatively scarce when compared to their current distribution. Currently, these fossil records only include those from Ceará, Minas Gerais, and Bahia states (Camolez and Zaher, 2010; Hsiou et al., 2012). These species are typical 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) in Lajedo de Soledade has interesting implications. 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, further studies with additional comparison specimens and species are necessary for greater taxonomic precision and to enhance our understanding of the Squamata fauna in the region.

The taxa described here are mostly compatible with faunal assessments made for the Chapada do Apodi and Rio Grande do Norte (Lima Verde, 1976; Costa et al., 2021). As said previously, *Crotalus durissus* and *Tropidurus* are characteristic of drier 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, corroborated by many anuran vertebrae in this assemblage, including a Siluriform pectoral spine.

Utida et al. (2020) investigated the Holocene paleoclimate of the Chapada do Apodi, and their study revealed that several climate change events occurred throughout the Holocene. The investigations demonstrated that the period between 11,000 and 5000 years ago represented the wettest phase, followed by an arid phase between 5000 and 3000 years ago. The identified species are consistent with both the climatic inferences from the late Pleistocene and those pertaining to the interval between 5000 and 3000 years ago. Thus, to better understand the climatic details at Lajedo de Soledade, it is necessary to date the different sedimentary layers of the ravines.

4. Conclusion

This study presents the first description of Squamata fossils from Lajedo de Soledade Site, identifying at least four taxa: *Crotalus durissus*, *Epicrates* sp., Tupinambinae indet., and *Tropidurus* sp. The species found are compatible with both dry and wet environments. However, isotopic analyses are necessary for a more detailed understanding of the climatic conditions at Lajedo de Soledade. Notably, this study also reports the first record of a fossil snake embryo (*Boidae* indet.) in Brazil, highlighting the exceptional preservational conditions and the potential of the site for future paleobiological and ontogenetic investigations. Once again, Lajedo de Soledade stands out as a highly diverse fossil deposit, with the addition of Squamata fossils.

CRediT authorship contribution statement

Sílvia Oliveira Lomba: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **João Paulo da Costa:** Writing – original draft, Investigation, Conceptualization. **Kleberson de Oliveira Porpino:** Writing – review & editing, Supervision. **Hermínio Ismael de Araújo-Júnior:** Writing – review & editing, Supervision, Project administration. **Annie Schmaltz Hsiou:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2025.105606.

Data availability

No data was used for the research described in the article.

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