

# The vertebrate fossil record from the Feliz Deserto Formation (Lower Cretaceous), Sergipe, NE Brazil: paleoecological, taphonomic, and paleobiogeographic implications

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## ABSTRACT

The Feliz Deserto Formation (Berriasian–Valanginian, Sergipe–Alagoas Basin, NE Brazil) preserved some of the earliest South American fossil records of the rifting stages which resulted in the Gondwana supercontinent break-up during the Early Cretaceous. Recently, the first spinosaurid theropod record of this formation was described, based on a tooth recovered from Canafistula 01 locality in Sergipe State. We add herein twenty-seven isolated specimens to the fossil record of the Lower Cretaceous Feliz Deserto Formation. The new material includes seven isolated spinosaurid theropod teeth of the spinosaurine clade, as well as an indeterminate theropod preungual pedal phalanx. In addition, we describe an isolated crocodyliform osteoderm, as well as eighteen isolated teeth, some of which were taxonomically identified in three distinct morphotypes of neosuchian crocodyliforms. These findings expand the Gondwanan fossil record of both spinosaurine theropods and neosuchian crocodyliforms. Despite the fragmented nature of the specimens, these new fossils allowed the characterization of their general taphonomic features with low fluvial transport of bioclast prior to the burial. The depositional paleoenvironment of the Canafistula 01 locality is compatible with the deltaic system unit, that characterizes part of the Feliz Deserto Formation during the Early Cretaceous. These fossil findings exemplify the co-occurrence of spinosaurid dinosaurs and more than one taxon of crocodyliforms in the deltaic-lacustrine paleoenvironment represented by the Feliz Deserto Formation. These new occurrences reinforce the fossiliferous potential of the Canafistula 01 locality, especially related to the paleovertebrates from the Lower Cretaceous of Brazil.

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## 1. Introduction

The Sergipe–Alagoas Basin is a marginal geological unit outcropping in Northeastern Brazil, whose origin is related to the

rifting process of the opening of the South Atlantic Ocean and the split between Africa and South America – which together formed the western part of Gondwana during the Paleozoic and Early Mesozoic (Milani et al., 1988; Campos Neto et al., 2007; Borba et al., 2011). This basin is elongated in N45°E direction, covering a total area of 53 000 km<sup>2</sup>. Approximately 25% of it is formed by onshore outcrops, which started to develop in a graben, extending across the states of Alagoas and Sergipe (Milani et al., 1988; Campos Neto et al., 2007; Kifumbi et al., 2017). Although the beginning and final

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moments of the rift phase within the basin are still controversial (Campos Neto et al., 2007), the Sergipe–Alagoas Basin preserves a detailed Jurassic–Cretaceous stratigraphy of the early rifting stages, providing clues about the rift opening and the tectonic–stratigraphic evolution during the break-up of Gondwana (pre-rift, rift and post-rift phases; Milani et al., 1988; Campos Neto et al., 2007; Kifumbi et al., 2017).

Most of the fossil record of the Sergipe–Alagoas Basin comes from post-Aptian marine stratigraphic levels (Sales et al., 2017), which includes well known ammonites (e.g., Bengston et al., 2018), gastropods (e.g., Andrade and Felix, 2012), and mosasaurs from the Upper Cretaceous levels (e.g., Bengston and Lindgren, 2005). Its Barremian assemblages contain fishes (e.g., Figueiredo, 2009; Gallo et al., 2010) and turtles (e.g., Romano et al., 2014), reported from geological units formed in a lacustrine or near-shore paleoenvironment (Campos Neto et al., 2007; Gallo et al., 2010; Garcia et al., 2018).

Until recently, little attention has been paid to the fossil vertebrates from the deltaic-lacustrine units of the Lower Cretaceous of the Sergipe–Alagoas Basin. Among those units, the Feliz Deserto Formation, possibly formed during the Berriasian–Valanginian in a deltaic-lacustrine depositional paleoenvironment (Campos Neto et al., 2007; Borba et al., 2011; Kifumbi et al., 2017), has already yielded invertebrates, lepisosteiform fish scales (Brito, 1984; Sales et al., 2017), and a recently described spinosaurid dinosaur tooth (Sales et al., 2017). Highlighting its potential to uncover Lower Cretaceous paleofaunas from the western Gondwana supercontinent.

The present contribution provides the anatomical description and taxonomic identification of new vertebrate fossils from the Feliz Deserto Formation, including crocodyliforms, represented by an osteoderm and teeth, and theropod dinosaurs, represented by an indeterminate preungual pedal phalanx and spinosaurid teeth. All described materials are from the fossiliferous locality Canafistula 01 (Sergipe State, SE-204, Japoatã Municipality). This is the second work that provides description of fossil materials from this locality. In addition, we also present a taphonomic, paleobiogeographic and paleoenvironmental characterization of the new specimens, as well as brief comments on their implications for the growing knowledge about the Lower Cretaceous paleovertebrates from the Feliz Deserto Formation.

### 1.1. Geological background

The Feliz Deserto Formation (Coruripe Group) represents an approximately 420 m of maximum thick (Borba et al., 2011; see also Campos Neto et al., 2007). It is interpreted as a deltaic-lacustrine depositional system, related to the rift stage of the Sergipe–Alagoas Basin, which was established during the first of the three tectonic events of the rift stage (Campos Neto et al., 2007; Borba et al., 2011; Kifumbi et al., 2017; Rigueti et al., 2020).

At the base of this formation, the predominant lithology is composed of fine to medium sandstones, deposited in an anastomosed fluvial channel (Kifumbi et al., 2017) with high sedimentary depositional energy. Towards the top, there is an intercalated sequence of gray to greenish claystones and fine-grained sandstones, which characterizes a lower energy lacustrine deltaic depositional paleoenvironment (Campos Neto et al., 2007; Kifumbi et al., 2017). The Feliz Deserto Formation is stratigraphically under the Barra de Itiúba Formation and superimposed on the Serraria Formation, being covered in the marginal part of the basin by the sediments of the Penedo Formation. The main outcrops are near to the geographical limits of Sergipe and Alagoas states, between the municipalities of Japoatã (Sergipe) and Igreja Nova (Alagoas) (Campos Neto et al., 2007; Borba et al., 2011). The top of the Feliz

Deserto Formation is marked by the pre-Aratu Fault, which separates this geological unit from the Barra de Itiúba Formation, forming a depositional/erosive gap of approximately 3–5 Ma (Galm and Santos, 1994; Campos Neto et al., 2007).

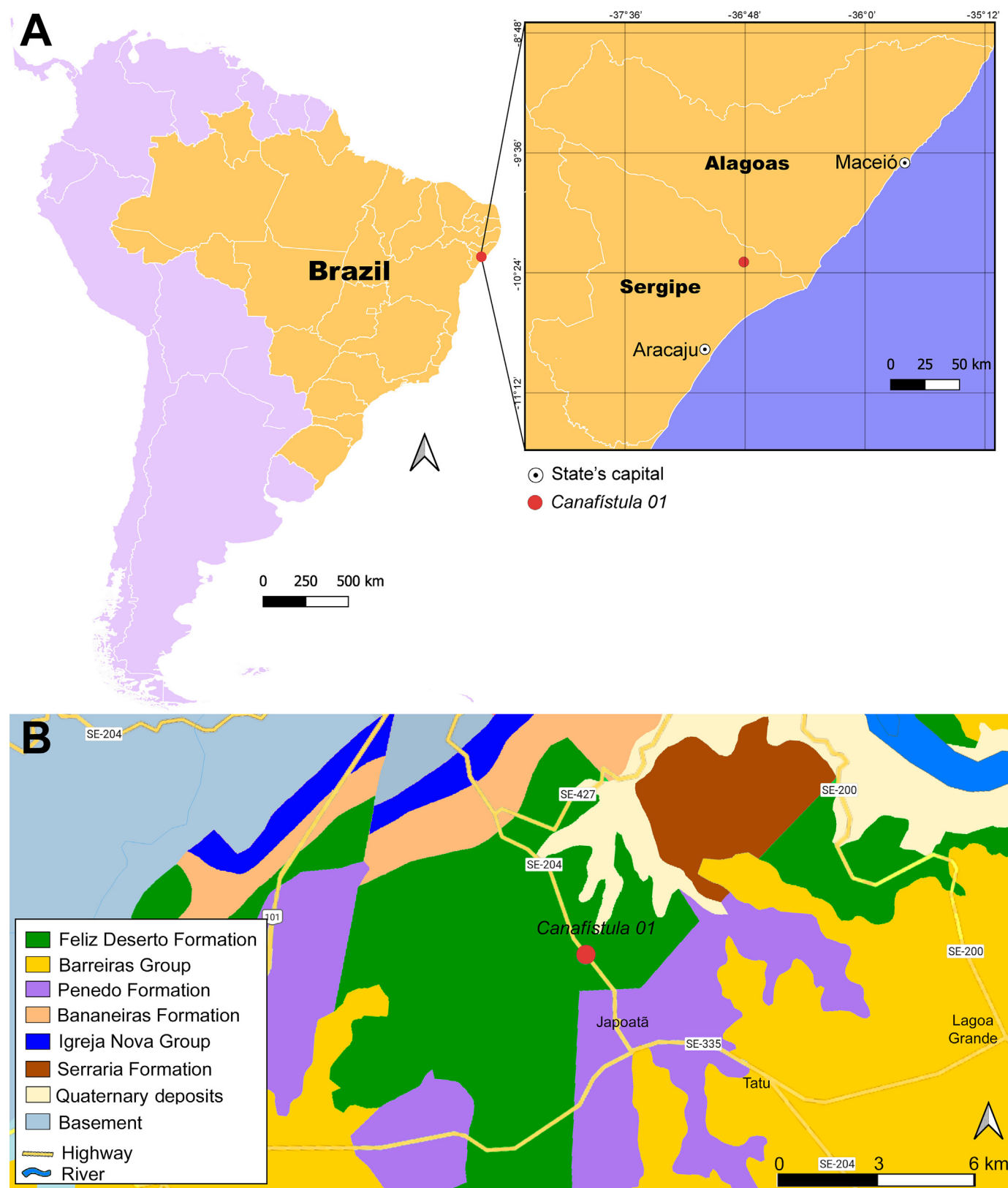
Recently, Kifumbi et al. (2017) refined the lithostratigraphic and the paleoenvironmental interpretation of the sedimentary facies. Based on lithology, sedimentary structures and paleocurrent patterns they concluded that the Feliz Deserto Formation represents a sedimentary succession, with at least four depositional facies, that can be associated with the following systems: (1) anastomosed fluvial channel, (2) floodplain – during the first stages of rifting with low tectonic activity, (3) distal delta front, and (4) proximal delta front – in a well established graben system bordering lacustrine bodies with increasing tectonic activity (Kifumbi et al., 2017). These four paleoenvironments fall into, at least, two distinct and successive depositional units, with the distal and proximal delta depositional phase being predominant in the Feliz Deserto Formation (Kifumbi et al., 2017). The Canafistula 01 fossiliferous site presented herein is geologically compatible to the facies association that represents the prodelta/distal delta front depositional paleoenvironment presented by Kifumbi et al. (2017) (further discussion below).

### 1.2. Study area

The material described here comes from Canafistula 01 site [Paleobiology Database ID 187200 (UTM DATUM WGS 84, Zone 24 L, 8 857 550 N/739 980 E, GPS error  $\pm 4$  m)], located 2 km from Japoatã Municipality, on the SE-204 highway, Sergipe State, Northeastern region of Brazil (Fig. 1).

This fossiliferous locality represents an exposure of the Feliz Deserto Formation, that we interpret as representative of its medial portion. Stratigraphically, Canafistula 01 is located midway above the fluvial Caioba sandstones – top of the Serraria Formation – and below the deltaic Pedreira Tatu sandstones, which constitute the top of the Feliz Deserto Formation (Borba, 2009). Canafistula 01 as a fossiliferous site was first reported by Sales et al. (2017), who further detailed the exposed rocks which cover ~200 m in width and a maximum height of ~6 m. Although Sales et al. (2017) indicated this outcrop on the “SE-202 Road”, in fact the location is on the SE-204 Highway. The general lithology of Canafistula 01 is composed of layers of fine sandstones (layers between ~300 and 500 mm in height) that are interbedded with fine-grained siltstones (layers of ~100 mm in height) containing numerous diminute isolated fossils, which include ganoid fish scales, small bone fragments, and teeth (Sales et al., 2017). A stratigraphic profile at the area where the fossils were recovered in this site was generated using SedLog v.3.0 program (Zervas et al., 2009) and is shown in Fig. 2A. At least three fossiliferous layers are discernible (Fig. 2A, 2B), however, at other points of the outcrop there is an increase of the fossiliferous layers, also occurring isolated teeth.

**Institutional abbreviations.** CCB – Coco Corta Barrabasa collection, Institut Royal des Sciences Naturelles de Belgique, Belgium; CPP – Centro de Pesquisas Paleontológicas “Llewellyn Ivor Price”, Brazil; DFMMh, Dinosaurier-Freilichtmuseum Münchenhagen, Germany; DGEO-CTG-UFPE – Departamento de Geologia, Universidade Federal de Pernambuco, Brazil; DGM – Divisão de Geologia e Mineralogia, Brazil; IRSNB – Institut Royal des Sciences Naturelles de Belgique, Belgium; IWCMS – Isle of Wight County Museums Services, United Kingdom; LabCEMM/PUCRS – Laboratório Central de Microscopia Eletrônica e Microanálises/Pontifícia Universidade Católica do Rio Grande do Sul, Brazil; LPUFS – Laboratório de Paleontologia da Universidade Federal de Sergipe, Brazil; MHNC – Museo de Historia Natural de Cochabamba, Bolivia; MHNM – Muséum d'Histoire Naturelle de Marrakech, Morocco;



**Fig. 1.** Map of South America (purple), highlighting the Canafistula 01 fossiliferous outcrop (UTM DATUM WCS 84, Zone 24 L, 8 857 550 N/739 980 E), Japoatã Municipality, Sergipe State, Brazil (orange) (A); Geological map indicating the outcrop location within the Feliz Deserto Formation (B).





