



A microvertebrate assemblage from the Adamantina Formation (Bauru Group, Upper Cretaceous) in São Paulo State, Brazil

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ABSTRACT

The Adamantina Formation is the most extensive and taxonomically rich unit within the Bauru Group (Upper Cretaceous). This unit is considered one of the most complete fossil records of vertebrate continental communities during the Cretaceous Gondwanan landmasses. However, this important fossil record is mainly based on large and articulated remains, and few works attempted to better understand its microvertebrate assemblages. This study reports a diverse microvertebrate assemblage from a new site in the Adamantina Formation in São Paulo, Brazil. The geological context in which the fossils were collected was analyzed, and all fossils were recovered in channel facies of the outcrop. The fossil assemblage described here includes elements commonly found in previous works in the Adamantina Formation, such as lepisosteiforms, amiids, dinosaurs, and crocodyliforms. But in this assemblage were also identified elements rarely recovered from Adamantina Formation, such as siluriforms, anurans, and a putative mammal. Furthermore, the taxa identified here indicate a humid environment, contributing to recognizing a diversity of paleoenvironments in the Adamantina Formation and highlighting the importance of microvertebrate assemblages to understanding the paleoecological aspects of fossil communities.

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1. Introduction

The Adamantina Formation (sensu Batezelli, 2017) is the most extensive, better-explored, and taxonomically richest unit of the Bauru Basin. Yielding one of the best-known Mesozoic continental paleofauna of South America (Fig. 1) and one of the most important Upper Cretaceous vertebrate assemblages worldwide, it offers a unique window to the Cretaceous faunal composition of south-western Brazil (e.g., Price, 1950; Bertini et al., 1993; Zaher et al.,

2003; Candeiro and Martinelli, 2006; Kellner et al., 2006; Montefeltro et al., 2011; Bittencourt and Langer, 2011; Marsola et al., 2014; Castro et al., 2018; Pinheiro et al., 2018; Alves et al., 2019, 2021; Brito et al., 2020; Fachini et al., 2020; Darlim et al., 2021). The study of that rich fossil record is, however, focused on larger and articulated specimens (Bandeira et al., 2018), whereas microvertebrate assemblages, i.e., those composed by a multi-individual concentration of skeletal material in which 75% or more of the elements are 5 cm in maximum dimension (sensu Eberth et al., 2007) tend to be neglected.

Microvertebrate remains are commonly found in bonebeds, where the accumulated skeletal remains are usually disarticulated

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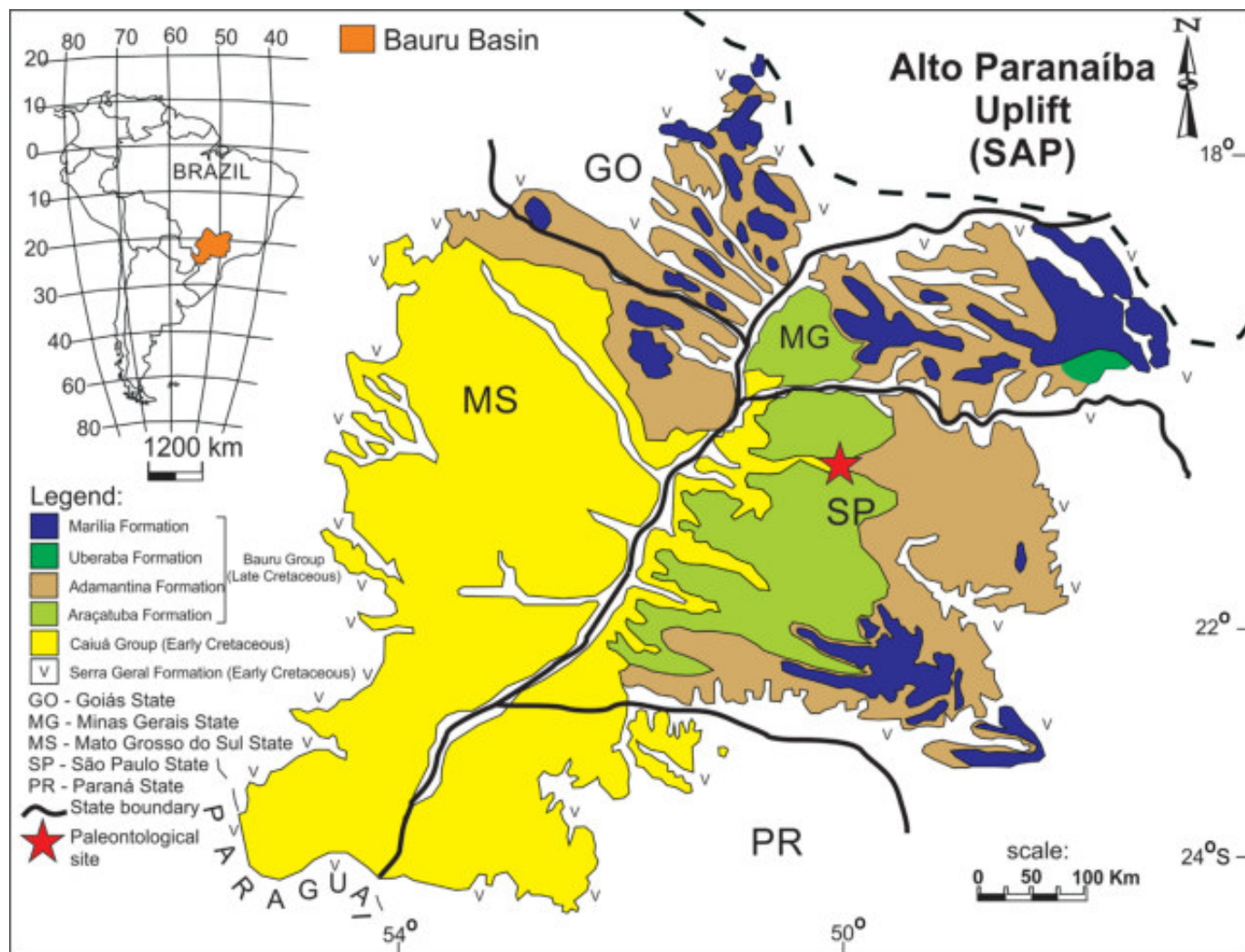


Fig. 1. Lithostratigraphic map of the Bauru Basin and study area in Auriflama City (After Batezelli et al., 2019).

and incomplete (Schiebout, 1997; Rogers and Kidwell, 2007; Rogers and Brady, 2010). Despite the inherent preservational biases of the microvertebrate fossil record, such assemblages tend to reveal rarer occurrences when compared to the record of more complete and articulated specimens (Wings et al., 2016; Alves et al., 2016; Castro et al., 2018). Therefore, such data is crucial for a more comprehensive understanding of any geological unit's diversity, paleoecology and correlation (Kaye and Padian, 1994). Here we describe fossil remains recovered from a new microvertebrate locality of the Adamantina Formation in São Paulo state, Brazil, dominated by semiaquatic taxa and provide new insights into this geological unit's fauna and depositional environment.

2. Geological settings

The Bauru Basin in southeastern Brazil covers an area of up to 370,000 km², including western Paraná, western São Paulo, northeastern Mato Grosso do Sul, south of Mato Grosso and Goiás, and western Minas Gerais (Fig. 1). The basin was formed during the Late Cretaceous by flexural subsidence akin to uplifts in the central-eastern portion of South America. Those uplifts resulted from the Trindade Mantle Plume (Gibson et al., 1995; Batezelli, 2017), and the current configuration of the Bauru Basin is related to Paleogene erosion.

In western São Paulo State, the Bauru Basin includes the Araçatuba, Adamantina (or Vale do Rio do Peixe sensu Fernandes and Coimbra, 2000), and Marília formations. Based on stratigraphic data, paleontological and radiometric dating, Batezelli (2017) proposed the chronostratigraphic column presented in Fig. 2.

The fossils described in this work were collected from an outcrop of the Adamantina Formation (Bauru Group) between the Tietê and São José dos Dourados rivers, at Km 84 of SP-463 road in the municipality of Auriflama, São Paulo, Brazil (20° 55'21.7''S, 50° 26'46.1''W, Figs. 1–2). The outcrop bears three facies associations: Channel (CH), Floodplain (OF), and Aeolian (Ae) (Figs. 3–7) (Tables 1 and 2).

The Channel facies association (CH facies) consists of clast and matrix-supported conglomerates (Gt facies) and yellowish, coarse to fine-grained sandstones, reaching a maximum thickness of three meters (Fig. 4). The conglomerates are composed of sub-angular to sub-rounded clay clasts, with diameters varying from 5 to 35 cm. The sandstones are well-sorted, formed by sub-rounded quartz grains, with trough cross-stratification (St facies) (Figs. 4–5). All the fossils were collected in the Channel facies association.

The Floodplain facies (OF facies) association overlays the channel deposits as a layer of greenish to greyish, massive mudstones with root marks. The mudstone facies (Fm facies) appear as lenticular bodies on the top of the channel deposits or as a three meters-thick tabular layer (Figs. 1 and 6).

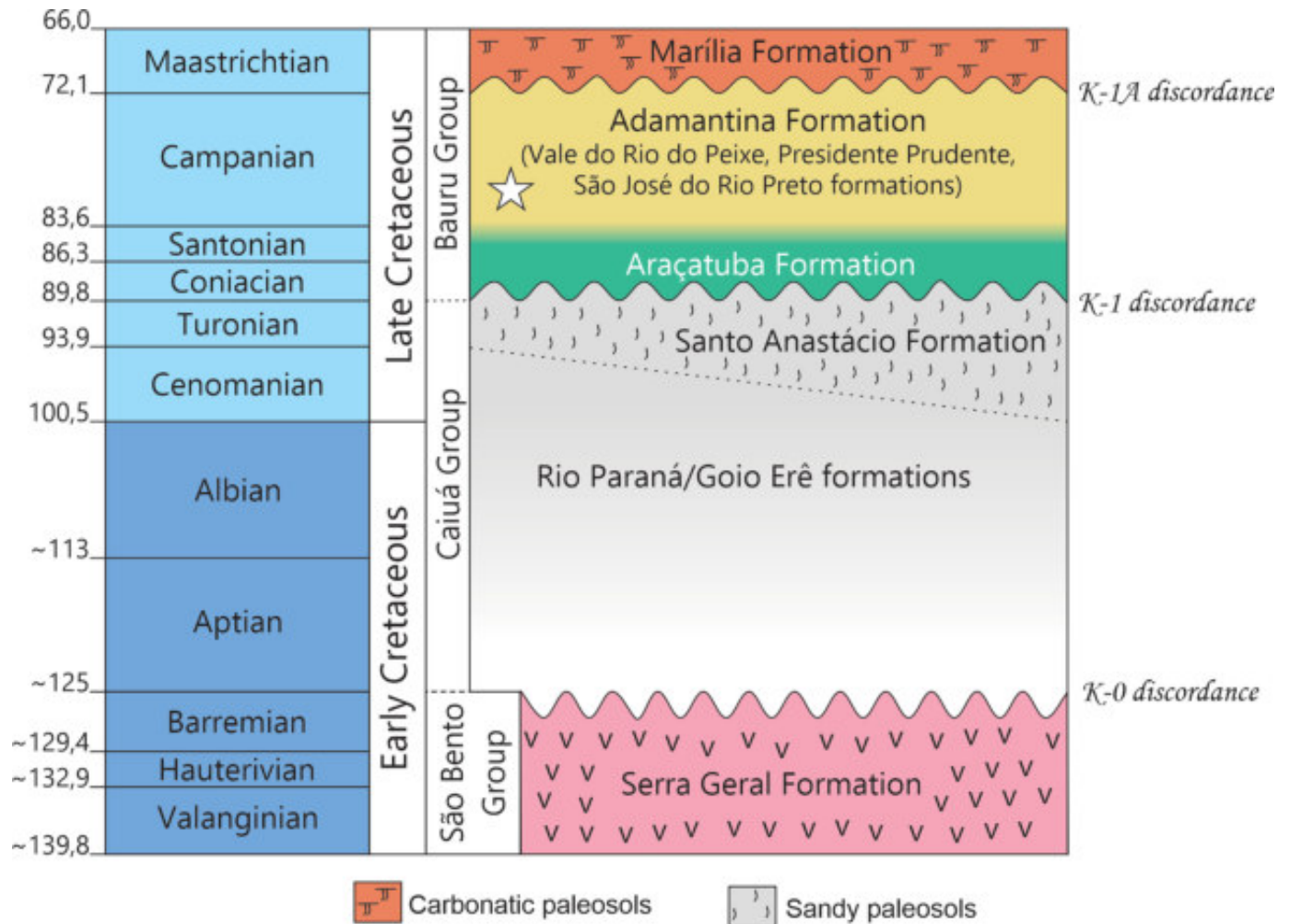


Fig. 2. Chronostratigraphic chart of the Cretaceous sequence in southern Brazil. The white star indicates the stratigraphic unit of the sampling site (After Langer et al., 2022).