**Fig. 2.** Canafistula 01 fossiliferous outcrop (Japoatã Municipality, Sergipe State, NE Brazil). Stratigraphic profile (A); Panoramic view of the northeastern portion of the site (B) also illustrated in Sales et al. (2017). Arrows indicate the fossiliferous layers.

MNHN – Muséum National d'Histoire Naturelle, France; MTM – Hungarian Natural History Museum, Hungary; NHMUK – Natural History Museum, United Kingdom; ONM – Museum of Geology at the Office National des Mines, Tunisia; PPC – Sahatsakhan Dinosaur Research Center of the Department of Mineral Resources, Thailand; PVL – Fundación Miguel Lillo, Argentina; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; UA – Université d'Antananarivo, Madagascar; ZIN PH – Zoological Institute of the Russian Academy of Sciences, Russia.

## 2. Material and methods

### 2.1. Studied material

All fossil specimens studied here are housed at the paleontological collection of the Laboratório de Paleontologia of the Universidade Federal de Sergipe (LPUFS), São Cristóvão, Sergipe State, Brazil. The fossil materials were collected by the LPUFS team lead by A. Liparini. Here we taxonomically identify and describe the general morphology of twenty-seven isolated fossils encompassing teeth, an osteoderm and a nearly complete phalanx, all from the same outcrop, Canafistula 01. In addition to these, a large and isolated scale of *Lepidotes* sp. (LPUFS 5902), associated with one of the teeth is included in the fossil record recovered. Some teeth were collected *in situ* (materials: LPUFS 5857, LPUFS 5858, LPUFS 5863, LPUFS 5865, and LPUFS 5866) in the uppermost exposed fossiliferous layer, which presented friable sedimentary matrix of siltstones interbedded, in some parts, with fine sandstone (Fig. 2). However, the remaining fossils described in this work have been rolled, being collected at the base of the fossiliferous locality, and the original fossiliferous layer has been lost.

For the study, when necessary, the fossils were prepared mechanically. The isolated tooth crowns and postcranial specimens described here were morphologically compared with several archosauriforms housed in different scientific institutions, allowing an adequate comparison of their morphology and enabling the systematic identifications. The species and specimens used in the comparisons are detailed in Table 1.

### 2.2. Anatomical nomenclature and dental measurements

The anatomical nomenclature of morphological structures adopted in this work for the description of teeth follows the previous terminology of Smith and Dodson (2003), Andrade et al. (2010), and dental abbreviations/measurements follows the standardization proposed by Hendrickx et al. (2015). The dental measurements defined by Hendrickx et al. (2015) and used here are exemplified in Fig. 3. Whenever possible, postcranial descriptions follow the terminology of Romer (1956), Ostrom (1969), and Tavares et al. (2015). The measurements of the specimens were performed with a digital caliper (measuring range: 0–150 mm; resolution: 0.01 mm).

### 2.3. Scanning electron microscope

The enamel of seven isolated tooth crowns LPUFS 5736, LPUFS 5739–5740, LPUFS 5743, LPUFS 5747, LPUFS 5749–5750 was observed with a scanning electron microscope (SEM). Samples were gold coated with a Q150R ES-plus coater and scanner with an Inspect F50 SEM, at the LabCEMM/PUCRS facility.

## 3. Results

### 3.1. Systematic paleontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930 (*sensu* Benton and Clark, 1988)

Crocodyliformes indet.

*Referred specimens.* LPUFS 5736; LPUFS 5738; LPUFS 5746; LPUFS 5749; LPUFS 5874; and LPUFS 5877 (Fig. 4).

*Morphological description.* The specimens vary in size (measurements are given in Table 2), but share a circular crown base and lack of denticles and flutes on the crown surface (Fig. 4).

Specimen LPUFS 5736 (Fig. 4A) is a small partial crown, lacking its apicalmost portion. In the mesial and distal planes, a poorly developed carina with diminutive apical crenulations is observed



**Table 1**

List of species and specimens used for morphological comparisons and taxonomic identification.

Clade	Species	Specimens	Reference
Crocodylomorpha	Dyrosauridae	Indet.	MHNC.14065 <sup>b</sup>
	Goniopholididae	<i>Anteophthalmosuchus</i> cf. <i>escuchae</i>	CCB-1 <sup>b</sup>
		<i>Anteophthalmosuchus epikrator</i>	IWCMS 2001.446 <sup>a</sup>
		<i>Anteophthalmosuchus hooleyi</i>	NHMK PV R 3876 <sup>a</sup>
	Indet.	<i>Siamosuchus phuphokensis</i>	IRSNB R47 <sup>b</sup>
		Indet.	PPC 1–63 <sup>b</sup>
		Indet.	ZIN PH 10/176 <sup>b</sup>
	Itasuchidae	<i>Roxochampsia paulistanus</i>	DGM 258-R <sup>a</sup> ; DGM 259-R <sup>b</sup>
	Mesoeucrocodylia	Indet.	DGEO-CTG-UFPE 6647 <sup>b</sup> ; DGEO-CTG-UFPE 6651 <sup>b</sup> ; DGEO-CTG-UFPE 6742 <sup>b</sup> ; DGEO-CTG-UFPE 8573 <sup>b</sup> ; DGEO-CTG-UFPE 8574 <sup>b</sup>
		Indet.	MTM V.97.38 <sup>b</sup>
Dinosauria	Pholidosauridae	<i>Magyarosuchus fitosi</i>	MNHN MRS 3100 <sup>b</sup>
	Indet.	<i>Elosuchus cherifiensis</i>	MNHN INA 40 <sup>b</sup>
		<i>Elosuchus felixi</i>	MNHN-kh01 <sup>b</sup>
		Indet.	ONM KAM 1 <sup>b</sup>
	Teleosauridae	<i>Sarcosuchus</i> sp.	DFMMh FV 330 <sup>b</sup>
		<i>Machimosaurus buffetauti</i>	NHMK PV R36793 <sup>b</sup> ; SMNS 55211 <sup>a</sup>
	Abelisauridae	<i>Machimosaurus</i> sp.	CPP 692 <sup>b</sup>
		Indet.	UA Bv-1265 <sup>b</sup>
	Ceratosaurs	<i>Majungasaurus crenatissimus</i>	MSNM V3664 <sup>b</sup>
		<i>Saltriavenator zanellai</i>	AODF604 <sup>b</sup>
	Megaraptora	<i>Australovenator wintonensis</i>	PVL 4822 <sup>a</sup>
	Sauropodomorpha	<i>Lessemsaurus sauropodoi</i>	USP GP/2T-5 <sup>a</sup>
	Spinosauridae	<i>Angaturama limai</i>	NHMK PV R9951 <sup>b</sup>
		<i>Baryonyx walkeri</i>	NHMK PV R9151-26 <sup>b</sup>
		<i>Spinosaurus</i> sp.	MSNM V6422 <sup>b</sup>
	Indet.	GMNH-FV. 2400 <sup>b</sup>	LPUFS 5737 <sup>a</sup>

<sup>a</sup> Specimens analyzed personally by the authors.<sup>b</sup> Specimens evaluated through bibliography.

(Fig. 4A2). These crenulations are composed only of enamel, as part of the exposed dentin is smooth (thus, they are not “true” denticles). The enamel surface is slightly irregular (Fig. 4A4). The greater crown curvature in LPUFS 5736 is present on the labiolingual plane, but a slight curvature is also seen in the mesiodistal plane (Fig. 4A3, 4A4).

LPUFS 5738 (Fig. 4B) is a partial crown lacking the cervix portion. The mesial and distal sides present a subtle carina, more evident on the distal surface in which the dentin is exposed (Fig. 4B2). The enamel was widely worn out, with only small portions appearing mainly on the labial surface and bearing an irregular texture. The labiolingual plane curvature is very subtle as well as the mesiodistal one (Fig. 4B3, 4B4). The apicalmost portion presents a large wear facet, being ~7.36 mm in diameter (Fig. 4B4, 4B5).

LPUFS 5746 (not figured) is a fragmentary crown preserving its apicalmost portion. The specimen is a small and blunt tooth, preserving most of its labial side. In the labial view, the apicalmost portion presents small enamel ornamentation, although the presence of flutes is inconclusive in this specimen. The cross section of LPUFS 5746 is circular and the enamel texture is irregular.

LPUFS 5749 (Fig. 4C) preserves the apicalmost portion of a crown without the cervix. The enamel texture has an irregular pattern. Prominent carinae are noted in the mesial and distal surfaces, with one of them exhibiting diminutive crenulations (Fig. 4C1, 4C6), which is composed only of enamel not being “true” denticles. No plane of curvature is evident on the LPUFS 5749, preventing defining properly the labial and lingual sides.

The specimen LPUFS 5874 (Fig. 4D) is an isolated crown. The base of the crown is circular in cross section (Fig. 4D6). The labiolingual curvature is the most evident and the apex of the crown has its inclination towards the lingual surface (Fig. 4D1, 4D2). A subtle mesiodistal curvature is also noted (Fig. 4D3, 4D4). The unserrated carina, present on the mesial and distal surfaces, symmetrically

divides the crown. In general, the LPUFS 5874 specimen has no ornamentation, therefore the enamel is smooth.

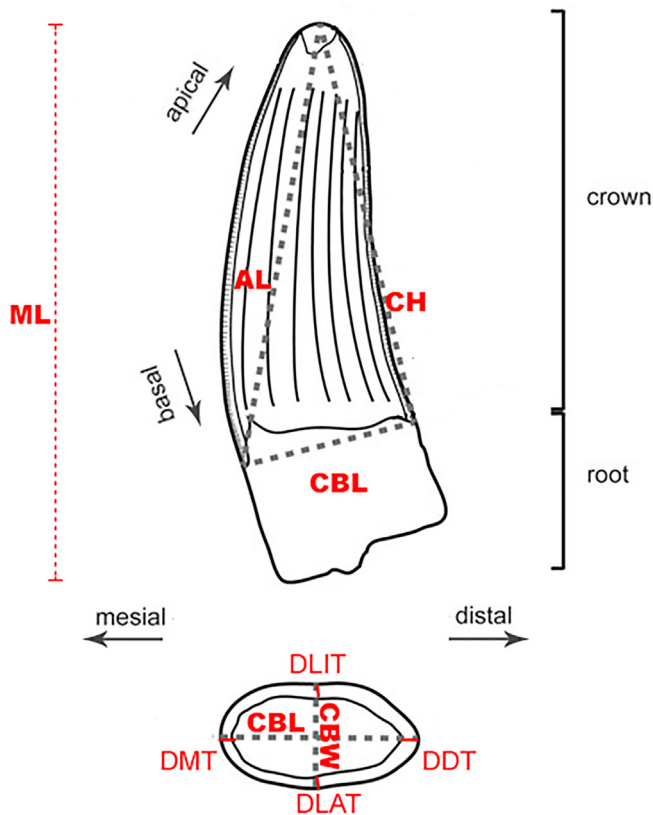
Specimen LPUFS 5877 (Fig. 4E) is a fragmented crown without the basalmost portion. The cross section of LPUFS 5877 appears to be subcircular in shape (Fig. 4E5, 4E6). A subtle unserrated carina is present on the mesial and distal surfaces, being more pronounced in the apicalmost portion of the crown (Fig. 4E1, 4E2). Most of the tooth crown is smooth and the basalmost portion preserves some macroscopic projections, which are remnants of the crown flutes. However, this is only seen clearly in a small portion of the distal side (Fig. 4E2) and is not a feature similar to other fluted crowns. Interestingly, the more pronounced flutes only at the base of the crown appear to be similar to some extant crocodylians (based on figured tooth in Ristevski, 2019, p. 11), but conservatively, we do not consider this as a key feature in identification at a less inclusive level. The enamel surface in specimen LPUFS 5877 has an irregular microscopic texture, which is distributed throughout the crown.

**Remarks.** The general morphology of these teeth (Fig. 4), which are the presence of enamel covering the entire crown, the conodont morphology, the circular shape of the basal cross section, the presence of carina in the plane of curvature, and the principal curvature of the crown being present in the labiolingual plane allow to identify these specimens as Crocodyliformes teeth (Sánchez-Hernández et al., 2007; Buffetaut et al., 2008; Sales et al., 2017; Souza et al., 2019). However, the absence of diagnostic features distinguishing these isolated teeth does not allow a more precise taxonomic determination.

Mesoeucrocodylia Whetstone and Whybrow, 1983  
Mesoeucrocodylia indet.

Referred specimen: LPUFS 5854 (Fig. 5).

**Morphological description.** The specimen LPUFS 5854 is an isolated osteoderm (Fig. 5). It has an irregular hexagonal shape (i.e., trapezoid) with 56.03 mm width of its major base and 35.20 mm length



**Fig. 3.** Dental measurements and anatomical position exemplified in a spinosaurid tooth. Anatomical abbreviations: AL – apical length; CBL – crown base length; CBW – crown base width; CH – crown height; DDT – dentin thickness distally; DLAT – dentin thickness labially; DLIT – dentin thickness lingually; DMT – dentin thickness mesially; ML – maximum length. Image modified from [Alonso and Canudo \(2016\)](#).

in its minor base. The maximum length is 47.69 mm and thickness is about 7.46 mm. The osteoderm has highly rounded edges, especially those present at its major base, in which the smaller facets have their borders diagonally to the main axis of the specimen. These rounded edges may have caused abrasion due to hydraulic transport. The best preserved side (medial/lateral) does not reveal any clues of suturing with adjacent osteoderms. The dorsal surface is strongly ornamented (Fig. 5A, 5B), composed of at least twenty-seven pits, ranging from rounded to oval in shape, some of which are quite large (e.g., 8.09 mm) and deep. The dorsal surface of the LPUFS 5854 is regular, the specimen thickness being homogeneous, with no sagittal crest or keel. The ventral surface of the osteoderm is still embedded in the rigid siltstone matrix with several minute remains of *Lepidotes* fish, which prevents the examination of foramina and other ventral features.