Aeolian facies association is at the top of the outcrop, composed of two 1.5 m thick layers of very fine to fine, well-sorted sandstones, whitish to yellow, with low angle cross-bedding, inclined to up to 5° with up to 3 m long foresets (Facies St) (Figs. 1–7).

Facies analyses identified processes that suggest the interaction between rivers and aeolian dunes, probably in a fluvial environment under a semi-arid climate. For example, the basal conglomerate layer grading to sandstone indicates subaqueous flows with a gradual decrease in energy and is responsible for building the sand sheet bodies (Miall, 2014). In addition, the facies distribution in the study area, concave-up geometry, and depositional architecture indicate the presence of unconfined fluvial deposits (Fisher et al., 2007; Davidson et al., 2013).

Previous works in the same area revealed paleocurrents indicative of north-to-southwest sediment transport (Fernandes and Magalhães-Ribeiro, 2015; Batezelli, 2017). The depositional model proposed here is similar to that of Fernandes and Magalhães-Ribeiro (2015) and Batezelli et al. (2019), with significant changes from north to south of the Bauru Basin, including a decrease in grain size in the deposits, changes in the size and architecture of the channels and high dispersion of paleocurrents. For these authors, such characteristics define the evolution of an alluvial system dominated by braided rivers (sensu Stanistreet and McCarthy, 1993) or a distributive fluvial system (sensu Hartley et al., 2012).

The Aeolian facies association overlays the floodplain deposits indicating the interaction between fluvial deposits and small aeolian dunes fields. The characteristics of this facies association suggest deposition by the wind on a flat surface above the fluvial deposits. Aeolian facies in the Adamantina Formation were first described by Fernandes (1998, see also Fernandes and Coimbra, 2000, Fernandes et al., 2003, Fernandes and Magalhães-Ribeiro, 2015). Fig. 8 illustrates the reconstructed paleodepositional environment of the site.

3. Material and methods

The fossils were excavated inside the rock matrix from the outcrop and later mechanically removed in the Laboratório de Paleontologia e Evolução de Ilha Solteira (LAPEISA). They were prepared with the aid of appropriate pneumatic pens (Paleotools®) and pin vices. The fossils were coated with Paraloid (B72) before and after the removal from the rock matrix. The most relevant specimens were photographed with a Leica S8APO stereomicroscope. We also took images of specimens with a Zeiss EVO® LS 15 Scanning Electron Microscope (SEM) at the Scanning Electronic Microscopy Laboratory of São Paulo State University (UNESP). The specimens analyzed under SEM were coated with gold in a Quorum Q150T. The fossils are housed at the LAPEISA, Department of Biology and Animal Science of UNESP, Ilha Solteira, SP, Brazil. The

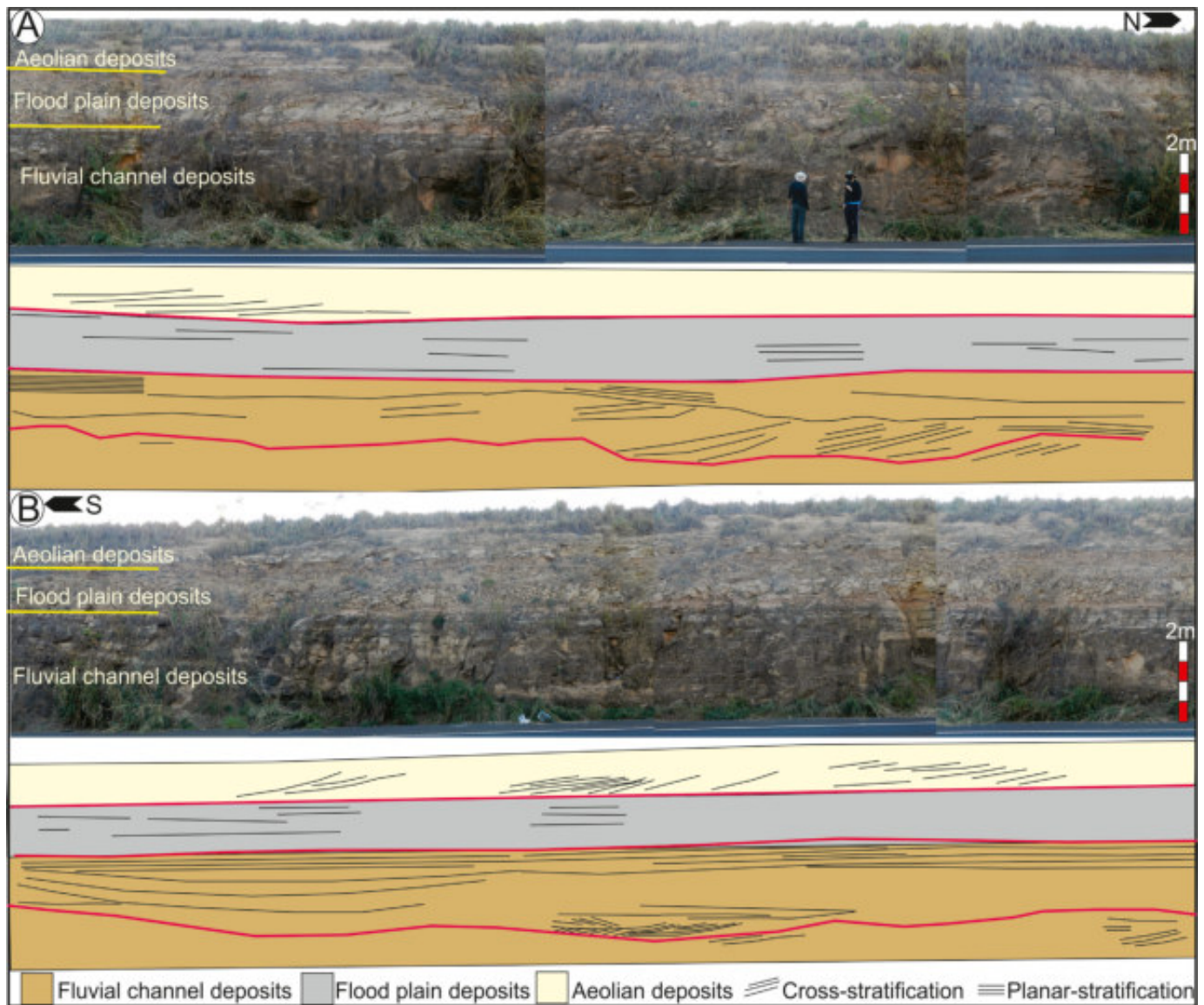


Fig. 3. Panoramic view of the outcrop in Auriflama city (Road SP-463, Km 84). A and B correspond to the north and south part of the outcrop.

specimens were identified based on comparisons with living and fossil species and with data from the literature.

4. Results

Osteichthyes Huxley, 1880
 Actinopterygii Woodward, 1891
 Lepisosteiformes Hay, 1929
Atractosteus Rafinesque, 1820

Material: isolated scales and teeth (LAPEISA-Pal 0005P, LAPEISA-Pal 0005Q, and LAPEISA-Pal 0005R, Fig. 9A–C).

Most of the microvertebrates collected in this new outcrop are represented by 200+ partial or complete ganoid scales attributed to *Lepisosteiformes* (Fig. 9B–C). The scales are lepisosteoid-type like others found in the Bauru Group (Martinelli and Teixeira, 2015; Alves et al., 2016, 2021), varying in size from 0.5 to 2 cm. Several teeth attributed to the clade were also found (Fig. 9F–G). These have a conical shape and longitudinal ridges in the basal portion,

associated with plicidentin, and an acrodine cap covering the most apical region of the crown (Fig. 9A).

The species *Lepisosteus cominatoi* was described for the Adamantina Formation (Silva Santos, 1984) and later reported by Gayet and Brito (1989) and Bertini et al. (1993). However, Alves et al. (2016) argued against such identifications, suggesting that none of the fossils mentioned in those studies allows classification to the species level. Based on scale and tooth samples from the same outcrop, Alves et al. (2021) attributed the scales to *Atractosteus* based on the ultrastructural arrangement of the ganoin tubercles and their individual sizes (0.3–10.9 μm and 3.3–10.5 μm respectively). These parameters differ from others, such as the living *Lepisosteus*, the fossil *Paralepisosteus* and obaichthyds (Alves et al., 2021). Therefore, we extend the taxonomic assignment proposed by Alves et al. (2021) to all the lepisosteiforms found in the outcrop.

Osteichthyes Huxley, 1880
 Actinopterygii Woodward, 1891
 Amiiiformes Hay, 1929 (sensu Grande and Bemis, 1998)

Vidalamiinae Grande and Bemis, 1998

Material: isolated teeth (LAPEISA-Pal 0003A and LAPEISA-Pal 0003B Fig. 9D–E).

Two Amiiformes teeth (Fig. 9 D–E) were collected from the outcrop and identified based on comparison with living specimens of the taxon (Grande and Bemis, 1998). The teeth are triangular in labial and lingual views and have an acrodyne cap, similar to the teeth previously described from Bauru Basin (Martinelli et al., 2013; Brito et al., 2017; Cidade et al., 2022). Skeletal remains of this group were reported for the Adamantina and Marília formations and assigned to Vidalamiinae (Martinelli et al., 2013; Brito et al., 2017; Cidade et al., 2022). This is also potentially the case for the teeth described here. However, we refrained from supporting a less inclusive classification for the newly reported specimens and assigned them as Amiidae. Other Upper Cretaceous Amiiformes were recognized in Argentina (Bogan et al., 2010), Morocco (Forey and Grande, 1998), Israel (Chalifa and Tchernov, 1982), Canadian Arctic (Friedman et al., 2003), Canada (Brinkman and Neuman, 2002), United States (Brinkman et al., 2013) and Hungary (Szabó and Ósi, 2017).

Osteichthyes Huxley, 1880

Actinopterygii Woodward, 1891

Characiformes Regan, 1911

Material: Isolated scales (LAPEISA-Pal 0007B, Fig. 9F).

Four cycloid scales attributed to Characiformes were collected (Fig. 9F) and identified by comparisons with living species of the group. The association with Characiformes is based on the morphology of the scales that are circular cordate in shape, flattened in the anterior field, scalloped in the anterior margin, sinusoidal in lateral margins, flattened in the posterior field, and smooth in the posterior margin. The focus position is posterior-central, with distinct and discontinuous circuli and longitudinal radii, bearing around ten primary radii and from five to eight secondary radii (Bräger and Moritz, 2016).

Elements referred to as Characiformes have been previously reported from the Adamantina and Marília formations (Gayet and Brito, 1989; Bertini et al., 1993). Some referred elements were initially described as similar to Erythrinidae but later reassigned to Amiidae (Gayet and Brito, 1989; Martinelli et al., 2013). Alves et al. (2016) reported Halecostomi materials, assigned either to Amiiformes or Characiformes. Late Cretaceous specimens of the latter group are known from South American sites in Argentina and Bolivia (Gayet and Meunier, 2001; Gayet et al., 2001), whereas the oldest Characiformes come from the Cenomanian of Africa (Werner, 1994). Although their Gondwanan origins are suggested by molecular data (Arroyave et al., 2013; Melo et al., 2022), the group is also known in the Late Cretaceous of France (Otero et al., 2008) and Canada (Newbrey et al., 2009).

Osteichthyes Huxley, 1880

Actinopterygii Woodward, 1891

Siluriformes Hay, 1929

Material: six pectoral fin spines, one dorsal-fin spine, and twenty isolated teeth (LAPEISA-Pal 0006A, LAPEISA-Pal 0006B, LAPEISA-Pal 0006J, LAPEISA-Pal 0006D, and LAPEISA-Pal 0004A, Fig. 9G–K). Seven spines were attributed to Siluriformes, six pectoral, and the fragment of the proximal portion of a single dorsal spine (Fig. 9G–J). Additionally, twenty villiform teeth (Fig. 9G–K) were attributed to Pimelodidae. The identification was achieved based on a comparison with living species. The best-preserved pectoral fin spines have the same features described by Alves et al. (2019) for the spines identified in another site of the Adamantina Formation. They show a dorsoventrally compressed body with irregular longitudinal striations in lateral view. Its anterior ridge is smooth

without denticles, whereas the posterior denticles are set inside a longitudinal groove. The posterior denticles are compressed, enlarged, retrorse, hooked, and irregularly spaced.

Siluriformes have been previously reported in the Bauru Basin (Gayet and Brito, 1989; Bertini et al., 1993; Brito et al., 2006; Alves et al., 2016; Alves et al., 2019), which tentative taxonomical assignments include Pimelodidae (Alves et al., 2019). Pimelodidae is a typical element of the extant neotropical ichthyofauna with more complete fossils found mainly in Miocene deposits in North of South America (Lundberg, 2005; Pérez et al., 2007; Aguilera et al., 2013). The new records presented here further support a Mesozoic origin for the group, as inferred by molecular data (Hardman and Lundberg, 2006; Chen et al., 2013; Kappas et al., 2016). Alongside the specimens, Alves et al. (2019) reported the Pimelodidae teeth described here are the oldest record of this clade worldwide.

Lissamphibia Haeckel, 1866

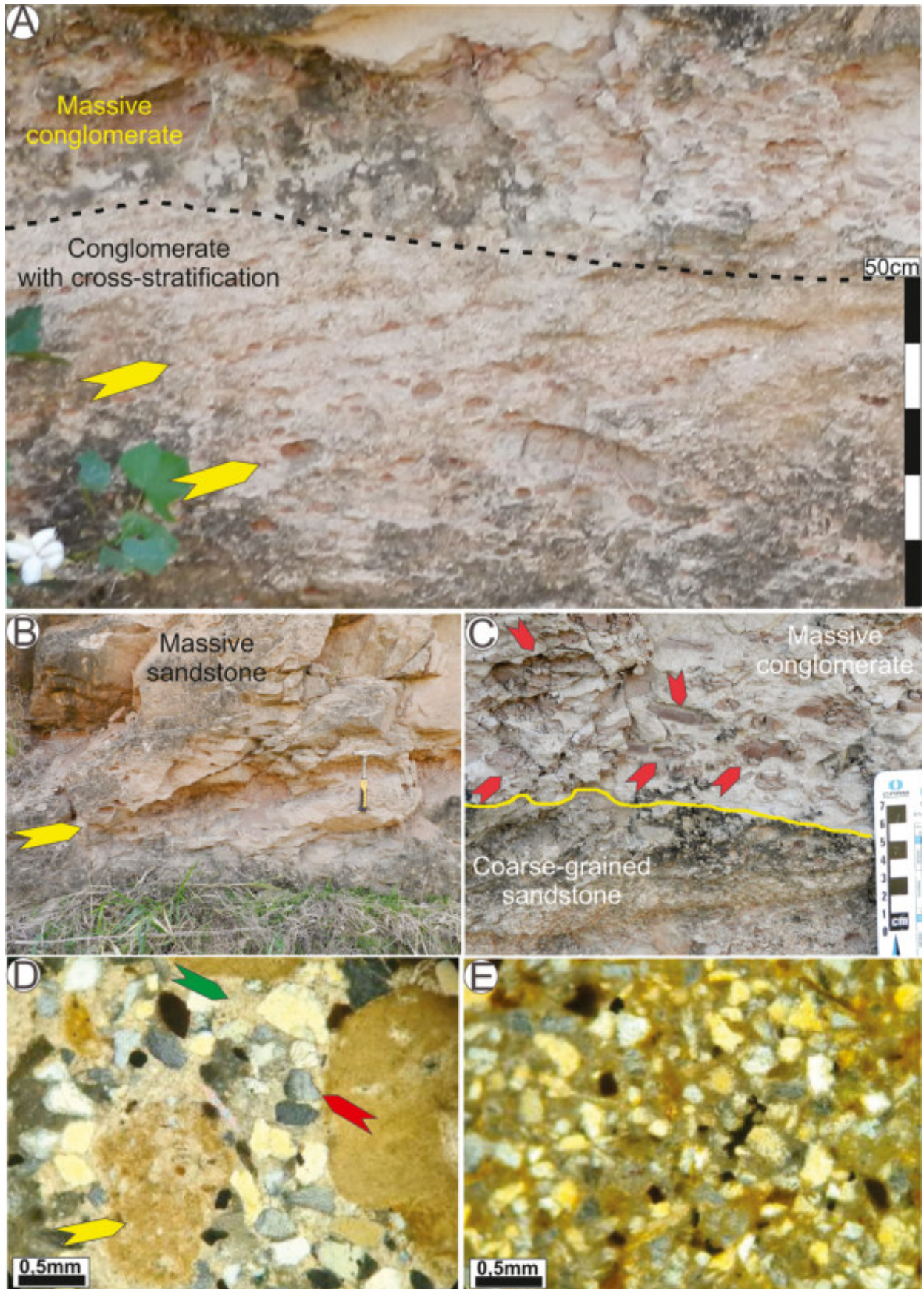
Anura Fischer von Waldheim, 1813

Neobatrachia Reig, 1958

Material: isolated left humeri (LAPEISA-Pal 0008A, LAPEISA-Pal 0008B, and LAPEISA-Pal 0008C, Fig. 10).

The humeri are robust and well-ossified. The diaphysis is slightly bowed ventrally and strongly curved laterally in the most complete specimen. It bears a well-developed deltoid crest (deltopectoral crest or crista ventralis) that extends along the proximal two-thirds of its ventral surface. The deltoid crest is flanked by a short and subtle parietal crest (crista paraventralis). The distal ends of the three humeri are uniform in their morphology. In ventral view, they bear a protuberant and rounded humeral condyle (eminentia capitata) with a diameter representing more than half the maximum distal width of the bone. The condyle is roughly aligned to the main axis of the distal portion of the diaphysis. It is unclear if LAPEISA-Pal 0008A (Fig. 10A–C) and LAPEISA-Pal 0008B (Fig. 10D–E) have a distinct ventral fossa proximal to the condyle because this area is covered by sediment in both specimens. A shallow ventral fossa is present in LAPEISA-Pal 0008C (Fig. 10F–G). The humeral condyle is bordered by prominent medial (radial epicondyle or entepicondyle) and lateral (ulnar epicondyle or ectepicondyle) epicondyles. The medial epicondyle is larger and more projected than the lateral epicondyle and almost reaches the distal margin of the humeral condyle. A shallow groove separates the tip of the medial epicondyle from the humeral condyle. The specimens lack distinct medial and lateral crests.

The material can be assigned to Anura based on the presence of an elongated diaphysis, a large and rounded humeral condyle, and a long deltoid crest (Sigurdson and Bolt, 2009). The most distinguishing feature among the fossil humeri is the strongly curved diaphysis of LAPEISA-Pal 0008A. In the basal lineages (“Archaeobatrachia”), the humeral diaphysis is typically straight or slightly curved (e.g., Ritland, 1955; Worthy, 1987; Blain and Villa, 2006; Martínez-Navarro et al., 2014; Biton et al., 2016; Gómez, 2016; Vasilyan et al., 2019). Similar strongly curved diaphyses are commonly associated with Neobatrachia clades (e.g., Keeffe and Blackburn, 2020; Muzzopappa et al., 2020; Gómez and Turazzini, 2021). In addition to the diaphysis curvature, the recovered fossils also differ from Pipimorpha, the only “archaeobatrachians” group known in the South America fossil record, in having a more prominent humeral condyle and a medial epicondyle more developed and projected than the lateral epicondyle. By contrast, in Pipimorpha, the distal end of the humerus is typically almost symmetrical, with a small humeral condyle flanked by similarly developed medial and lateral epicondyles (Báez et al., 2012a; Rage et al., 2013; Gómez, 2016). Among Neobatrachia, the fossil humeri reported here resemble the extant *Calyptocephalella*, having a