**Comparisons.** There is little taxonomic information to adequately identify isolated osteoderms at genus or species level ([Andrade et al., 2011](#); [Pinheiro et al., 2011](#)). With some exceptions, such as *Simosuchus* ([Hill, 2010](#)), *Montealtosuchus* ([Tavares et al., 2015](#)), *Knoetschkesuchus* ([Schwarz et al., 2017](#)), and some baurusuchids ([Montefeltro, 2019](#)), few taxa have their detailed dermal morphology described so far.

Regardless, the strongly ornamented dorsal surface composed of deep pits in LPUFS 5854 is similar to the morphology observed in mesoeucrocodylian taxa ([Pinheiro et al., 2011](#); [Carvalho et al., 2021](#)). The trapezoid shape of LPUFS 5854 is also a feature present in the mesoeucrocodylian dermal plates: according to [Pinheiro et al. \(2011\)](#) it refers to the ventral part of the body (gastral or ventral shield). Such shape of the osteoderm is also observed in some

gastral dermal plates of semiaquatic goniopholidids neosuchian such as *Anteophthalmosuchus* ([Martin et al., 2016](#); [Ristevski et al., 2018](#)), *Siamosuchus* ([Lauprasert et al., 2007](#)), as well as other undetermined goniopholidids ([Kuzmin et al., 2013](#); [Puértolas-Pascual et al., 2015](#)). In general terms, this gastral osteoderm morphology observed in LPUFS 5854 (Fig. 5) and in some goniopholidids, differs from other neosuchians such as thalattosuchians (e.g., [Ösi et al., 2018](#)), dyrosaurids ([Jouve et al., 2020](#)), and some tethysuchian pholidosaurids (e.g., [Broin, 2002](#); [Jouve and Jalil, 2020](#)). It also differs from the rectangular or oval dorsal osteoderms that are present in several crocodyliform clades (e.g., [Lauprasert et al., 2007](#); [Tavares et al., 2015](#)).

Interestingly, the nearly trapezoidal morphology of LPUFS 5854 is compatible with some of the osteoderms of the peripheral mesoeucrocodylian shield ([Martin et al., 2016](#)), differing from the dorsal osteoderms in both shape and the absence of a sagittal keel. However, several fragmented and non-diagnostic dermal plates have been reported as goniopholidids over the past years, including some dubious South American occurrences ([Andrade et al., 2011](#)). Given the absence of diagnostic features in isolated crocodyliform osteoderms ([Andrade et al., 2011](#); [Pinheiro et al., 2011](#)), the aforementioned distinctive characteristics of LPUFS 5854 allow, in a conservative manner, to identify this specimen as an indeterminate Mesoeucrocodylia, presumably a dermal plate of the peripheral or gastral shield.

Neosuchia [Benton and Clark, 1988](#)

Neosuchia indet.

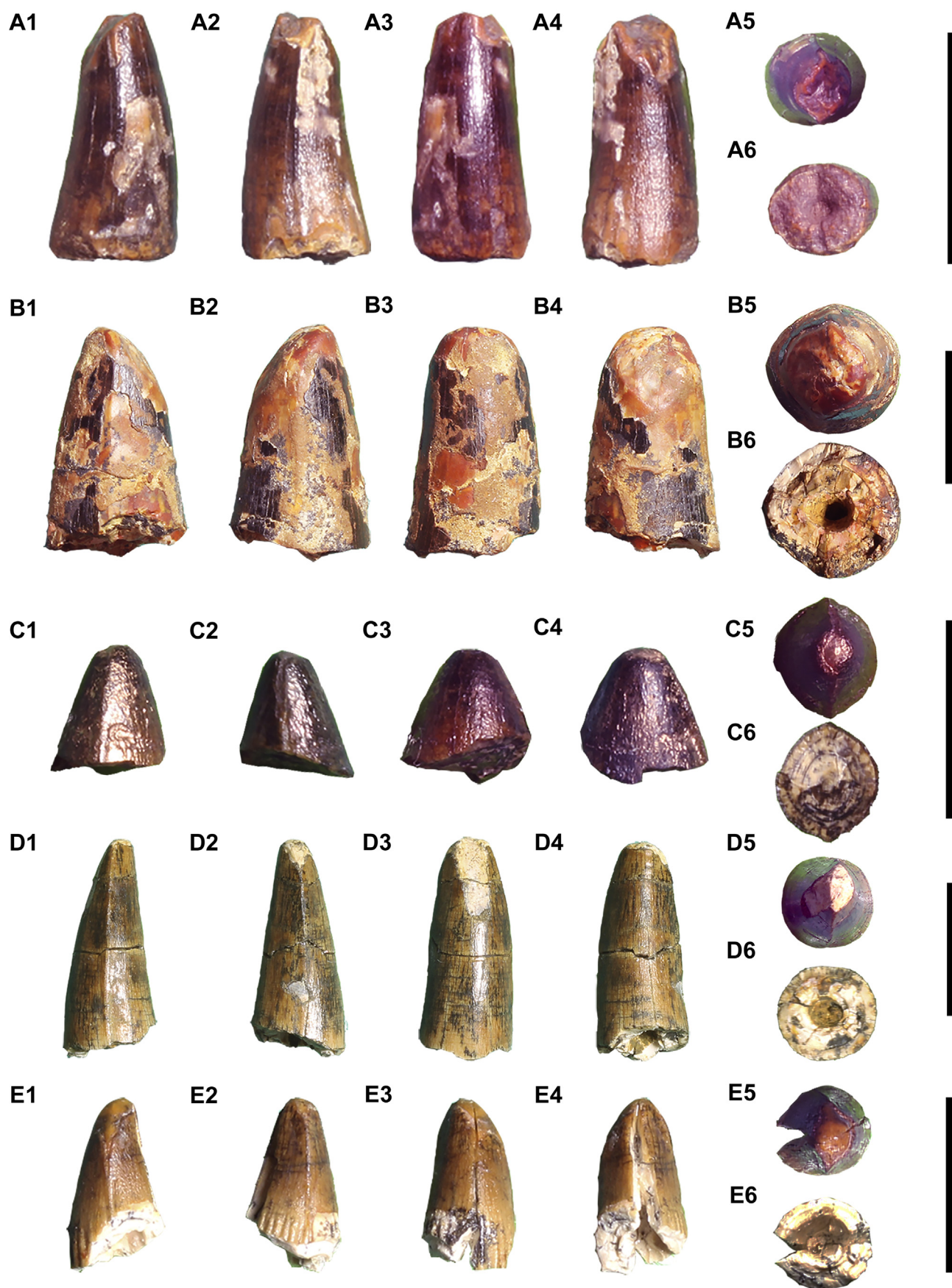
**Referred specimens.** LPUFS 5739; LPUFS 5740; LPUFS 5741; LPUFS 5743; LPUFS 5747; LPUFS 5750; LPUFS 5856; LPUFS 5857; LPUFS 5858; LPUFS 5859; and LPUFS 5876 (Figs. 6, 7).

**Morphological description.** The teeth referred to Neosuchia vary in size (Table 2) and completeness. The enamel is usually thick, getting thicker towards the apex. The crowns have apicobasal ornamentation, without denticles in the carinae (Figs. 6, 7). Three morphotypes are distinguished.

**Morphotype I.** The LPUFS 5740 (Fig. 6B) is a small crown without the cervix. It is circular in basal cross section (Fig. 6B5, 6B6). No carina is present in the specimen, although a gracile structure is observed in the apicalmost portion of the mesial and distal surface (Fig. 6B1, 6B2). The enamel is composed of several flutes, at least eight on the labial and lingual surfaces (Fig. 6B3, 6B4). However, some of them do not entirely reach the apicalmost portion of the crown, while others are distributed along the longitudinal axis (Fig. 6B4). At least some of the flutes seem to be composed of dentin. The most evident curvature of the crown is in the labiolingual plane (Fig. 6B1, 6B2). The enamel is almost smooth, but a slightly irregular texturing is seen on LPUFS 5740 surface.

Specimen LPUFS 5747 (Fig. 6E) is a blunt and completely preserved crown. The cross section is subcircular in shape (Fig. 6E5, 6E6). Only a small carina is seen in this specimen (Fig. 6E2). The surface of the crown is very ornamented, composed of several flutes, some of which being entirely distributed from the base of the crown to the apex, whereas others do not reach the apical part of the specimen (Fig. 6E3, 6E4). No curvature is seen in this specimen, preventing identification of the labial and lingual surfaces properly. However a small curve of the flutes and the pattern of the wear facet seem to demarcate the labial side (Fig. 6E2). The enamel of LPUFS 5747 is thick and the texture has a braided pattern.

LPUFS 5859 (Fig. 7C) is the tip of a crown. It has a circular outline at the base of the crown and an elliptical one at the top (Fig. 7C5, 7C6). Labiolingually there is a smooth curvature (Fig. 7C1, 7C2). Both mesial and distal sides have unserrated carinae that are more pronounced on the apical portion of the tooth (Fig. 7C1, 7C2). The surface of the LPUFS 5859 is composed of seven flutes on the labial



**Fig. 4.** Teeth of *Crocodyliformes* indet. from the Berriasian–Valanginian of Canafistula 01: LPUFS 5736 (A); LPUFS 5738 (B); LPUFS 5749 (C); LPUFS 5874 (D); LPUFS 5877 (E). Mesial view (1), distal view (2), labial view (3), lingual view (4), apical view (5), and basal view (6). Scale bars: 10 mm.



and lingual surfaces, that are irregular in size and arranged in the apicobasal orientation (Fig. 7C3, 7C4). The enamel generally has a smooth surface in LPUFS 5859. However, some portions have a regular to braided ornamentation.

**Morphotype II.** LPUFS 5739 (Fig. 6A) preserves the apicalmost portion of a crown. The specimen appears to have a circular cross section (Fig. 6A5, 6A6), however the lingual surface has a large excavated pit formed by the replacement tooth (occupying almost entirely the lingual surface, Fig. 6A4). The main crown curvature is in the labiolingual plane. There is no sign of carina composed of dentin and enamel. However, in the apicalmost portion of the LPUFS 5739, a gracile structure asymmetrically divides the crown in the mesiodistal plane, with the labial side being larger than the lingual one (Fig. 6A1, 6A2). Only the enamel of the apicalmost portion is preserved, which is marked by thirteen flutes on the labial surface (Fig. 6A3) and twelve on the lingual one (Fig. 6A4). The flutes on the labial side are exclusively composed of the thick layer of enamel, but on the lingual side some flutes appear to be also composed of dentin. The enamel texture has an irregular pattern.

The specimen LPUFS 5741 (Fig. 6C) is a completely preserved crown. The specimen has a blunt morphology with a circular shape in cross section (Fig. 6C5, 6C6). A small curvature is noted in the labiolingual plane (more evident in the crown flutes, Fig. 6C2). LPUFS 5741 does not preserve any carina, in fact there is a groove on the mesial and distal surfaces, making these surfaces slightly flatter (Fig. 6C1, 6C2). The crown is composed of several flutes formed by both enamel and dentin, which are present above the cervix to the apicalmost portion of the tooth, below an almost rounded wear facet (Fig. 6C3, 6C4). The enamel texture of LPUFS 5741 is braided.

LPUFS 5750 (Fig. 6F) is the apicalmost portion of a crown. There is no plane of curvature in this specimen, but the flutes on the surfaces show some degree of curvature, allowing to distinguish the labial and lingual surfaces. Only the mesial side preserves a diminute carina (Fig. 6F1). The flutes are well demarcated, being more spaced at the base of the crown becoming less spaced mainly in the apicalmost portion (Fig. 6F3, 6F4). A braided pattern is seen on the enamel surface of LPUFS 5750.

The specimen LPUFS 5857 (Fig. 7A) is a fragment of the apicalmost portion of a circular crown in cross section (Fig. 7A5, 7A6). The specimen is gently curved in the labiolingual plane, evidenced by the curvature of the labial side (Fig. 7A1, 7A2). Both distal and mesial carinae are conspicuous, especially in the portion immediately below to the apical wear facet of the crown (Fig. 7A1, 7A2). The enamel surface has at least thirty-two flutes, being sixteen on both labial and lingual sides (Fig. 7A3, 7A4). The flutes are regularly spaced, some of them do not reach the apicalmost portion. Close to the carinae, the flutes are obliquely oriented, while the other flutes are arranged in the apicobasal orientation. The enamel ornamentation in LPUFS 5857 is very subtle and arranged in a braided pattern.

Specimen LPUFS 5876 (Fig. 7D) is a completely preserved crown. The specimen is blunt and subcircular in cross section (Fig. 7D5, 7D6). The evident curvature is on the labiolingual plane (Fig. 7D1, 7D2). Only in the apicalmost portion of the crown in distal plane a subtle carina is noted, which does not reach the base of the crown. Similar to other described specimens, the surface of the tooth is composed of several flutes that reach the apicalmost portion of the crown (Fig. 7D3, 7D4). The enamel is texturized with a braided and almost anastomosed pattern, being more evident immediately above the cervix.

**Morphotype III.** LPUFS 5743 (Fig. 6D) is an almost completely preserved crown, lacking the apicalmost portion. A gracile carina is present on the apical region of the mesial and distal surfaces

(Fig. 6D1, 6D2), this structure being derived from a sulcus located below in the crown. Small flutes are present on the labial and lingual surfaces of LPUFS 5743, mainly in the portion above the cervix (Fig. 6D3, 6D4). The enamel surface has a smooth texture. LPUFS 5856 (not figured) is a poorly preserved crown with 27.27 mm of maximum length. Due to incompleteness, its anatomical orientation is not possible. There is no sign of preserved enamel. However, the surface of the dentin has at least seven grooves or striae, irregularly distributed along the crown surface. The dentin is also characterized by numerous tiny pits which are dispersed throughout the exposed tissue.