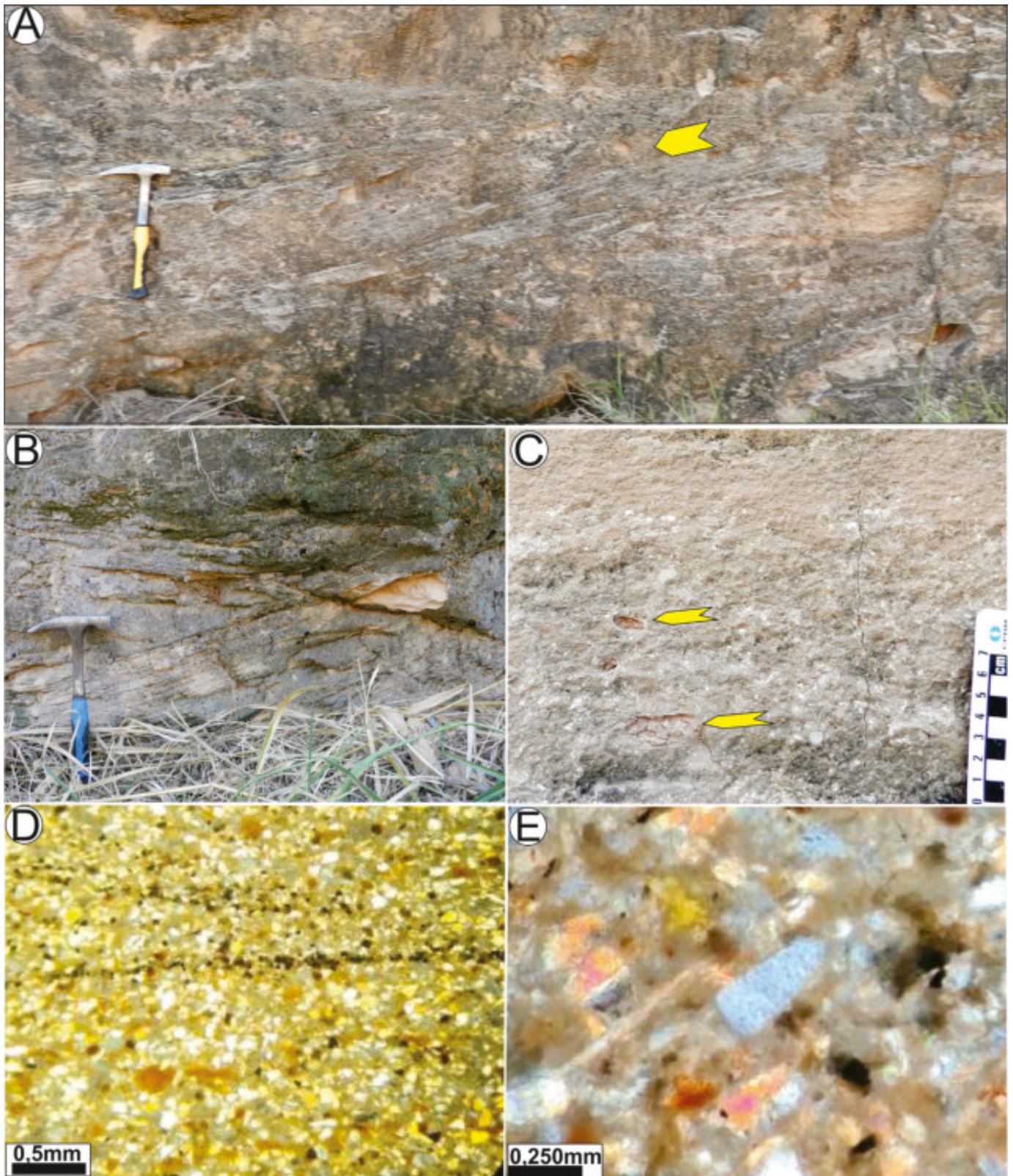


Fig. 5. Channel facies association. A) Fine-to-medium-grained sandstone with trough cross-stratification (Facies St). B) Detail of the sandstone with trough cross-stratification (Facies St) (yellow arrow indicates the paleoflow). Detail of the massive sandstone with clay clasts (Facies Sm) (yellow arrow). C) Sandstone photomicrography, presenting very fine-to-fine-grained quartz sandstone. E) Subangular-oriented quartz grains. Outcrop in Auriflama city (Road SP-463, Km 84) (Fig. 1).

Fig. 4. Channel facies association. A) Conglomerate matrix support with trough cross-stratification exhibit clay clasts in foresets (Facies Gt) (yellow arrow). B) Caves formed by the erosion of the clay-clasts (Facies Gm) (yellow arrow), grading to massive sandstone (Facies Sm). C) Detail of contact between massive sandstone (Facies Sm) and intraformational conglomerate with clay clasts (Facies Gm). Red arrows indicate the clay clasts. D) Thin-section photomicrography presenting clay-clast (yellow arrow), quartz grain (red arrow), and micrite cement (green arrow) of the Gt and Gm facies. E) Sandstone photomicrography, presenting fine-to-coarse-grained quartz sandstone. Outcrop in Auriflama city (Road SP-463, Km 84) (Fig. 1).

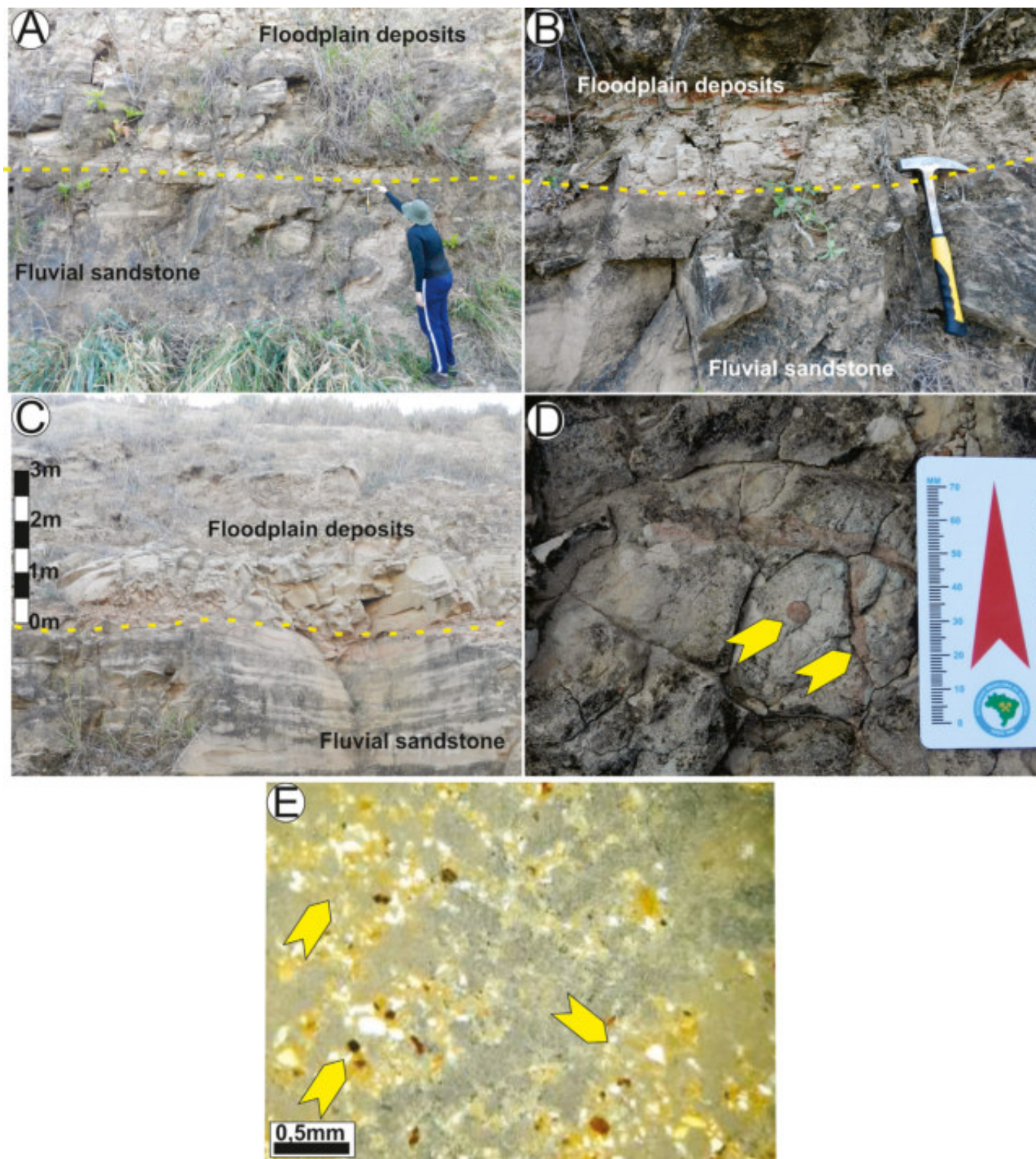


Fig. 6. A) Mudstone layer in the top of the fluvial deposits. B) Detail of the greyish mudstone layer overlaying the fluvial deposit. C) 3 m thick of the greenish mudstone overlying the fluvial deposits. D) Detail of the root marks in greyish mudstone (yellow arrow). E) Photomicrography showing the texture of the floodplain mudstone (Facies Fm). The yellow arrows indicate the irregular quartz grains distribution. Outcrop in Auriflama city (Road SP-463, Km 84) (Fig. 1).

pronouncedly curved diaphysis and a robust distal portion with a large humeral condyle. However, they differ from the humeri of *Calyptocephalella* by having the medial and lateral epicondyles differently developed (e.g., Báez, 1987; Muzzopappa and Báez, 2009; Agnolin, 2012; Otero et al., 2014; Muzzopappa et al., 2016).

They also resemble ceratophryids, especially the living *Lepidobatrachus* and *Ceratophrys*, in the presence of a significantly curved and solidly built diaphysis and a well-developed and rounded humeral condyle that is bordered by a prominent medial epicondyle and less developed lateral epicondyle. Nonetheless, these groups

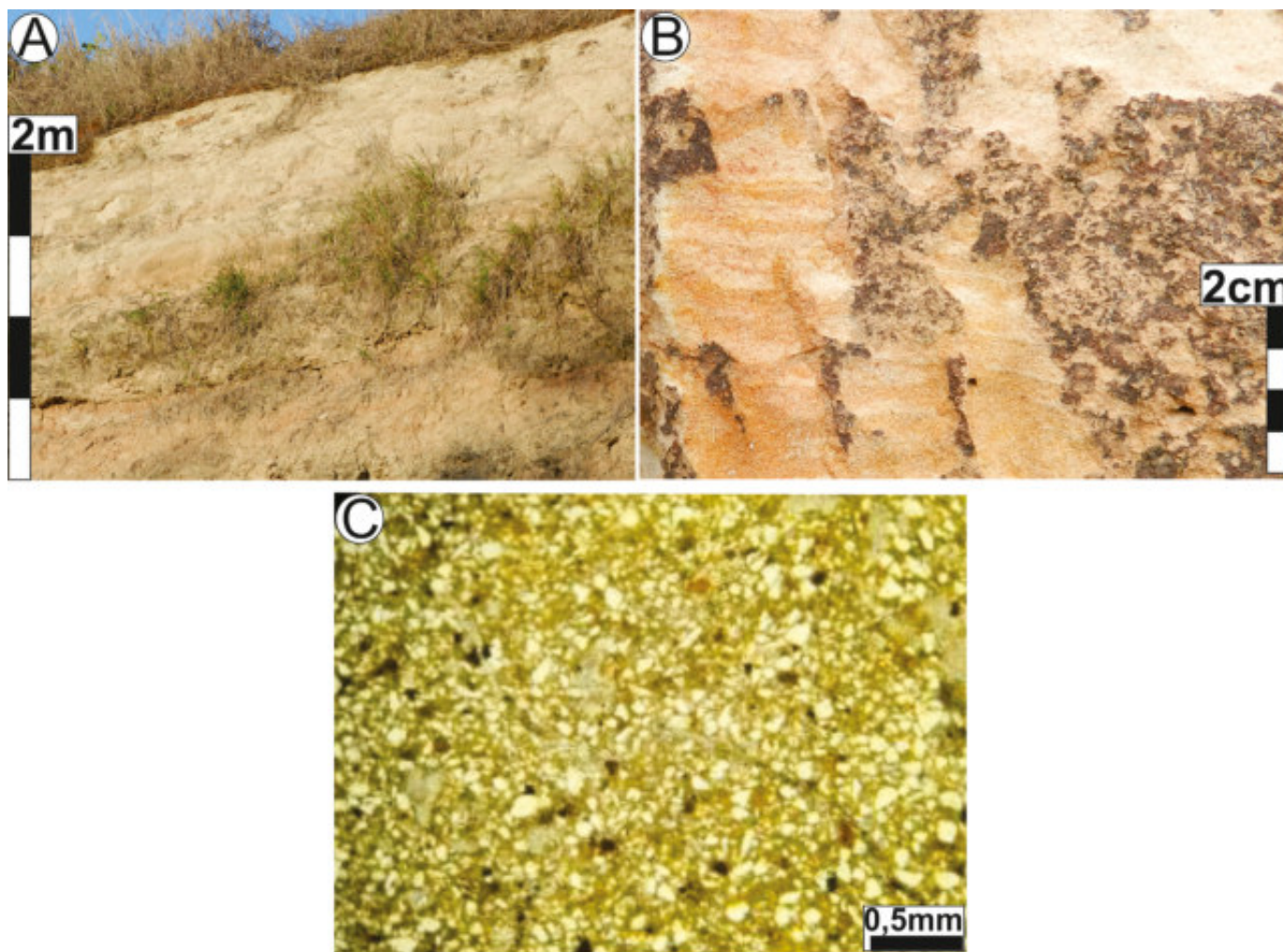


Fig. 7. A) Panoramic view of the Aeolian facies association (Facies Ae). B) Detail of the very fine-to-fine sandstone. C) Photomicrography showing the very-fine texture and well-sorted aeolian sandstone. Outcrop in Auriflama city (Road SP-463, Km 84) (Fig. 1).

Table 1
Facies described in the study area (based on Miall, 1985).

Facies	Characteristics
Gt	Clast-supported conglomerates constituted of pebbles and cobbles of clay. These facies occur as centimetric lenticular bodies or centimetric layers in the base of fining upward cycles. The conglomerates are massive and exhibit trough cross-stratification.
St	Moderate-sorted, fine to coarse-grained sandstone with trough cross-stratification, forming lenticular bodies with thicknesses varying from 0.30 to 1.50 meters. The grains are rounded, and the trough cross stratifications are medium-scale (up to 3 meters).
Sta	Well-sorted, fine to medium-grained sandstone with trough cross-stratification (foresets up to 3 m), forming lenticular bodies with thicknesses of 2.50 meters.
Sm	Fine to coarse, massive sandstone, with sub-rounded to rounded grains and thicknesses varying from 1 to 1.50 meters.
Fm	Greenish, massive mudstone with root marks. This facies occurs in tabular layers varying from 50 cm to 2 meters thick.

differ from the fossil specimens in their more ventrally bowed and less laterally tilted humeral diaphysis and shorter deltoid crest (Perí, 1994; Wild, 1997). Finally, LAPEISA-Pal 0008A differs from all

Table 2
Facies association and sedimentary environment interpretation.

Facies association	Architectural element	Interpretation
Gt and St	CH – Channel	Fluvial environment
St and Sm	SB – Sand bars	Fluvial environment
Fm	OF – Overbank deposits	Floodplain
St	Aeo – Aeolian deposits	Dunes field

well-preserved neobatrachian humeri from the Mesozoic of South America by their strongly laterally curved diaphysis and relatively long deltoid crest. Due to the absence of more diagnostic traits, no fossil remains can be considered a specific neobatrachian clade and are regarded as indeterminate neobatrachians. The Mesozoic fossil record of anurans in South America is patchy. The Pipimorpha (Pipoidea), which are among the early-diverging lineages of Anura (“Archaeobatrachia”), have been reported from the Early Cretaceous of Brazil (Báez et al., 2009; Carvalho et al., 2019; Báez et al., 2021), the Late Cretaceous of Argentina (e.g., Báez, 1981, 1987; Báez et al., 2000; Martinelli and Forasiepi, 2004; Gómez, 2016; Báez et al., 2022; Suazo-Lara and Gómez, 2022;

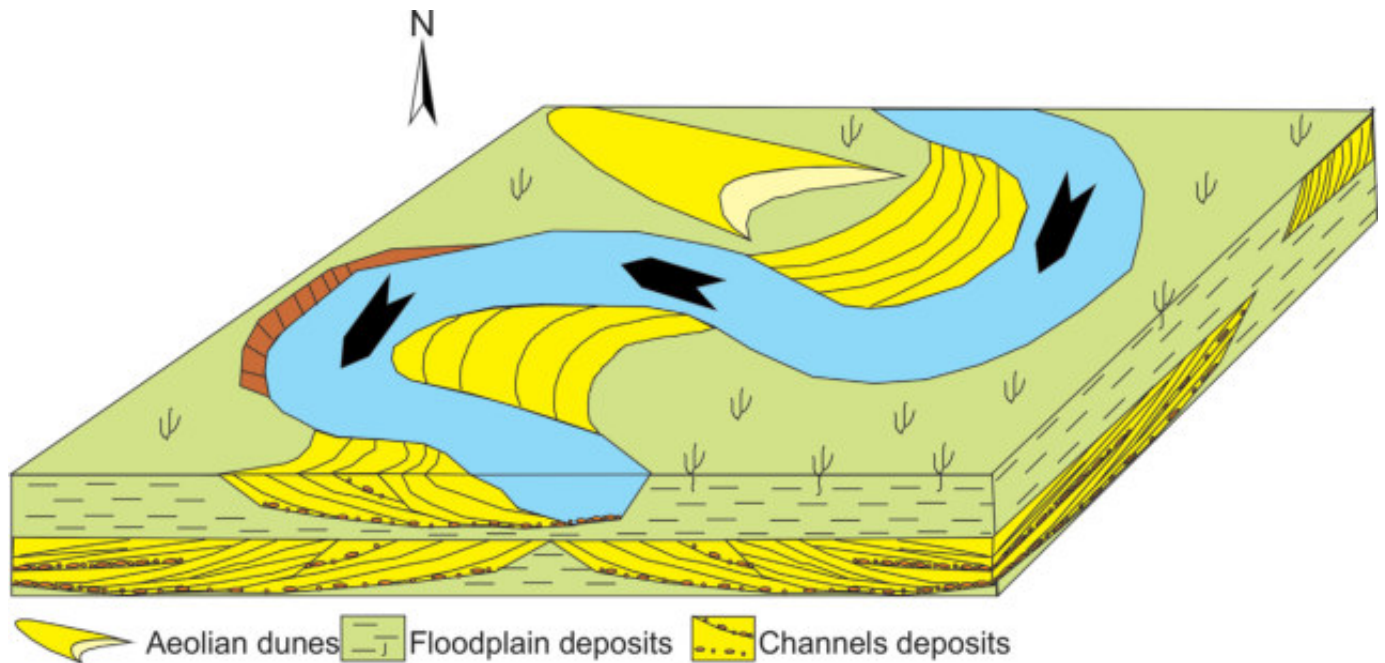


Fig. 8. Evolutionary model for the deposits of the Adamantina Formation in the study area.

Moyano-Paz et al., 2022) and Chile (Suazo-Lara and Gómez, 2022). The record of neobatrachians includes well-preserved specimens from the Early and Late Cretaceous of Brazil (e.g. Carvalho, 2006; Báez et al., 2009, 2012b; Agnolin et al., 2020; Moura et al., 2021; Muzzopappa et al., 2022). However, the exact phylogenetic placement of these specimens among less inclusive clades within Neobatrachia is still uncertain (e.g., Báez and Gómez, 2018; Moura et al., 2021; Muzzopappa et al., 2022). In addition, isolated and fragmentary remains from the Late Cretaceous of Argentina and Chile have been assigned to *Calyptocephalella* or regarded as indeterminate calyptocephalellids (Báez, 1987; de la Fuente et al., 2007; Agnolin, 2012; Novas et al., 2019; Suazo-Lara and Gómez, 2022; Moyano-Paz et al., 2022; Sterli et al., 2022).

Our findings expand the record of neobatrachians from the Bauru Basin. To date, two species have been described from the Marília Formation (Serra da Galga Formation sensu Soares et al., 2020), *Baurubatrachus pricei* (Báez and Perí, 1989) and *Uberabatrachus carvalhoi* (Báez et al., 2012b). Also, the Adamantina Formation has yielded remains of a newly described species of *Baurubatrachus* (*B. santosdoroi*; Muzzopappa et al., 2022) and a still unnamed neobatrachian (Carvalho, 2006). Although LAPEISA-Pal 0008A could not be compared with *U. carvalhoi* because the humeri are missing in this species, the distinct morphology of the studied specimen indicates a higher diversity of neobatrachians in the Bauru Basin.

Testudines Batsch, 1788

Pleurodira Cope, 1865

Podocnemidoidea, Gaffney et al. 2006

Material: plastron and shell fragments (LAPEISA-Pal 0035).

Only a few shell and plastron fragments were collected and assigned to testudines. We have no morphological characters that allow a less inclusive assignment. However, we tentatively assigned the fossils discovered here to Podocnemidoidea (sensu França and Langer, 2005) because this is the only group of Testudines recognized in the Bauru Basin.

Archosauria Cope, 1869

Crocodyliformes Benton and Clark, 1988

Mesoeucrocodylia Whetstone and Whybrow, 1983

Peirosauridae Gasparini, 1982

Material: isolated teeth; jaw fragment (LAPEISA-Pal 0014A, LAPEISA-Pal 0014B, LAPEISA-Pal 0013A, LAPEISA-Pal 0013B, LAPEISA-Pal 0013C, and LAPEISA-Pal 0013D, Fig. 11A–F).

Sixteen complete or partial teeth and a jaw fragment from the symphyseal region were assigned to peirosaurid crocodyliforms. We attributed such dental elements to the peirosaurid clade *Pepesuchinae* due to the pseudozyphodont morphology of the carina and the presence of marked apico-basal striae along the crown (Campos et al., 2011; Pinheiro et al., 2018; Geroto and Bertini, 2019; Nicholl et al., 2021). In addition, the fragmentary mandible bear traits only seen in *Pepesuchus deiseae*, including alveoli D5 and D6 closer to one another and a smaller alveolus D6 (Campos et al., 2011; Geroto and Bertini, 2019, Fig. 11A).

A crocodyliform taxonomic composition including only peirosaurids is uncommon in the Adamantina Formation (Pinheiro et al., 2021). Previous extensive collections in that stratigraphic unit revealed abundant baurusuchids and sphagesaurids (Godoy et al., 2014; Bandeira et al., 2018; Pinheiro et al., 2021; Ruiz et al., 2021). For example, no Peirosauridae have been reported from the Buriti Farm area (Carvalho et al., 2005, 2010; Marinho and Carvalho, 2009; Pol et al., 2014; Darlim et al., 2021), located approximately 25 km from SP-463 road site, with a 30-years long collection history, which yielded three Baurusuchidae and two of Sphagesauridae species (Carvalho et al., 2005; Marinho and Carvalho, 2009; Nascimento and Zaher, 2010; Marinho et al., 2013; Pol et al., 2014; Darlim et al., 2021).