Specimen LPUFS 5858 (Fig. 7B) is a small crown, with an evident delimitation of the enamel by the cervix (Fig. 7B1). The apicalmost portion is broken, yet a small portion of the labiodistal wear surface is preserved. In the mesiodistal plane, LPUFS 5858 presents a very subtle curvature (Fig. 7B3), whereas the labiolingual curvature is pronounced and visible mainly on the labial surface of the crown (Fig. 7B1, 7B2). In cross section, the specimen is circular at the crown base (Fig. 7B5, 7B6). Both mesial and distal margins of the crown bear unserrated carina, except on the basalmost portions, which show short, apicobasally oriented mesiodistal grooves laterally to the carina (Fig. 7B1, 7B2). At least eight and twelve flutes are present on the labial and lingual surfaces, respectively (Fig. 7B3, 7B4). The enamel ornamentation is evident in the basal part of the crown, appearing as dense striations, with anastomosed pattern in the mid-crown portion.

**Comparisons.** All described teeth (Figs. 6, 7) have similar morphology sharing the following characteristics: enamel covering the entire dental crown, conodont morphology ranging from circular to subcircular (CBR values are given in Table 2) in cross section, presence of a carina in the principal plane of curvature, principal curvature of the crown present in the labiolingual plane, and the presence of flutes on the labial and lingual surfaces.

Notosuchian taxa with more elaborate/ornate enamel include *Sphagesaurus*, *Mariliasuchus* and *Notosuchus*, but their crown shape and the presence of ziphodont carinae clearly distinct them from the generic pattern of the teeth described. The accentuated development of ornamentation of conspicuous apicobasal flutes is limited to the Neosuchia clade, excluding Crocodylia, in addition to some groups, such as Atoposauridae, Metriorhynchidae, Dyrasauridae, Susisuchidae and Hylaeochampsidae (Andrade et al., 2010, 2011).

Furthermore, all specimens have non-serrated carinae, i.e. the non-ziphodont condition (Andrade et al., 2010). Some features such as the base of the subcircular crown in cross section, the enamel ornamentation with the presence of flutes and the irregular texture, are similar to what is known of the morphology for some goniopholidid neosuchians (Andrade et al., 2011; Kuzmin et al., 2013; Carvalho et al., 2021). However, *Goniopholis* presents finer ornamentation, without anastomose and more accentuated ramification by bifurcation of the ridges, from the middle region of the crown to the apex, which is a distinct pattern from the teeth described here. Some of these features are also observed in thalattosuchian neosuchians such as *Machimosaurus* (Young et al., 2014) and some teleosaurids, such as “*Steneosaurus*” (Foffa et al., 2015). However, these taxa differ from the material described here in having little to no curvature in the labiolingual plane and by the presence of serrated carinae, whether true or false, in addition to the apical texture of the crown (Young et al., 2014; Foffa et al., 2015). Some itasuchids such as *Roxochampsia* (Pinheiro et al., 2018) share characteristics with the material described here, however, the isolated crowns presented here also differs from this taxon due to the absence of crenulate carina and the general blunt shape of the apical portion of the crown observed in *Roxochampsia*. Peirosaurids have similar dental ornamentation. However, most of

**Table 2**

Teeth morphometrics (mm). Anatomical abbreviations: AL – apical length; CBL – crown base length; CBR – crown base ratio (CBW:CBL); CBW – crown base width; CH – crown height; CHR – crown height ratio (CH:CBL); DDT – dentin thickness distally; DLAT – dentin thickness labially; DLIT – dentin thickness lingually; DMT – dentin thickness mesially; ML – maximum length.

LPUFS specimens	AL	CBL	CBR	CBW	CH	CHR	DDT	DLAT	DLIT	DMT	ML
5736	10.69 <sup>a</sup>	5.09	1.09	5.56	10.30 <sup>a</sup>	2.02 <sup>a</sup>	–	–	–	–	11.01
5738	–	10.44 <sup>a</sup>	0.99 <sup>a</sup>	10.35 <sup>a</sup>	–	–	3.64	3.80	3.95	3.53	17.21
5739	–	8.42	0.86 <sup>a</sup>	7.31 <sup>a</sup>	–	–	2.13 <sup>a</sup>	–	–	2.45 <sup>a</sup>	14.22
5740	–	4.44 <sup>a</sup>	1.09 <sup>a</sup>	4.86 <sup>a</sup>	–	–	–	2.00	1.77	–	8.98
5741	8.22	8.84	1.08	9.62	8.30	0.93	3.85	3.67	4.05	3.41	9.15
5743	7.43 <sup>a</sup>	4.27	0.90	3.86	7.65 <sup>a</sup>	1.79 <sup>a</sup>	–	–	–	–	8.26
5746	–	6.17	–	–	–	–	–	–	–	–	7.02
5747	–	4.22	1.02	4.31	–	–	–	–	–	–	5.14
5749	–	7.51 <sup>a</sup>	0.75 <sup>a</sup>	5.68 <sup>a</sup>	–	–	–	–	–	–	7.75
5750	–	6.60 <sup>a</sup>	0.95 <sup>a</sup>	6.32 <sup>a</sup>	–	–	–	–	–	–	7.75
5855	–	16.51	0.79	13.09	–	–	5.35	5.14	4.87	5.39	22.85
5857	–	6.86 <sup>a</sup>	1.09 <sup>a</sup>	7.50 <sup>a</sup>	–	–	–	–	–	–	9.19
5858	11.78	5.55	1.08	6.04	11.81	2.12	–	–	–	–	12.44
5859	–	6.17 <sup>a</sup>	1.14 <sup>a</sup>	7.09 <sup>a</sup>	–	–	–	–	3.24 <sup>a</sup>	–	10.89
5861	–	8.18	0.83 <sup>a</sup>	6.84 <sup>a</sup>	–	–	–	–	–	–	13.67
5862	–	11.10	0.97	10.80	–	–	1.98 <sup>a</sup>	2.90	2.22 <sup>a</sup>	2.36 <sup>a</sup>	22.09
5864	–	16.52	0.81	13.44	–	–	–	–	2.15	–	36.70
5865	–	10.51 <sup>a</sup>	0.90 <sup>a</sup>	9.47 <sup>a</sup>	–	–	–	–	–	–	15.38
5872	22.49 <sup>a</sup>	10.37	0.96	10.04	23.26 <sup>a</sup>	2.24 <sup>a</sup>	3.39	3.76	3.61	4.15	29.00
5873	14.00	7.37 <sup>a</sup>	1.01 <sup>a</sup>	7.45	12.47	1.69 <sup>a</sup>	–	–	–	–	15.03
5874	–	7.88 <sup>a</sup>	1.02 <sup>a</sup>	8.04 <sup>a</sup>	–	–	2.90	2.66	3.10	2.77	18.65
5876	7.73	7.82	1.11	8.75	7.72	0.98	2.90	2.97	3.40	–	8.83
5877	–	5.33 <sup>a</sup>	1.06 <sup>a</sup>	5.70 <sup>a</sup>	–	–	–	–	–	–	10.03
5878	17.30	7.64	0.92	7.08	16.38	2.14	3.27	2.86	2.65	3.17	18.96

<sup>a</sup> Incomplete measurements.

them differ from the specimens described here in having a ziphodont dentition, although the ziphodont morphology is less evident in the anterior teeth of some taxa, such as *Pepesuchus* and *Itasuchus* (Pinheiro et al., 2018; Carvalho et al., 2021). In addition to this, the non-ziphodont dentition is also present in some pholidosaurids such as *Sarcosuchus* (Dridi, 2018; Souza et al., 2019) but accurate identification is not possible. Crown-Crocodylia teeth also do not have the type of ornamentation found in the studied teeth.

Concerning the fossil material described here, at least three morphotypes can be distinguished based on the flute morphology. Morphotype I has narrow and distant carinae/flutes being well demarcated, potentially only composed of enamel, resulting in evident functional “U”-shaped grooves between the carinae, represented by specimens LPUFS 5740 (Fig. 6B), LPUFS 5747 (Fig. 6E), and LPUFS 5859 (Fig. 7C). Morphotype II presents poorly demarcated wide carinae, possibly formed by enamel and dentin, resulting in more subtle “V”-shaped gutters at the meeting point between carinae, represented by specimens LPUFS 5739 (Fig. 6A), LPUFS 5741 (Fig. 6C), LPUFS 5750 (Fig. 6F), LPUFS 5857 (Fig. 7A), and LPUFS 5876 (Fig. 7D). Morphotype III presents poorly demarcated carinae/flutes, the base of the crown has a groove and the carinae become more developed at the apex of the crown. This morphotype is represented by specimens LPUFS 5743 (Fig. 6D) and LPUFS 5858 (Fig. 7B). In general, there are no teeth with true denticles in the mesial or distal carinae, as well as no anastomosed enamel texture in the apical region of the crown. Besides, most of the specimens present relatively thin enamel at the base of the crown, but evidently thicker in the apical region.

The three morphotypes aforementioned have generic features that can be considered similar with goniopholidids, teleosaurids and pholidosaurids crocodyliiforms (and similar to Jurassic isolated mesoeucrocodylian teeth - Carvalho et al., 2021). However, based on the distinctions previously described, we cautiously identify those specimens as indeterminate Neosuchia. Based on the morphotypes, they presumably belong to more than one taxa.

Dinosauria Owen, 1842

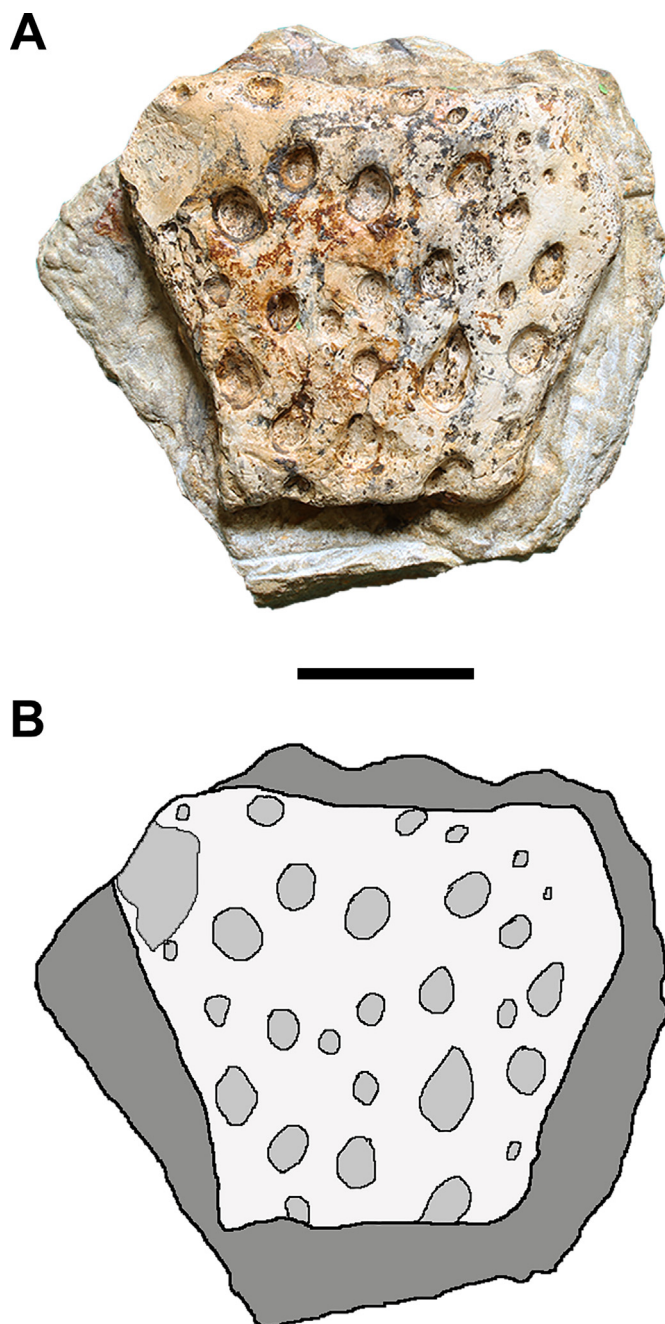
Saurischia Seeley, 1888

Theropoda Marsh, 1881

Theropoda indet.

*Referred specimen.* LPUFS 5863 (Fig. 8).

*Morphological description.* LPUFS 5863 is a proximal portion of a large left preungueal pedal phalanx (probably phalanx II–2 or III–2) (Fig. 8). The specimen is 53.14 mm in maximum length and 46.03 mm in maximum height. The proximal articulation is triangular in shape with a relatively deeply grooved ginglymus joint, presenting a medial keel between the posterodorsal and posteroventral processes, which delimits the two proximal articular surfaces (Fig. 8A, 8D, 8E, 8H). The medial surface is elliptical, whereas the lateral edge is broken, which extends to the lateral limit of the posterodorsal process (Fig. 8B, 8D, 8F, 8H), hampering description. The posteroventral process is well preserved with a flat projection forming a slightly rounded apex that extends posteriorly to the posterior limit of the posterodorsal process (Fig. 8C, 8G). On the dorsal surface of the phalanx LPUFS 5863, the posterodorsal process is quite evident; although it is more prominent than the posteroventral process, it does not project posteriorly to it (Fig. 8B, 8F). On the medial surface of the LPUFS 5863, there is a medial depression very close to the proximal portion of the phalanx, which becomes shallower anteriorly, or in the neck of the phalanx, until its medial rupture (Fig. 8D). Below the medial depression, at its ventral edge, the phalanx has at least 20 grooves that vary between ~1 and 12 mm in length, and are arranged at approximately 120° from the main axis of the phalanx (Fig. 8B, 8F). Since such grooves do not appear to be compatible with bony accidents (e.g., fleshy attachments) of pedal elements (e.g., Carrano and Hutchinson, 2002), these demarcations are considered as taphonomic feature. Interestingly, it cannot be ruled out that these grooves could be striated tooth marks produced by the crenulation of ziphodont tooth, as a result of defleshed carcasses (e.g., Rogers et al., 2003; Drumheller et



**Fig. 5.** Osteoderm of *Mesoeucrocodylia* indet. from the Berriasian–Valanginian of Canafistula 01: LPUFS 5854 (A) and corresponding interpretative drawing (B) in dorsal view. Scale bar: 20 mm.

al., 2020) or sets of parallel striations due to trampling (e.g., Behrensmeyer et al., 1986; Reynard, 2014).