The Adamantina Formation encompassed different habitats, and it is reasonable to assume that different crocodyliforms occupied different niches with variable paleobiology (Riff et al., 2013; Pol et al., 2014; Bandeira et al., 2018; Montefeltro, 2019; Montefeltro et al., 2020; Pinheiro et al., 2021). The fossiliferous assemblage reported here is composed mainly of aquatic and semiaquatic animals, whereas other outcrops of the Adamantina Formation in the region represent a drier environment (Fernandes and Coimbra, 2000; Carvalho et al., 2010). In the Presidente Prudente (sensu Fernandes and Coimbra, 2000) and Marília formations, also

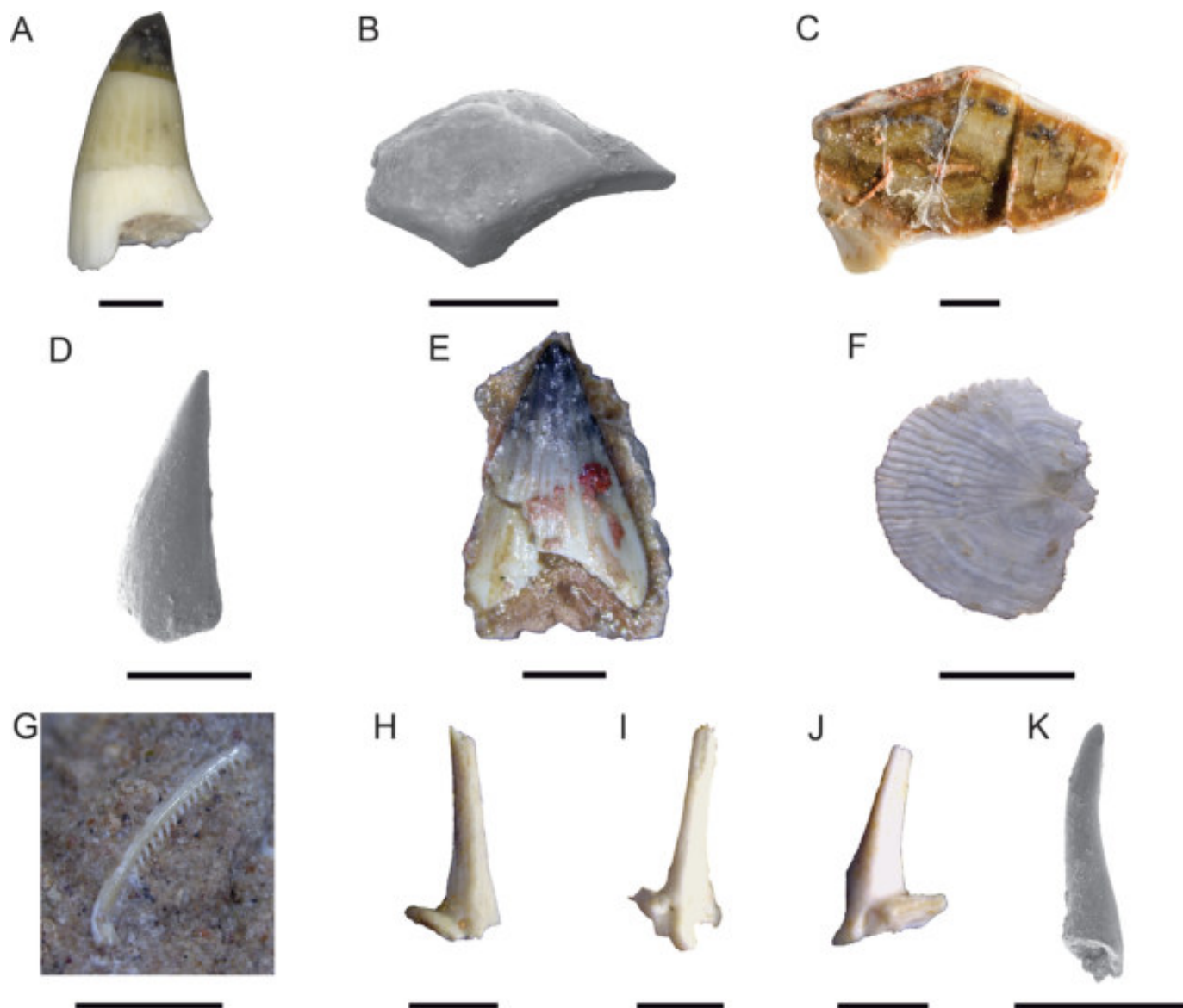


Fig. 9. Fish microremains of the Adamantina Formation, Bauru Group, São Paulo State, Brazil. *Antractosteus* tooth in lateral view LAPEISA-Pal 0005P (A); SEM photograph of *Antractosteus* scale LAPEISA-Pal 0005Q (B); *Antractosteus* scale LAPEISA-Pal 0005R (C); SEM photograph of Vidalamiinae tooth LAPEISA-Pal 0003A (D); Vidalamiinae tooth LAPEISA-Pal 0003B (E); Characiformes scale in external view LAPEISA-Pal 0007B (F); Siluriformes spine in dorsal view LAPEISA-Pal 0006A (G), LAPEISA-Pal 0006B (H), LAPEISA-Pal 0006J (I); LAPEISA-Pal 0006D (J); SEM photograph of Pimelodidae tooth in lateral view LAPEISA-Pal 0004A (K). Scales bars: 2 mm.

deposited in more humid environments (Fernandes and Magalhães-Ribeiro, 2015), peirosaurids are also more abundant, in the scarcity of Baurusuchidae and Sphagesauridae (Riff et al., 2013; Pinheiro et al., 2018, 2021).

Dinosauria Owen, 1842
 Saurischia Seeley, 1888
 Sauropodomorpha Huene, 1932
 Sauropoda Marsh, 1878
 Titanosauria Bonaparte and Coria, 1993

Material: isolated teeth (LAPEISA-Pal 0010A and LAPEISA-Pal 0010B, Fig. 12A–B).

Five sauropod teeth were recovered from the SP-463 road site. These were identified for their long, thin dental crowns, with a

subcircular cross-section and no serrated carina (Upchurch et al., 2004). Most teeth are fragmented, but two of the more complete ones (Fig. 12A–B) are relatively smaller (around 1.2 mm in the labio-lingual and mesio-distal axes and 7.75 mm in the height of the cusp) and probably represent juvenile specimens.

All sauropods known to the Bauru Group are included in the clade Titanosauria (Martinelli et al., 2015; Bandeira et al., 2016), with most of the species described from the Adamantina Formation (Kellner and Azevedo, 1999; Santucci and Bertini, 2001; Azevedo et al., 2007; Bittencourt and Langer, 2011; Machado et al., 2013; Bandeira et al., 2016; França et al., 2016). Among the species described for this geological unit, only *Maxakalisaurus topai* and *Brasilotitan nemophagus* have preserved teeth (Kellner et al., 2006; Machado et al., 2013). However, Titanosauria teeth tend to have

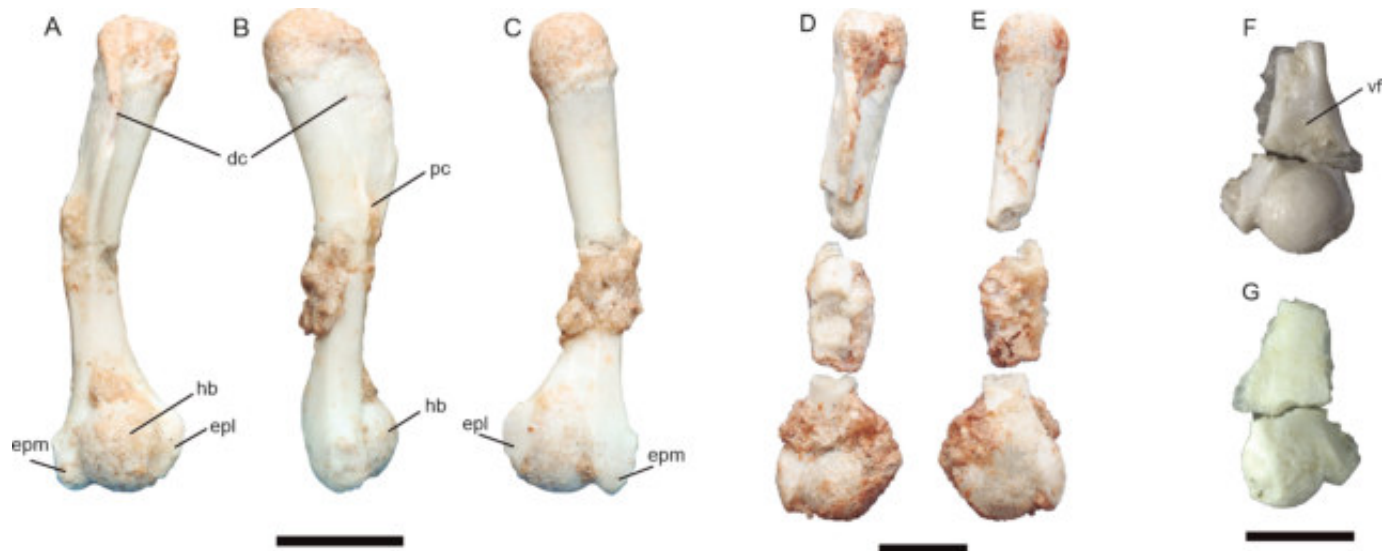


Fig. 10. Anura left humeri from the Adamantina Formation, Bauru Group, São Paulo State, Brazil. LAPEISA-Pal 0008A left humerus in anterior (A), dorsal (B), and ventral views (C), LAPEISA-Pal 0008B left humerus in anterior (D), and dorsal views (E), LAPEISA-Pal 0008C distal portion of left humerus in anterior (F) and ventral views (G). Abbreviations: dc, deltoid crest; hb, humeral ball; pc, parietal crest; epl, lateral epicondyle; epm, medial epicondyle; vf, ventral fossa. Scale bars: 1 cm (A–E); and 1 mm (F–G).