**Comparisons.** The LPUFS 5863 pedal phalanx (Fig. 8) lacks the distal end. However, its proximal portion is as wide as it is high, a feature allowing to exclude its identification to a manual phalanx of a large theropod. Usually, manual phalanges in theropods tend to have the proximal surface taller than wide, as seen in ceratosaurians, such as *Saltriovenator* (Dal Sasso et al., 2018), and tetanurans, such as *Baronyx* (Charig and Milner, 1997). LPUFS 5863 shows a robust proximal joint with advanced posteroventral and posterodorsal processes, a feature observed in the pedal phalanges of saurischian dinosaurs, such as *Lessemsaurus* (Bonaparte, 1999), *Australovenator* (White et al., 2013), as well as indeterminate abelisaurids (Novas

et al., 2008). In the more proximal phalanges (e.g., II–1, III–1) of theropods (e.g., abelisaurids – Novas et al., 2008; *Australovenator* – White et al., 2013; and *Majungasaurus* – Carrano, 2007), the proximal articulation, in general, is shallower, with the medial keel absent. In the more distal phalanges beyond the medial keel, the ginglymal surface becomes deeper (e.g., Ostrom, 1969).

Based on the (1) presence of a medial keel dividing two deeply grooved surfaces (ginglymus joint), and the (2) presence and (3) robustness of the posterodorsal and posteroventral processes of the LPUFS 5863, we identified the specimen as an indeterminate Theropoda. Interestingly, the size of LPUFS 5863 is compatible with large ceratosaurians as well as early-diverging tetanurans, differing from clades of small to medium-sized theropods such as noasaurid ceratosaurians and coelophysoids, among others. However, due to the lack of diagnostic features in isolated phalanges, we prefer to maintain a more conservative identification of specimen LPUFS 5863.

Tetanurae Gauthier, 1986

Megalosauroida Fitzinger, 1843

Spinosauridae Stromer, 1915

Spinosaurinae Stromer, 1915 (*sensu* Sereno et al., 1998)

Spinosaurinae indet.

**Referred specimens.** LPUFS 5855; LPUFS 5861; LPUFS 5862; LPUFS 5864; LPUFS 5865; LPUFS 5872; LPUFS 5873; and LPUFS 5878 (Figs. 9, 10).

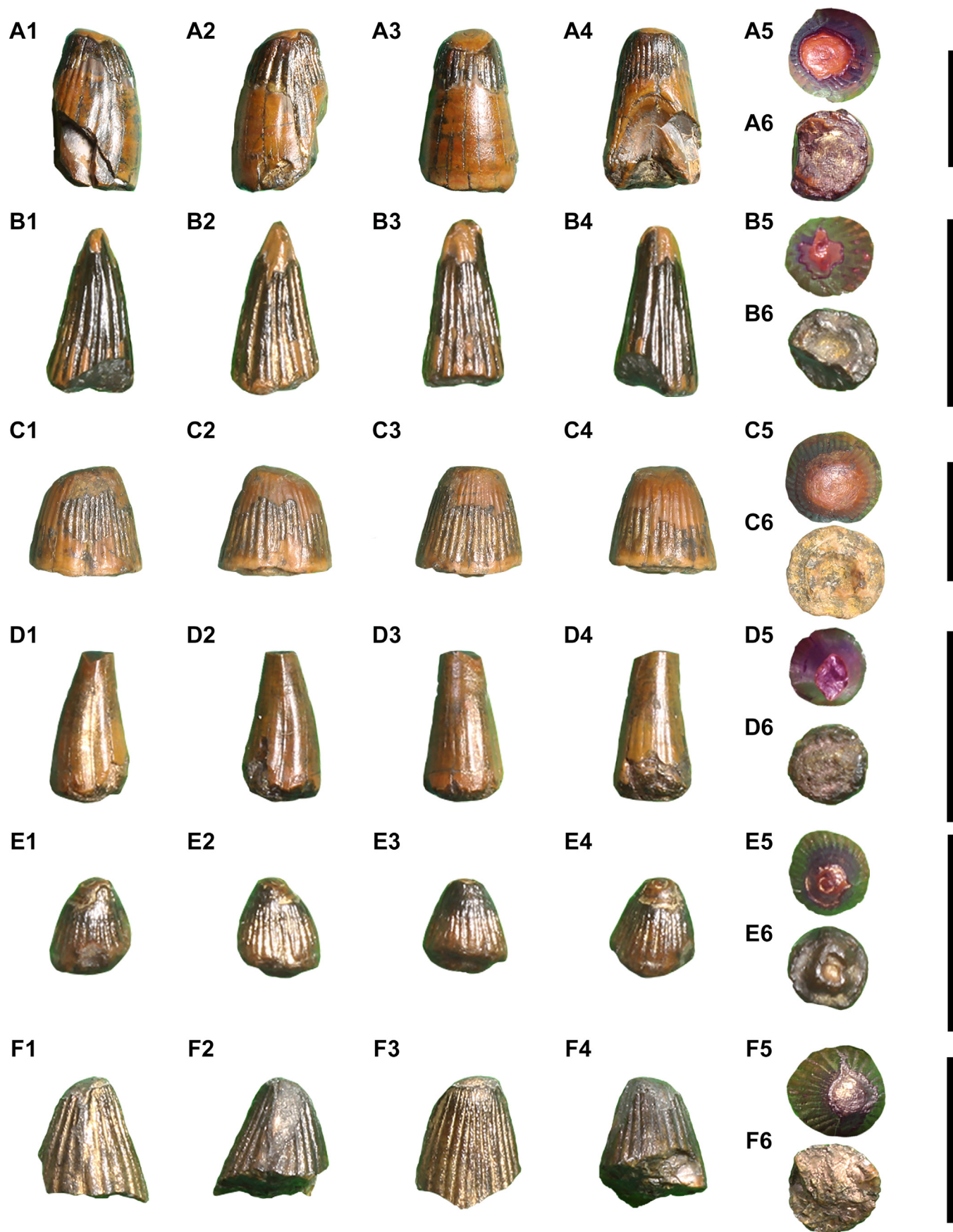
**Morphological description.** Although the specimens are isolated crowns that vary in size (Table 2), micromorphology and degree of preservation, a shared anatomical pattern can be observed, including: conodont morphology, presence of labial and lingual flutes, non-serrated mesial and distal carinae, veined (anastomosed) enamel texture, and carinae reaching the cervix/root (Figs. 9, 10).

LPUFS 5855 (Fig. 9A) is an isolated and large partial tooth, with only the crown base preserved. The most evident curvature is in the mesiodistal plane, being more evident in the mesial surface (Fig. 9A3). In cross section, LPUFS 5855 is subcircular, being slightly flattened in the labiolingual portion at the base of the crown (Fig. 9A6), whereas in the apicalmost portion, the cross section is semicircular (Fig. 9A5). In the mesial surface, the carina is evident only in the most basal portion of the crown, but this structure is better preserved in the distal surface, without serrations (Fig. 9A2). Taking into account the carina located at the base of the crown, they seem to subdivide the specimen symmetrically (Fig. 9A1, 9A2). On the lingual surface, which has the best preserved surface, there are sixteen flutes (Fig. 9A4), whereas the labial side bears nine regularly spaced flutes (Fig. 9A3). Small portions of the enamel are preserved, exhibiting a veined texture.

The specimen LPUFS 5861 (Fig. 9B) is a fragmented crown. At the base of the specimen, the delimitation between the crown and the root by the cervix is clearly discernible without any constriction (Fig. 9B1, 9B4). In cross section, the specimen has a subcircular shape in the base of the crown (Fig. 9B6). The mesiodistal curvature is subtle, but clearly discernible, however a even more quite subtle labiolingual curvature is also present. On the mesial side (Fig. 9B1), a well developed and unserrated carina is present. On the preserved lingual surface of LPUFS 5861, there are thirteen well arranged and spaced flutes (Fig. 9B4). The labial side is deteriorated (Fig. 9B3). The enamel is ornamented and the texture are distinct at the base, being a very irregular ornamentation with tiny veins, whereas in the most apical portion of the enamel has a texture with several canaliculi arranged in an anastomosed way, which are arranged apicobasally mainly in the flutes.

Specimen LPUFS 5862 (Fig. 9C) is represented by the basalmost part of a crown, with the region of the cervix being preserved. In





**Fig. 6.** Teeth of *Neosuchia* indet. from the Berriasian–Valanginian of Canafistula 01: LPUFS 5739 (A); LPUFS 5740 (B); LPUFS 5741 (C); LPUFS 5743 (D); LPUFS 5747 (E); LPUFS 5750 (F). Mesial view (1), distal view (2), labial view (3), lingual view (4), apical view (5), and basal view (6). Scale bars: 10 mm.

cross section, LPUFS 5862 has a circular crown base (Fig. 9C5, 9C6). In the mesiodistal plane, an accentuated curvature, especially on the mesial surface, is noted (Fig. 9C3, 9C4). Another slightly milder curvature is present in the labiolingual plane. Both distal and mesial unserrated carinae seem to divide LPUFS 5862 symmetrically (Fig. 9C1, 9C2). However, the mesial carina is better preserved. The surface of the crown is composed of irregular flutes, some of which are arranged in the apicobasal direction along the entire length of the crown. By contrast, other flutes are only present at the base of the crown, and do not reach the apicalmost portions of the preserved crown. On the labial surface, there are at least seven flutes (Fig. 9C3), whereas on the lingual side there are at least sixteen flutes (Fig. 9C4). It is interesting to note that on the lingual surface at least six of these flutes do not reach the apicalmost portion of the crown. The main texture of the enamel is quite anastomosed.

LPUFS 5864 (Fig. 9D) is a partially preserved tooth. It has basically the crown and a small part of the root, lacking its apicalmost portion. Both tooth broken surfaces from apical and basal region are oblique in relation to the main axis of the specimen (Fig. 9D3). The cross section from both the crown and the preserved part of the root has a subcircular shape (Fig. 9D5, 9D6). A slight mesiodistal curvature is observed in the crown region, especially on the mesial surface which is better preserved (Fig. 9D4). In the labiolingual plane, another even smoother curvature is observed in LPUFS 5864. The margin of the mesial surface has a well developed carina that extends from the cervix to the preserved apical margin of the tooth (Fig. 9D1). However, there is a wear mark on the outer margin of the carina, especially in the apicalmost portion of the crown, forming a large wear facet. In the region immediately above the cervix, in the mesial side, the carina is well preserved, making the absence of serrations evident. In the distal margin of the LPUFS 5864, there is no clear evidence of the presence of a carina, although the wear of the enamel at the base of the cervix suggests the presence of an anatomical delimitation of the carina (Fig. 9D2). Except at the distal margin of LPUFS 5864, the enamel is well preserved and has a veined texture, consisting of multiple tiny anastomosed ridges. The tooth surface has several flutes; on the lingual surface, which is better preserved, it is possible to count twelve flutes (Fig. 9D4), while in the labial view there are only two flutes that are demarcated in the dentin (below enamel wear) (Fig. 9D3). The flutes are almost equally spaced, and extend from the cervix to the preserved apicalmost region. In the labiodistal portion of LPUFS 5864, there are two lingual depressions, corresponding to the double tooth replacement (Fig. 9D2), which represents the typical process in spinosaurids (Lacerda et al., 2022). Finally, from a sagittal broken surface, it is noted that the dentin packaging occurs in at least four distinct and easily discernible layers (Fig. 9D5), which seem to be the lines of von Ebner (see Heckeberg and Rahut, 2020).

The LPUFS 5865 (Fig. 10A) specimen represents the most apical part of a crown. In cross section the specimen is subcircular (Fig. 10A5, 10A6). Both mesial and distal carinae were probably worn away (Fig. 10A1, 10A2). The preserved portion of the crown shows mesiodistal curvature and no evidence of labiolingual curvature is discernible. Therefore, the determination of which surfaces are labial and lingual is difficult, but they are tentatively inferred based on the crown flutes morphology. On the surface of the crown, one of the sides (?lingual) has nine longitudinal flutes, while on the other side (?labial) there are at least twelve flutes that are arranged regularly in the apicobasal direction (which are also visible on the dentin surface) (Fig. 10A3, 10A4). The enamel ornamentation is anastomosedly arranged. The entire apical portion of the tooth has a large wear area (Fig. 10A5). In a cross section of the basalmost portion of the crown, it is noted that the dentin packaging occurs with the distinction of at least four tissue layers (Fig. 10A6).

LPUFS 5872 (Fig. 10B) is an almost complete preserved crown with a small portion of the root. The cross section of the crown base is subcircular (Fig. 10A5, 10B6). The most evident curvature is seen in the mesiodistal plane, besides the subtle labiolingual curvature (Fig. 10B3, 10B4). The unserrated and well developed carina symmetrically divides the crown and reaches the cervix (Fig. 10B1, 10B2). The LPUFS 5872 has ten and eleven on the labial and lingual surfaces, respectively. The enamel texture has an anastomosed pattern, being more evident at the base of the crown and becoming more subtle apically.