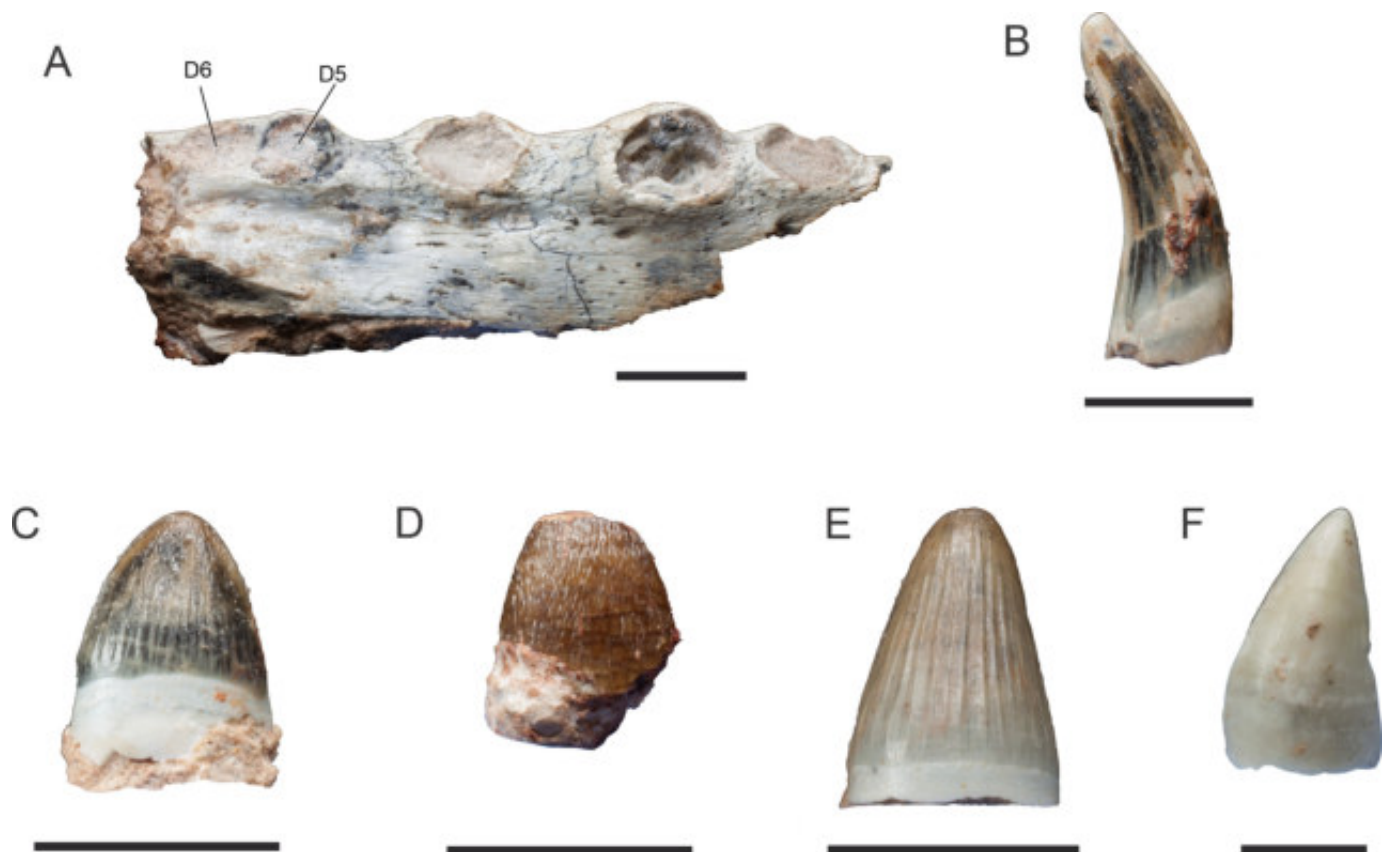


Fig. 11. Crocodyliformes remains of the Adamantina Formation, Bauru Group, São Paulo State, Brazil. LAPEISA-Pal 0014A jaw fragment of *Pepesuchinae* crocodyliform in occlusal view; isolated *Pepesuchinae* teeth LAPEISA-Pal 0014B (B), LAPEISA-Pal 0013A (C), LAPEISA-Pal 0013B (D), LAPEISA-Pal 0013C (E), LAPEISA-Pal 0013D (F). Scale bars: 1 cm (A–F).

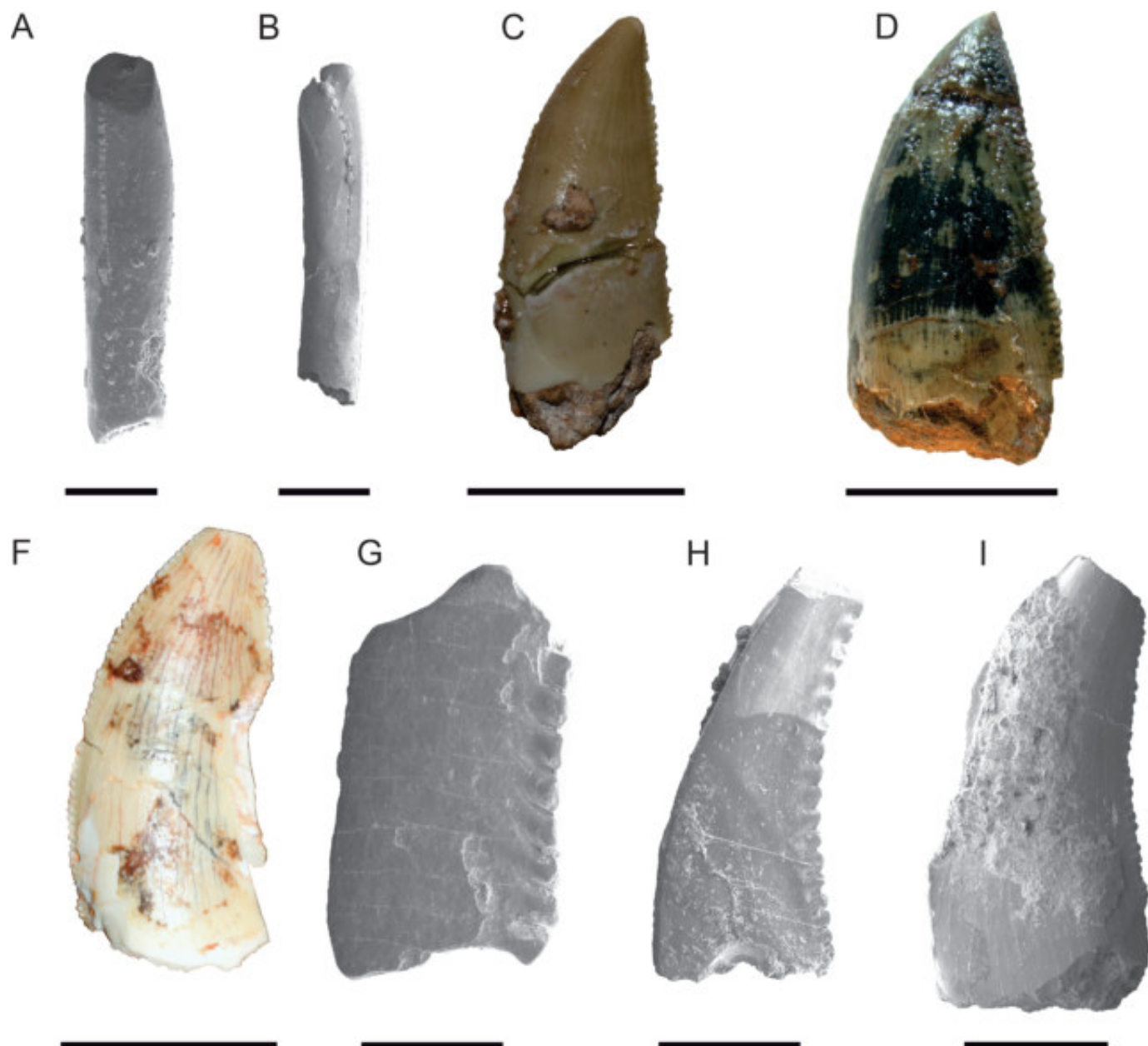


Fig. 12. Dinosauria microrremains of the Adamantina Formation, Bauru Group, São Paulo State, Brazil. Electronic microphotography of Sauropoda teeth LAPEISA-Pal 0010A (A), LAPEISA-Pal 0010B (B); Stereophotograph of Theropoda teeth LAPEISA-Pal 0011A, (C), LAPEISA-Pal 0011B (D), LAPEISA-Pal 0011C (F), Electronic microphotography of Theropoda teeth LAPEISA-Pal 0011D (G), LAPEISA-Pal 0011E (H), LAPEISA-Pal 0011F (I). Scale bars: 1 mm (A–B, G–I), 1 cm (C–E).

similar general characteristics (Mocho et al., 2017). Thus, we attribute the Sauropoda teeth reported to Titanosauria indet.

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881

Material: Six isolated teeth (LAPEISA-Pal 0011A, LAPEISA-Pal 0011B, LAPEISA-Pal 0011C, LAPEISA-Pal 0011D, LAPEISA-Pal 0011E, and LAPEISA-Pal 0011F, Fig. 12C–H).

Six teeth from the SP-463 road site are referred to as Theropoda (Fig. 12C–H) given their tightly labiolingually compressed crown, serrated carinae, denticles with uniform size and shape, and no apicobasal ridges (Hendrickx et al., 2015). However, none of these teeth is complete, so their assignment to less inclusive clades

within Theropoda is tentative. It is based on comparing previously described specimens and identifying traits putatively unique to certain theropod groups.

Three collected teeth are conodont without conspicuous crown ornamentations (LAPEISA-Pal 0011A, 0011B, 0011C). In addition, none of them has preserved roots, indicating they could have been lost *in vivo* (Hendrickx et al., 2015), nor cervices and cinguli in the crowns.

In LAPEISA-Pal 0011A and 0011B, the crown is complete enough to measure its inclination concerning the tooth base (71° and 70°, respectively). In LAPEISA-Pal 0011A, the mesial carina is more markedly worn than the distal one. The mesial denticles are not preserved, but both carinae reach the apex of the tooth. The crown apex presents an irregular enamel, typically associated with

abrasion due to contact with food during feeding (Hendrickx et al., 2015). Distoapical denticles are missing in LAPEISA-Pal 0011A, but distocentral denticles are present. They are chisel-shaped, roughly quadrangular, with the apex curving apically and symmetrically convex in the external outline. The interdenticular spaces are shallow but long, with a shallow diaphysis. The interdenticular slits are deep and subtriangular, with laminae between neighbor denticles.

In LAPEISA-Pal 0011B, most mesial denticles are worn out, and only their bases are preserved. The denticles of the distal carina reach the apex of the tooth, though they are worn in this region. Distoapical denticles are of regular size, with a lanceolate shape, and directed perpendicular to the carina profile. The distocentral denticles are better preserved, with a lanceolate profile, proximodistally expanded bases, and directed to the tooth apex, i.e., oblique relative to the carina. The interdenticular spaces of the distocentral denticles are deep and large, the diaphyses are shallow, and the interdenticular slits are subtriangular, with a lamina joining the denticles that are closer to one another. In LAPEISA-Pal 0011C, the denticles of the mesial carina are entirely worn out, and it is not possible to confirm if they reached the tooth base. Mesoapical distal denticles are chisel-shaped, proximodistally subquadrangular, and symmetrically convex, but measuring their inclination relative to the tooth base is impossible. The mesoapical diaphyses are deep, and the interdenticular slits are subtriangular and deep, without a lamina joint neighboring denticles. Mesocentral denticles show reduced wear, being proximodistally subrectangular and chisel-shaped, with apically directed apices and an asymmetrically convex profile. The interdenticular spaces of the mesocentral denticles are shallow and long, the diaphyses are shallow, and the interdenticular slits are subtriangular, without a lamina connecting the denticles. Only a few mesobasal denticles are preserved but lanceolate, asymmetrically convex, with short and deep interdenticular spaces and deep diaphyses. The interdenticular slits are subtriangular, without a lamina connecting the denticles. The set of characters presented by LAPEISA-Pal 0011A, 0011B, and 0011C suggest that they belong to abelisaurids.

LAPEISA-Pal 0011F is a very fragmented tooth, without a preserved apex, with sediment adhered to the crown surface. It seems that the condont morphotype is not possible to confirm due to its bad preservation. Its crown presents a slight labial inclination so that the distal carina is almost not visible in a strict lateral view. The distocentral denticles are chisel-shaped, proximodistally elongated and subrectangular, apically inclined concerning the carina, with the labial and lingual outlines symmetrically convex. The interdenticular spaces of the distocentral denticles are shallow and short, the diaphyses are deep, and the interdenticular slits are subtriangular, without a lamina joining neighboring denticles. This set of traits also suggests an Abelisauridae affinity (Hendrickx et al., 2015, 2019).

LAPEISA-Pal 0011D and 0011E are more fragmented. Therefore, it is not possible to define the overall morphology of their crowns. In LAPEISA-Pal 0011D, only the middle portion of the distal carina is preserved. The mesocentral denticles lost their apices, but a proximodistal curvature is observed. These denticles are lanceolate and proximodistally elongated. The inclination of the denticles is basal concerning the mesodistal carina, but given its fragmentary nature, it is not possible to define its orientation concerning the crown. The interdenticular spaces are long and shallow, with deep diaphyses. LAPEISA-Pal 0011E is a ziphodont tooth with the crown original surface mostly worn-out. The crown narrows towards the apex and presents irregular enamel flaking. This specimen differs from the other teeth sampled in the presence of two basomedially crests forming a triangular concavity. This concavity can be associated with a resorption pit to

accommodate the replacement tooth (Hendrickx et al., 2015). The distoapical denticles in LAPEISA-Pal 0011E are chisel-shaped, subrectangular in profile, perpendicular to the carina, and with a convex labial profile. The interdenticular spaces of the distoapical denticles are deep and long, with deep diaphyses and concave and deep interdenticular slits, without a lamina linking neighboring denticles. The distocentral denticles are chisel-shaped, subquadrangular, perpendicular to the carina, with deep interdenticular space (but shorter than the distoapical denticles). The diaphyses of the distocentral denticles are deep, and the interdenticular slits are convex, without a lamina connecting the nearby denticles. Most basal denticles are heavily worn but resemble the distocentral denticles in general morphology. Based on Hendrickx et al. (2015, 2019), the set of traits present in LAPEISA-Pal 0011D and 0011E suggests Dromaeosauridae or Troodontidae affinities for both teeth. However, given the geographic distribution of troodontids, mostly absent from Gondwana (Goswami et al., 2013), we suggest they probably represent a Dromaeosauridae.