The specimen LPUFS 5873 (Fig. 10C) is a complete crown, circular in cross section (Fig. 10C6). Similar to previous descriptions, LPUFS 5873 has a mesiodistal curvature as well as a subtle labiolingual curvature (Fig. 10C3, 10C4). The carina symmetrically divides the crown, beginning at the cervix region and reaching the apicalmost portion of the specimen (Fig. 10C1, 10C2). There are ten flutes on the labial surface of the crown and twelve on the lingual one. The enamel of specimen LPUFS 5873 is worn (Fig. 10C1, 10C4), but at the base of the crown and on the lingual side (Fig. 10C2, 10C3), the anastomosing texture pattern is evident.

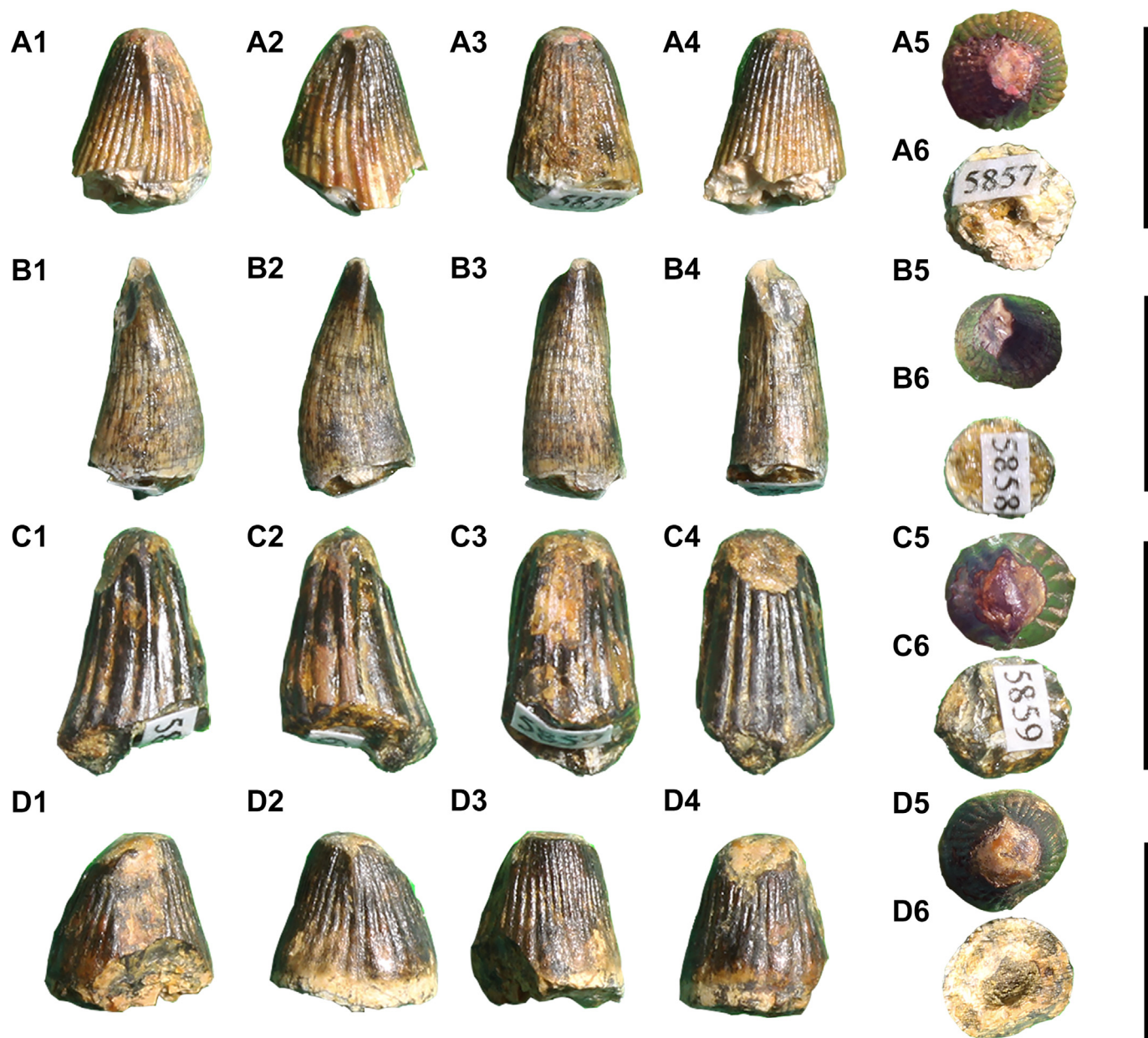
LPUFS 5878 (Fig. 10D) is an entirely preserved crown, being subcircular in cross section (Fig. 10D6). The most evident curvature is in the mesiodistal plane. The unserrated carina of the crown symmetrically divides the specimen and reaches the cervix (Fig. 10D1, 10D2), distributing ten flutes on the labial surface and ten on the lingual one (Fig. 10D3, 10D4). The enamel texture is anastomosed and this pattern is most evident just above the cervix in LPUFS 5878.

**Comparisons.** The specimens LPUFS 5855, LPUFS 5861, LPUFS 5862, LPUFS 5864, LPUFS 5865, LPUFS 5872, LPUFS 5873, and LPUFS 5878 (Figs. 9, 10) have the typical conodont morphology (conical crown and flutes distributed on the enamel surface), rather than the ziphodont morphology (narrow crown curved labiolingually and distally, serrated carinae and absence of a cervix constriction) observed in some archosaur taxa (Andrade et al., 2010; Hendrickx et al., 2015). In addition, the teeth present the mesiodistal plane as the main plane of curvature of the crown, a feature typically present in theropods (Sánchez-Hernández et al., 2007; Buffetaut et al., 2008; Sales et al., 2017).

Interestingly, the specimens LPUFS 5861, LPUFS 5862, LPUFS 5872, LPUFS 5873, and LPUFS 5878 show basal extent of the carina below the cervix (Fig. 11), which is a common feature shared among spinosaurids (Hendrickx et al., 2019). Additionally, one specimen (LPUFS 5864) has two marks of tooth replacement (Fig. 9D2), a pattern already observed in spinosaurids (Isasmendi et al., 2022; Lacerda et al., 2022). In general terms, all described teeth share the morphology of flutes and enamel texture similar to spinosaurids, such as *Angaturama* (Kellner and Campos, 1996), *Spinosaurus* (Hasegawa et al., 2010; Hendrickx et al., 2015) and the indeterminate spinosaurine from the same locality and previously described (Sales et al., 2017). In contrast to baryonychine spinosaurids such as *Baryonyx* (Charig and Milner, 1997) and *Iberospinus* (Mateus and Estraviz-López, 2022), the teeth presented here lack the denticles in the mesial and distal carinae, which is a discernible feature shared among spinosaurines (Serenó et al., 1998; Hendrickx et al., 2015; Alonso and Canudo, 2016). Besides, the overall texturization of the enamel of the described specimens is anastomosed, which seems to be a common feature in spinosaurines (Hendrickx et al., 2019).

Based on the conodont morphology, the mesiodistal plane of curvature, the veined/anastomosed texture of the enamel covering the entire crown, the presence of mesial and distal carinae that reaches the cervix at the base of the crown, and the distribution of flutes in the labial and lingual planes, it is safe to assign the aforementioned specimens to spinosaurids. Moreover, the presence of non-denticulated carinae allows us to attribute the specimens to indeterminate Spinosaurinae.





**Fig. 7.** Teeth of *Neosuchia* indet. from the Berriasian–Valanginian of Canafistula 01: LPUFS 5857 (A); LPUFS 5858 (B); LPUFS 5859 (C); LPUFS 5876 (D). Mesial view (1), distal view (2), labial view (3), lingual view (4), apical view (5), and basal view (6). Scale bars: 10 mm.

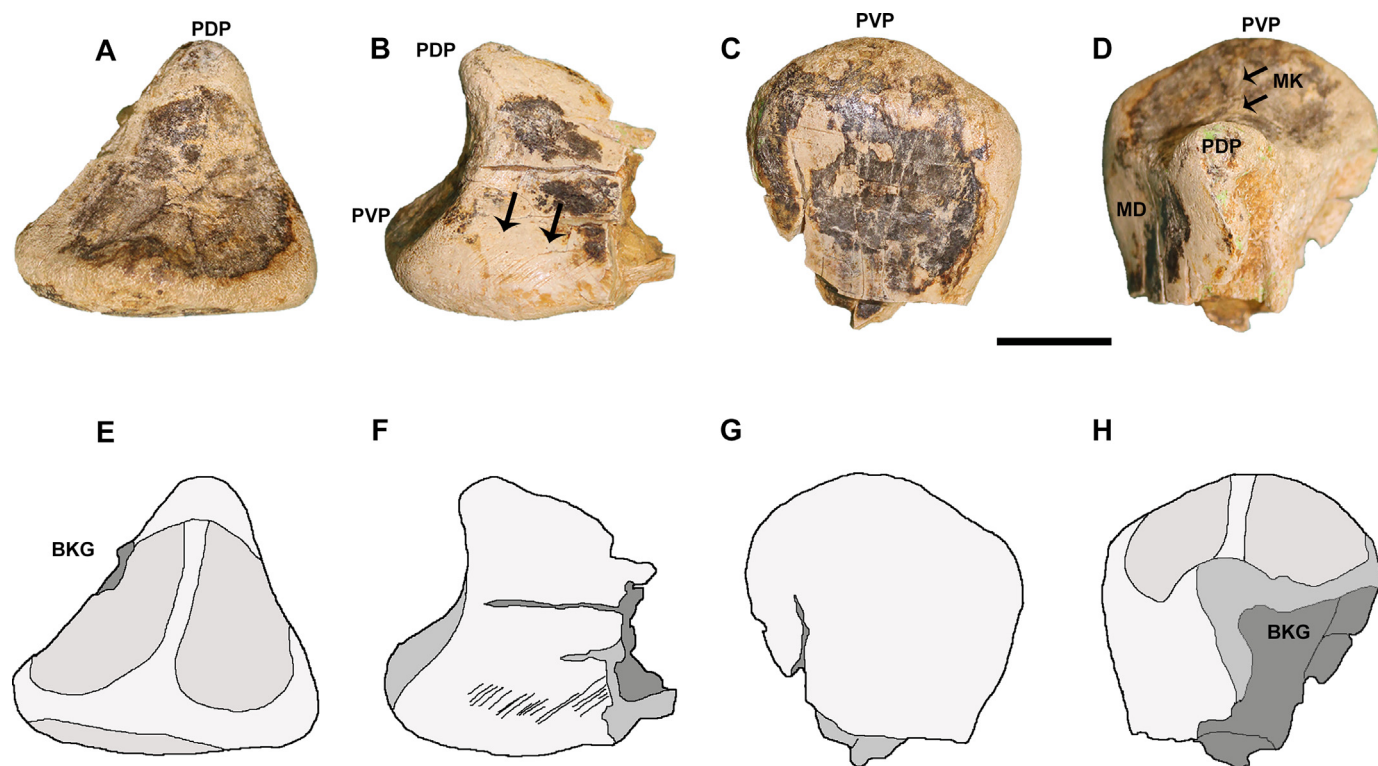
### 3.2. Taphonomic characterization

The studied sample comprises twenty-five isolated teeth (mostly composed of the crown - LPUFS 5736, LPUFS 5738–5741, LPUFS 5743, LPUFS 5746–5747, LPUFS 5749–5750, LPUFS 5855–5859, LPUFS 5861–5862, LPUFS 5864–5865, LPUFS 5872–5874, LPUFS 5876–5878), an isolated osteoderm (LPUFS 5854) and an isolated pedal phalanx (LPUFS 5863). There are also several scales of ganoid fish, of various shapes and sizes. Most of these scales have smooth edges, with a smooth layer of ganoine (a hypermineralized tissue distinct from the “true” enamel - [Schultze, 2016](#)) and the presence of surface cracks, probably caused by the fragmentation of the material after the fossil diagenesis. A large ganoid scale (LPUFS 5902) was associated with the medium-grained sandstones present at the base of the tooth root of the

spinosaurid LPUFS 5864 specimen. In addition, part of the rocky matrix composed of fine sandstones interbedded with siltstones associated with osteoderm LPUFS 5854, preserved at its base several ganoid scales (some semi-articulated) and small bone fragments, exemplifying the mixing of bioclasts in processes prior to burial.

From the imaged sample of the seven isolated crocodyliform crowns (LPUFS 5736, LPUFS 5739–5740, LPUFS 5743, LPUFS 5747, LPUFS 5749–5750) observed with a scanning electron microscope, at least six crowns show short, generally straight and unbranched marks without preferential orientation ([Fig. 12A, 12C, 12D](#)). On some specimens, they are parallel or sub-parallel ([Fig. 12A](#)), while they combined different orientations on other specimens ([Fig. 12C, 12D](#)). The broken regions mainly affected the apex ([Fig. 12E, 12F](#)), or apex and average height of the crown ([Figs. 6, 9, 10](#)).





**Fig. 8.** Phalanx of Theropoda indet. from the Berriasian–Valanginian of Canafistula 01, photos (A–D) and corresponding interpretative drawings (E–H): LPUFS 5863 (A, E) proximal view; (B, F) medial view; (C, G) ventral view; (D, H) dorsal view. Scale bar: 20 mm. Anatomical abbreviations: BKG – breakage; PDP – posterodorsal process; PVP – posteroventral process; MD – medial depression; MK – medial keel.

## 4. Discussion

### 4.1. Taphonomy

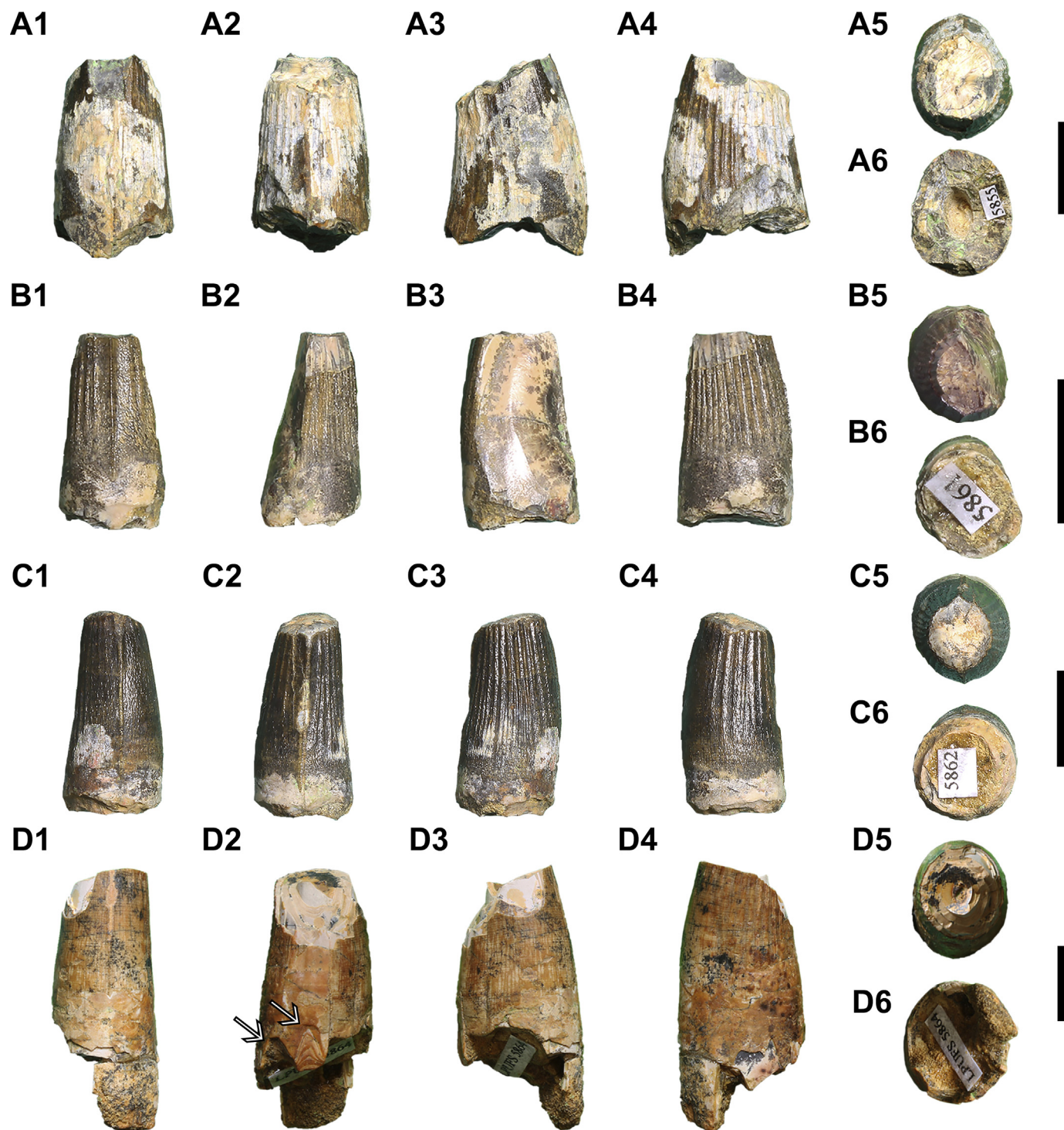
The described fossil material is generally small, ranging from 5.14 mm for the smallest specimen (LPUFS 5747) to 36.70 mm for the largest specimen (LPUFS 5864), regarding the most representative records, which are isolated tooth crowns. The largest specimen described here are the phalanx (LPUFS 5863 - 53.14 mm) and the osteoderm (LPUFS 5854 - 56.03 mm) (Table 2). The discrepancy in size of both bone elements compared to dental ones has been interpreted as a result of hydraulic equivalence between bone and dental tissues. Indeed, the lower densities of the former makes the deposition of larger bone elements simultaneously with teeth of smaller sizes possible in the same hydraulic regime (Behrensmeyer, 1975).

Generally, the fossils are usually very fragmented; for example teeth do not have the root preserved in its entirety. The prevalence of tooth crown preservation has been attributed to the presence of a harder component, enamel, combined with the fact that they are less hollow than the roots, which have no enamel and thinner walls, with a larger internal cavity. Those features make the tooth crown more resistant to breakage, increasing its potential for preservation (Enax et al., 2013). In addition, all material described here have sharp broken edges without sign of abrasion, expected if long to moderate transport in a fluvial system had occurred. Besides that, the external surface of the fossils is well preserved, which is an evidence for the absence of expansive recrystallization process during the fossil diagenesis, and thus the original bioclast structure is preserved (see different fossilization modes in Holz and Schultz, 1998).

In most cases, the teeth observed with SEM (e.g., Fig. 12F) present apical breaks that do not correspond to the type of mark expected as a result of the fracture *in vivo*, during the feeding process (=spalling), with conchoidal fracture of apicobasal orientation originated from occlusal impact. Instead, there were “sharp corner” fractures, perpendicular to the crown orientation, more consistent with side impact damage and/or crushing subsequent to loss of the crown. However, concerning the specimens LPUFS 5739 (Fig. 6A), LPUFS 5747 (Fig. 6E), and LPUFS 5750 (Fig. 6F), the apex loss is associated with a roundness that may result from *in vivo* use, consistent with the feeding of hard items, such as chelonivorous feeding.

Regarding spinosaurid teeth, although they both have enamel, dental macrostructure and similar composition with crocodyli-forms teeth (Kundanati et al., 2019), it is interesting to note that the relative time of tooth formation is short, and replacement rates are relatively faster when compared to other large theropod dinosaurs (Heckeberg and Rauhut, 2020) in addition to double tooth replacement (Lacerda et al., 2022). These features generally helps to explain the abundance of spinosaurid remains in Mesozoic assemblages (e.g., Heckeberg and Rauhut, 2020).

Finally, the general shape and arrangement of break marks, as well as the transport marks on the surfaces of the crocodyli-form crowns (Fig. 12A, 12C, 12D) is congruent with a moderate transport of the material in a fluvial system, due to few surficial alterations (Dauphin, 2022). However, there is no evidence of marks, on the surface of the crowns, caused by long distances transporting, and the pre-burial exposure time should not have been long due to absence of weathering and the general well preservation of the tooth crown surfaces. Nevertheless, the association of the material with rapid burial event(s) can be excluded due to the notable presence of breakages and transport marks mentioned above.



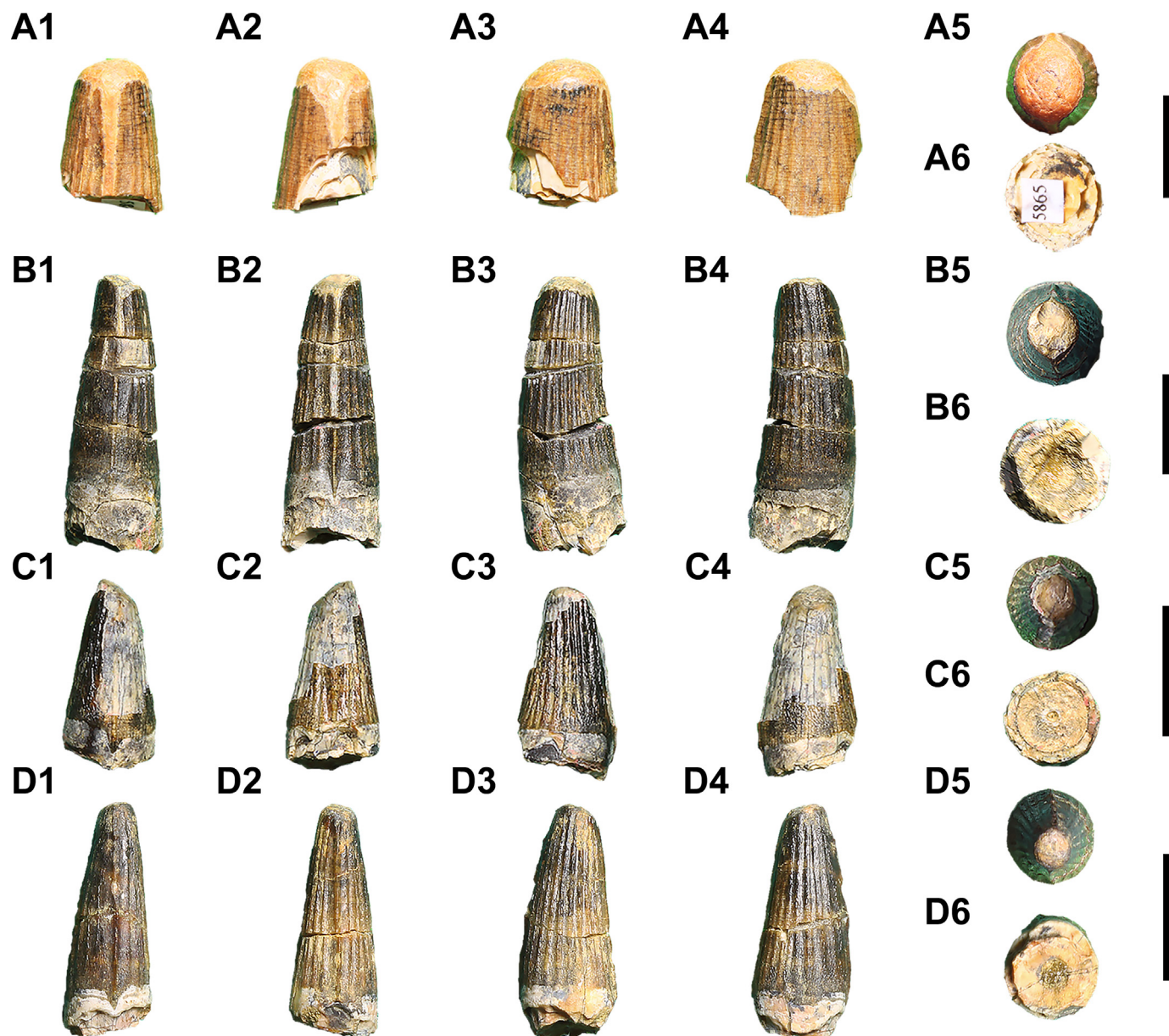
**Fig. 9.** Teeth of Spinosaurinae indet. from the Berriasian–Valanginian of Canafistula 01: LPUFS 5855 (A); LPUFS 5861 (B); LPUFS 5862 (C); LPUFS 5864 (D). Mesial view (1), distal view (2), labial view (3), lingual view (4), apical view (5), and basal view (6). Arrows indicate the double mark of tooth replacement. Scale bars: 10 mm.

#### 4.2. Paleoenvironment and paleoecology of the Canafistula 01 locality

The interpretation of the depositional environment of the Feliz Deserto Formation, according to Kifumbi et al. (2017), is systematized in at least four depositional facies, which occur in the following paleoenvironments: (1) anastomosed fluvial channel, (2) floodplain, (3) distal delta front, and (4) proximal delta front.

Interestingly, these paleoenvironments fall into at least two distinct and successive depositional units during the rifting stages, with the distal/proximal deltaic depositional phase predominant in the stratigraphy of Feliz Deserto Formation (Kifumbi et al., 2017). The geology of the prodelta/distal delta front deltaic phase of the Feliz Deserto Formation is characterized by the abundance of mudstones interbedded with fine polymodal-oriented sandstones, indicating the deposition of sediments in a system of quiet waters with





**Fig. 10.** Teeth of Spinosaurinae indet. from the Berriasian–Valanginian of Canafistula 01: LPUFS 5865 (A); LPUFS 5872 (B); LPUFS 5873 (C); LPUFS 5878 (D). Mesial view (1), distal view (2), labial view (3), lingual view (4), apical view (5), and basal view (6). Scale bars: 10 mm.

periodic entry of sand, coming from different portions of the sedimentary basin (Kifumbi et al., 2017).

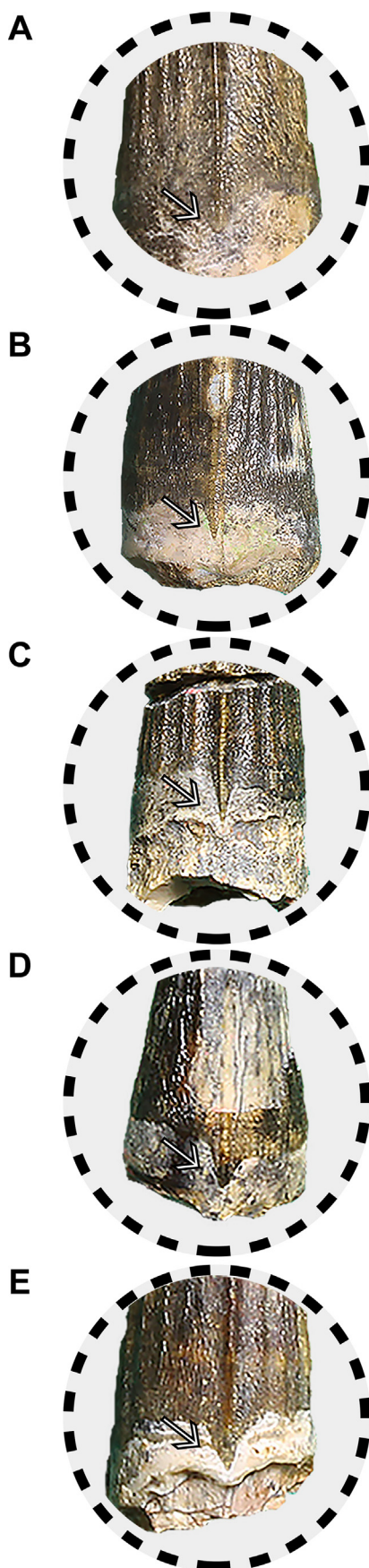
The deltaic depositional paleoenvironment seems to be predominant in the studied locality, based on its general lithological features (see section 1.1; Fig. 2; and Sales et al., 2017). Thus, Canafistula 01 appears to be an accumulation of bioclasts in a deltaic paleoenvironment, with the potential to reveal a great amount of biological information from the Lower Cretaceous of Brazil, adding more scientific information related to the paleodiversity of the Feliz Deserto Formation (Fig. 13).