Theropods in the Adamantina Formation are known based on relatively incomplete and fragmentary specimens. This record mainly comprises isolated materials such as teeth and isolated/fragmented bones attributed to Abelisauridae (Candeiro, 2007; Machado et al., 2013; Brum et al., 2016). Few abelisaurids have been formally described for deposits of the Bauru Group (Kellner and Campos, 2002; Bittencourt and Langer, 2011). Yet, none of them have preserved teeth. Other dental records of Theropoda from the Bauru Group include Noasauridae, Maniraptora, and possibly Carcharodontosauridae (Candeiro et al., 2004; Candeiro et al., 2012; Delcourt and Grillo, 2014; Brum et al., 2018; Martinelli et al., 2019). The occurrence of Theropoda in the SP-463 road site is relevant because, at this point, they are the only top predators recovered in the assemblage. Baurusuchid crocodyliforms are generally recognized as top predators in most communities in the Bauru Group (Bandeira et al., 2018; Montefeltro et al., 2020), but they have not been identified in fossil-sampled sites.

Mammalia Linnaeus, 1758

Material: isolated tooth (LAPEISA-Pal 0009, Fig. 13).

Records of Brazilian fossil mammals are most common in Quaternary deposits (e.g., Auler et al., 2006), extremely rare for the Cretaceous deposits (Bertini et al., 1993; Castro et al., 2018). Aside from the mammalian footprints recorded in the Lower Cretaceous deposits of the Araraquara region (Leonardi 1981), the only somatofossils known for the Upper Cretaceous in the Bauru Group are from the Adamantina Formation. Bertini et al. (1993) reported a jaw fragment with a premolar *in situ*, referred to as Placentalia, and Castro et al. (2018) described the tribosphenidan *Brasilestes stardusti* from an isolated premolar. The new material reported herein is the third known specimen in the Bauru Group. It shows some similarities to the ones described by Castro et al. (2018) and reported by Bertini et al. (1993).

The new specimen shows a main cusp and an accessory lingual cusp. It measures 2.5 mm along the mesio-distal axis, 1.4 mm along the labio-lingual axis, and 1.95 mm as the maximum height. In comparison to the holotype of *Brasilestes stardusti*, both share the asymmetric mesio-distal profile. Additionally, preliminary analysis indicates that LAPEISA-Pal 0009 has a reduced enamel layer not covering the entire dental surface of the new tooth, as occurs in *B. stardusti*. On the other hand, the specimen described herein lacks double roots and a flat talonid, which is present in *B. stardusti*. The absence of double roots is not attributed to a taphonomic question since the base of the dental crown is complete. However, this condition indicates that the specimen represents a deciduous premolar with the roots

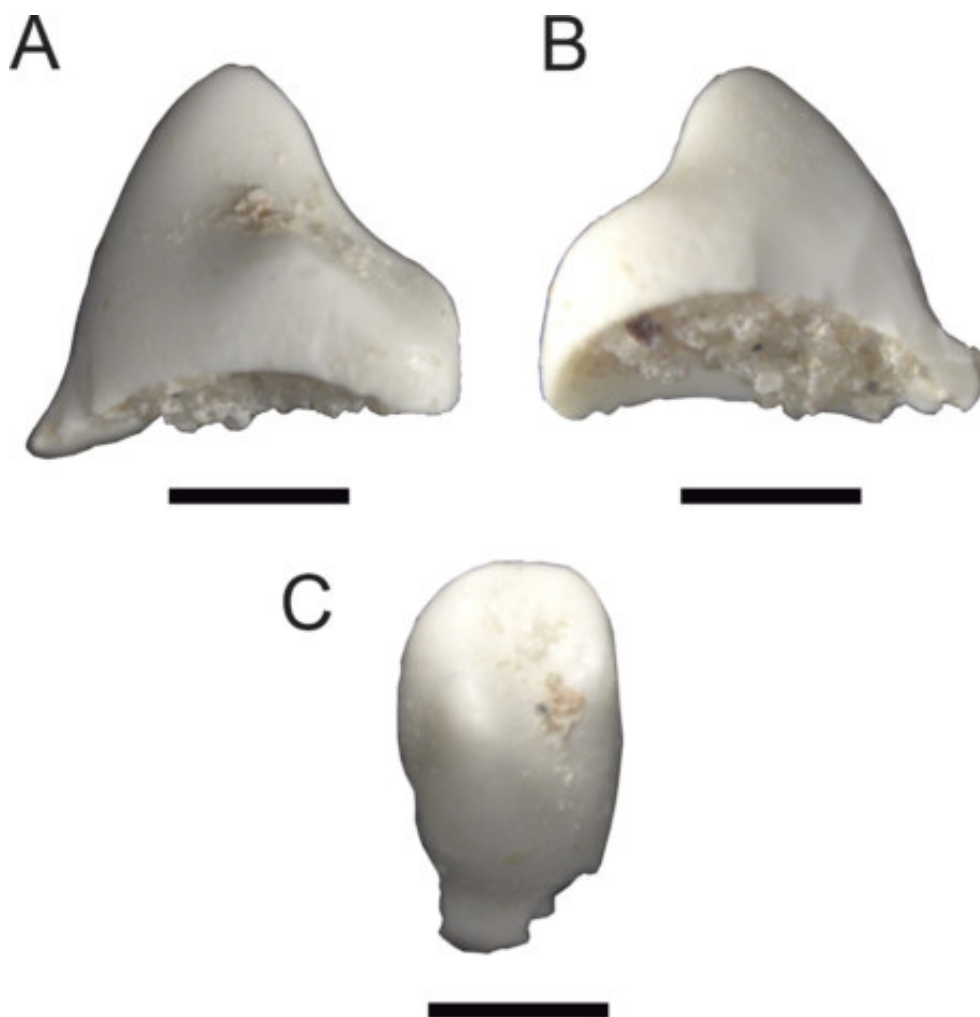


Fig. 13. Putative deciduous mammalian premolar LAPEISA-Pal 0009 in lingual (A), labial (B), and occlusal views (C). Scale bars: 1 mm.

reabsorbed by the permanent tooth of the same locus. Considering that deciduous mammalian teeth tend to have a slightly different morphology than permanent teeth (Kielan-Jaworowska et al., 2005), the deciduous nature of the new tooth, if confirmed, could explain the differences in size, talonid morphology and position of accessory cusp concerning the holotype of *B. stardusti*, and their association cannot be ruled out.

South American Mesozoic mammals have been known since the Early Jurassic from localities in Argentina, Bolivia, Brazil, Chile, and Peru, comprising about 30 species of several lineages (see the recent review of Rougier et al., 2021). However, concerning the Late Cretaceous, biogeographic differences are recognized between southern and northern South America, as illustrated by the lack of tribosphenidans' records in the fossil-rich sites of Patagonia (Castro et al., 2018).

Considering the abundant fauna of Crocodyliformes of the Bauru Group and the multicusp dentition found in some of the taxa (Montefeltro et al., 2009), we also compared the new specimen with teeth of Crocodyliformes. The comparison was focused on Eunosuchia teeth from the Adamantina Formation, which represents the most extreme case of multicusp teeth among Crocodyliformes and with abundant records in this unit (Montefeltro et al., 2009; Melstrom and Irmis 2019). In this sense, Rougier et al. (2021) mention that the affinity of *B. stardusti* to juvenile sphagesaurid notosuchian cannot be ruled out. However, we

observed that the teeth of multicusp eunosuchians bear multiple apico-basal ridges, tend to have thicker enamel, and usually have three or four cusps (Montefeltro et al., 2009; Melstrom and Irmis 2019). Thus, we propose the attribution of the new tooth to Mammalia.

5. Discussion

The microvertebrate assemblage described here for the Adamantina Formation suggests a complex community living in this region during the Upper Cretaceous. This assemblage includes commonly reported taxa for the Bauru Group, such as Actinopterygii, Podocnemididae, Crocodyliformes, Sauropoda and Theropoda, and scarcely reported taxa, such as Anura and possibly Mammalia.

The vertebrate remains from the new locality were excavated from the channel facies association. They are disarticulated and dissociated, and most have some degree of fragmentation. Fish scales and teeth are the most abundant skeletal remains recovered at the site. Isolated teeth mainly represent crocodyliforms, dinosaurs, and mammal, whereas a few isolated shell fragments and humeri represent turtles and anurans. The prevalence of isolated and fragmented elements that are both numerous in the skeleton and physically resistant is typical of many assemblages preserved in channel deposits (e.g., Rogers and Kidwell, 2007; Rogers and Brady,

2010). Abraded bones might be present due to transport and reworking in channel settings, but the new specimens show no significant abrasion. This is not surprising considering that teeth, one of the most common elements in the assemblage, show very low abrasion rates by transport processes (Argast et al., 1987). The genesis of fluvial bone accumulations is highly influenced by the active flows, which might transport, sort, and mix bioclasts (Eberth et al., 2007; Rogers and Brady, 2010). Bioclasts deposited in fluvial contexts may derive from the local biocoenoses or enter the channel after the reworking and transporting of preexisting assemblages at channel margins or floodplains (Rogers and Kidwell, 2007; Rogers and Brady, 2010). The resulting fossil sample, therefore, most likely represents time-averaged, autochthonous to allochthonous accumulations.

The record of aquatic and semi-aquatic forms (e.g., fishes, turtles, anurans, pepesuchines) in the SP-463 road site is more abundant than that of terrestrial taxa (theropods, sauropod, and possibly the mammal), as expected for an assemblage preserved in a fluvial environment. Food and water resources might have attracted terrestrial vertebrates to the area, but the probability of preservation is lower because they do not inhabit the river channels. This might help explain the absence of notably terrestrial notosuchians, such as Baurusuchidae and Sphagesauridae, which are vastly reported in other Adamantina Formation outcrops. Instead, the crocodyliform faunas in the new outcrop are dominated by Peirosauridae, which includes putative semi-aquatic species such as the pepesuchines recorded herein. The absence of other terrestrial vertebrates, such as Squamata and Aves, might be related to the fragility of their small bones.

Aquatic vertebrate faunas remain poorly known in the Adamantina Formation. Our new fossil sample emphasizes microremains' importance for fully understanding the Bauru Group's faunal composition.

6. Concluding remarks

The Adamantina Formation is considered one of the richest units in terms of vertebrate record from the Upper Cretaceous in Brazil. However, this record is overwhelmingly known from larger and articulated fossils. As such, microvertebrates are largely unknown from that unit. The new and diverse microvertebrate fossil community reported is composed by a mixture of well-known and rare taxa from the Adamantina Formation. Our results provide new insights into the Adamantina Formation's fauna and depositional environment, in particularly the identification of a community dominated by aquatic and semi-aquatic taxa. Our new information emphasize the importance of microvertebrate data even for intensely and extensively explored geological units.

Data availability

Data will be made available on request.

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