Based on the previous occurrence of spinosaurid (Sales et al., 2017) and the descriptions provided in this work, it is possible to trace a faunal association for Canafistula 01 which in turn extends to the Feliz Deserto Formation. Based on the occurrences (Table 3), it is noted that crocodyliforms make up a large part of the studied assemblage, followed by spinosaurids theropods (Fig. 13). Another

relevant element in this scenario are the *Lepidotes* fishes (Brito, 1984; Sales et al., 2017). Similar fossiliferous assemblages are common in the literature (e.g., Fanti et al., 2014) and are mainly related to estuarine or coastal paleoenvironments. Moreover, spinosaurids theropods are recognized as semiaquatic animals that spend much of their time in the water feeding on fish (Charig and Milner, 1997; Dal Sasso et al., 2005; Amiot et al., 2010; Sales et al., 2016).

In this context, spinosaurids appear to have been important components, as well as crocodyliforms, in the food web of the large deltaic system of the Lower Cretaceous that is preserved in the Feliz Deserto Formation (Fig. 13). Spinosaurids and crocodyliforms are two potential predatory competitors, both of which have the potential for a generalist diet, but with a direct influence of the semiaquatic fauna. Nonetheless, Kundanati et al. (2019) investigated mechanical properties of the teeth of spinosaurid theropods





(*Suchomimus*) and pholidosaurid crocodyliforms (*Sarcosuchus*), and found that the teeth of spinosaurids are less rigid (lower elasticity), more prone to wear, yet stronger when compared to the teeth of pholidosaurids. It is worth noting that the results may be evidence of an actual biological signal which implies that both taxa adopted different strategies processing food, or the result from distinct taphonomic processes on both material (Kundanati et al., 2019). Even though, if the results indicate different feeding strategies between spinosaurids and crocodyliforms, this suggests potential clues to understand if there was some degree of niche partitioning (Kundanati et al., 2019) which can help to expand the paleoecological interpretations about the Canafistula 01 locality.

#### 4.3. Paleodiversity and paleobiogeography of the Lower Cretaceous Feliz Deserto Formation fauna

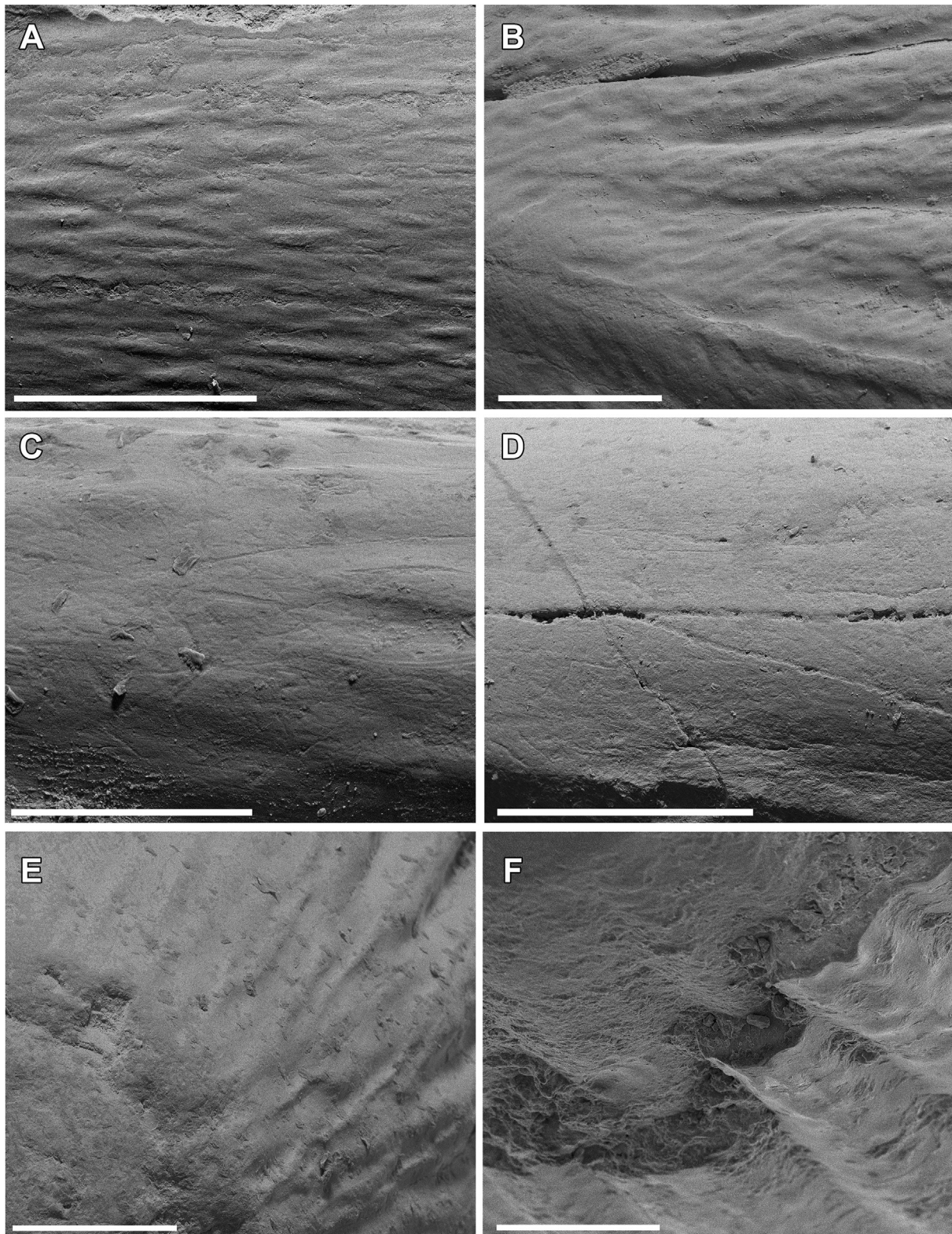
The fossil record of Crocodylomorpha in Brazil is quite representative, with at least 50 species recovered from different regions in a temporal range from the Triassic to the present day (Cidade et al., 2019; Carvalho et al., 2021). The most evident mesoeucrocodylian fossil record from Brazil is from the Upper Cretaceous (Santonian to Maastrichtian) of the Bauru Basin (Candeiro and Martinelli, 2006) revealing a significant diversity. Meanwhile, the Upper Jurassic and Lower Cretaceous crocodyliform records are still less representative than the Upper Cretaceous occurrences, although research is increasing (e.g., Fortier and Schultz, 2009; Montefeltro et al., 2013; Souza and Campos, 2018; Souza et al., 2019; Carvalho et al., 2021).

The material described in this work, although not systematically identified at less inclusive levels due to the fragmented nature of the fossils, includes important Lower Cretaceous Gondwana occurrences, due to the paucity of the fossil record (Salisbury et al., 2006). The described material of crocodylomorphs can be distinguished into at least three morphotypes of teeth attributed to Neosuchia as well as remains of an indeterminate crocodyliform specimens and an indeterminate mesoeucrocodylian, which suggests that more than one crocodyliform species inhabited the deltaic system of the Feliz Deserto Formation during the Early Cretaceous (Fig. 13).

The presence of non-Crocodylia Neosuchia in the Gondwanan sedimentary deposits is limited, which justifies the predominant interpretation of the group as a Laurasian lineage with a late dispersal to the southern hemisphere (see Salisbury et al., 2006; Montefeltro et al., 2013). However, regarding the evolution of Eusuchia, the probable origin of the group is considered to be Laurasian, although some paleobiogeographic inferences for the clade do not consider some Gondwanan fossil material (Salisbury et al., 2006). In addition, taxa from South America and Australia are growing indicators that point to a neosuchian–eusuchian transition in Gondwana landmasses (Salisbury et al., 2006), or even reinforces the hypothesis of a cosmopolitan distribution of the clade during the Early Cretaceous (Montefeltro et al., 2013). Thus, these new crocodyliforms findings from the Feliz Deserto Formation shed light on both the paleobiodiversity recovered from this formation and the paleogeographical distribution of crocodyliforms. The new material amplifies the occurrences of crocodyliforms in western Gondwana, as well as the number of crocodyliforms assemblages from the Lower Cretaceous of Brazil.

Similarly, the fossil record of spinosaurids in South America comes from several localities in northeastern Brazil (e.g., Kellner

**Fig. 11.** Carina extending beneath the cervix in teeth of Spinosaurinae indet. from the Berriasian–Valanginian of Canafistula 01, indicated by arrows: LPUFS 5861 (A); LPUFS 5862 (B); LPUFS 5872 (C); LPUFS 5873 (D); LPUFS 5878 (E). Out of scale.



**Fig. 12.** Teeth of *Crocodyliformes* indet. from the Berriasian–Valanginian of Canafistula 01 under SEM. Enamel ornamentation and transport marks near the base of the crown in LPUFS 5736 (A), scale bar: 1 mm; Enamel ornamentation near the crown apex in LPUFS 5739 (B), scale bar: 1 mm; Enamel ornamentation and transport marks in the mid-crown of LPUFS 5740 (C), scale bar: 300 µm; Enamel ornamentation and transport marks in the mid-crown of LPUFS 5743 (D), scale bar: 1 mm; Enamel ornamentation near to the apical wear facet of the crown LPUFS 5747 (E), scale bar: 500 µm; Apical wear facet of the crown LPUFS 5750 with apparent enamel ornamentation (F), scale bar: 500 µm.





**Fig. 13.** Early Cretaceous paleoenvironmental reconstruction of the Feliz Deserto Formation, exemplifying the deltaic depositional paleoenvironment and recording the paleovertebrate occurrences of crocodyliforms and spinosaurine theropods (art by Renata Cunha UFPR).



**Table 3**

List of paleovertebrate taxa recovered from the Lower Cretaceous of Feliz Deserto Formation (Sergipe—Alagoas Basin, NE Brazil).

Clade		Material	Specimens	Reference
Actinopterygii	<i>Lepidotes</i> sp.	Scale	Unnumbered LPUFS 5902	Cited by Brito (1984); Sales et al. (2017) This work
Crocodylomorpha	Crocodyliformes indet.	Tooth	LPUFS 5736; LPUFS 5738; LPUFS 5746; LPUFS 5749; LPUFS 5874; LPUFS 5877	This work
	Mesoeucrocodylia indet.	Osteoderm	LPUFS 5854	
	Neosuchia indet.	Tooth	LPUFS 5739; LPUFS 5740; LPUFS 5741; LPUFS 5743; LPUFS 5747; LPUFS 5750; LPUFS 5856; LPUFS 5857; LPUFS 5858; LPUFS 5859; LPUFS 5876	
Dinosauria	Spinosauridae indet.	Tooth	LPUFS 5737	Sales et al. (2017)
	Spinosaurinae indet.	Tooth	LPUFS 5855; LPUFS 5861; LPUFS 5862; LPUFS 5864; LPUFS 5865; LPUFS 5872; LPUFS 5873; LPUFS 5878	This work
	Theropoda indet.	Phalanx	LPUFS 5863	

and Campos, 1996; Medeiros et al., 2014; Sales et al., 2017). Based on our observations, the materials described here can be attributed to Spinosaurinae, which is the only spinosaurid clade recorded in Brazil to date. Also, the previous record (Sales et al., 2017) allied to the descriptions of this work represent the oldest Gondwanan spinosaurine theropods.

It is interesting to note that, according to the hypothesis of Sereno et al. (1998), the initial distribution of spinosaurids was cosmopolitan, with later vicarious and dispersal events from Laurasia. Recently, a biogeographic model proposed by Barker et al. (2021) suggests the origin of the group in the Laurasia landmasses as later dispersion pulses to Gondwana. However, the material described allied with previous material (Sales et al., 2017) may suggest alternative events to explain the biogeography of the group, since it demonstrates that spinosaurines were already present in the South American portion of Gondwana during the Berriasian–Valanginian. Thus, the new findings support the great fossiliferous potential and, hence, scientific relevance of the study area as a window to the Lower Cretaceous. Representing additional material of the oldest Gondwanan spinosaurids, it likely correspond to an important place and moment of the evolution and diversification of the spinosaurine clade in South America.

## 5. Conclusions

We described here twenty-seven isolated fossil specimens from the Lower Cretaceous Feliz Deserto Formation, including an indeterminate theropod preungual pedal phalanx and seven isolated teeth of spinosaurine theropods. These fossils complement the oldest Gondwanan records of this clade from South America. In addition, the first crocodyliform record from this formation is presented, referring to an isolated osteoderm and eighteen isolated teeth, some of which having been taxonomically classified as non-crocodylian neosuchians. These fossils extend the group's occurrence toward the western portion of the Gondwana landmasses. The depositional paleoenvironment of the Canafistula 01 locality represents a deltaic system unit, that characterized part of the Feliz Deserto Formation during the Early Cretaceous. The taxa presented here exemplify the co-occurrence of spinosaurids and more than one taxon of crocodyliforms in this paleoenvironment. These occurrences reinforce the fossiliferous potential of the studied area, Canafistula 01, located in Sergipe State, especially concerning paleovertebrates from the Lower Cretaceous of Brazil.

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