

## A new *Eocaiman* (Alligatoridae, Crocodylia) from the Itaboraí Basin, Paleogene of Rio de Janeiro, Brazil

André E.P. Pinheiro<sup>a\*</sup>, Daniel C. Fortier<sup>b,c1</sup>, Diego Pol<sup>d2</sup>, Diógenes A. Campos<sup>e3</sup> and Lílían P. Bergqvist<sup>a4</sup>

<sup>a</sup>Laboratório de Macrofósseis, Departamento de Geologia, Universidade Federal do Rio de Janeiro, Ilha do Fundão, Av. Athos da Silveira Ramos s.n, Rio de Janeiro, Brazil; <sup>b</sup>Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul, Campus do Vale, Av. Bento Gonçalves 9500, Cx.P. 15001, 91501-970, Porto Alegre, Brazil; <sup>c</sup>Instituto de Geociências, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, Pampulha, Belo Horizonte, Brazil; <sup>d</sup>CONICET - Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, Trelew 9100, Argentina; <sup>e</sup>Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Av. Pasteur 404, Rio de Janeiro, Brazil

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A new small species of *Eocaiman* is described on the basis of three anterior left mandibular rami and one isolated tooth. The specimens came from the middle-upper Paleocene Itaboraí Basin (Rio de Janeiro State, Brazil; Itaboraian South American Land Mammal Age). The new taxon differs from the other two *Eocaiman* species, such as its small size, likely participation of the splenial in the mandibular symphysis, a reduced angle between the longitudinal axis of the symphysis and the mandibular ramus, and enlarged ninth and tenth dentary teeth (in addition to the large first and fourth dentary teeth). The participation of the splenial in the mandibular symphysis is a unique character among caimanines (with the only possible exception being *Tsoabichi greenriverensis*). The new taxon provides new information on the taxonomic and anatomical diversity of the genus *Eocaiman*, a taxon of prime importance to understand the evolutionary origins of caimans given its position as the basalmost member of Caimaninae. Furthermore, the new taxon has a relatively small body size in comparison with other species of *Eocaiman*, a case paralleled by other Itaboraian reptilian groups (e.g. snakes), suggesting that this ecosystem provides critical data to test the relationship between reptilian body size and climate.

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**Keywords:** Crocodyliformes; Alligatoroidea; Caimaninae; *Eocaiman*; Itaborai; Paleogene

### 1. Introduction

Crocodylomorph archosaurs are an important and diverse group of reptiles that first appeared in the Late Triassic. Extant diversity is relatively low, consisting of 24–30 species (Martin 2008; Hekkala et al. 2011; Densmore III et al. 2011) with a worldwide distribution in tropical and subtropical regions. Extant species belong to Crocodylia (Gmelin 1789, *sensu* Benton and Clark 1988), a crown group that first appears in the Late Cretaceous (Benton and Clark 1988; Brochu 2003; Puértolas et al. 2011). The crocodylian body plan was established during the Mesozoic (Gasparini 1981), but it was during the Cenozoic that crown crocodylians likely achieved a worldwide distribution, replacing other crocodylomorph lineages that thrived during the Mesozoic (Buscalioni et al. 2003; Salisbury et al. 2006; Puértolas et al. 2011). As Brochu (2003) noted, the basal most members of Brevirostres (Crocodyloidea + Alligatoroidea) already have the stereotypical aspect of extant crocodiles, with long and dorsoventrally flattened snouts outwardly resembling the modern American alligator or the Nile crocodile. The crown-group Alligatoridae, first appears in the earliest

Paleocene and includes two major stem-based clades – Alligatorinae and Caimaninae (Brochu 1999).

Alligatorinae has a rich fossil record, especially in the Paleocene and Eocene of North America and Europe, but the group is currently restricted to only two living species of *Alligator* that inhabit the southeastern United States (*A. mississippiensis*) and eastern China (*A. sinensis*). The Paleogene fossil record of Caimaninae is, in contrast, much more incomplete (Brochu 2011) but is more speciose today, ranging from five to seven species depending on the division of some species complexes (Brochu 2010). The caimanine fossil record in the Paleogene of South America is discontinuous but indicates this clade was established very early in the Cenozoic (Brochu 2010, 2011). The oldest caimans, *Necrosuchus ionensis*, *Eocaiman palaeocenicus* and *Notocaiman stromeri*, are all known from the Paleocene of Patagonia (Simpson 1937; Bona 2007; Brochu 2011).

The genus *Eocaiman*, erected by Simpson (1933), was one of the first lineages that radiated in South America (Simpson 1933; Brochu 1999; Bona 2007). *Eocaiman cavernensis* was the first species described and the only one known from substantial cranial material found in

\*Corresponding author. Email: paleolones@yahoo.com.br

Colhué-Huapí Lake (middle Eocene of Chubut [Ré et al. 2010], Argentina; Casamayoran South American Land Mammal Age [SALMA]). Langston (1965) referred materials to this genus from La Venta (middle Miocene of La Venta, Colombia; Laventan SALMA). The first material tentatively referred to *Eocaiman* from the Paleocene was described by Gasparini (1981) from the lower Paleocene of Salamanca Formation (Chubut, Argentina; Peligran SALMA). More recently, the Salamanca Formation has yielded a more complete specimen, described as *E. palaeocenicus* (Bona 2007). Several authors have mentioned the presence of *Caiman* sp. in the paleofaunal lists of the mid–late Paleocene Itaboraí Basin for over 60 years (e.g. Price and Paula-Couto 1946, 1950; Price and Campos 1970; Palma and Brito 1974). This material is here described and recognised as a new species of the genus *Eocaiman* based on a phylogenetic analysis, constituting the smallest known species of the genus.

### 1.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, United States; DGM, Departamento de Geologia e Mineralogia, now designated as MCT; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MCT, Museu de Ciências da Terra; CPRM, Companhia de Pesquisas e Recursos Minerais; DNPM, Departamento Nacional de Produção Mineral, Rio de Janeiro; Brazil; MLP, Museo de La Plata, Argentina; MPEF, Museo de Paleontología Egidio Feruglio, Trelew, Argentina; UCPM, University of California Paleontological Museum, California, United States; UFRJ-DG, Universidade Federal do Rio de Janeiro, Departamento de Geologia, Rio de Janeiro, Brazil.

### 1.2. Anatomical abbreviations

**d3**, third dentary tooth; **d3–d10**, dentary teeth from third to tenth; **d3–d13**, dentary teeth from third to thirteenth positions; **d4**, fourth dentary tooth; **d4 a**, fourth dentary tooth alveolus; **d4a–d12a**, dentary teeth alveoli from fourth to twelfth positions; **d9**, ninth dentary tooth; **d10**, tenth dentary tooth; **d13**, thirteenth dentary tooth; **mc**, meckelian channel; **ms**, mandibular symphysis; **sl**, posterior end of mandibular symphysis; **sp ds**, splenial dorsal scar; **sp vs**, splenial ventral scar.

## 2. Itaboraí Basin: geology, paleontological context and age

The depressional margins of eastern of Brazil are related to the breakup of Western Gondwana: the separation of South America from Africa and the opening of the South Atlantic Ocean, a geologic structural process known locally as the

‘Continental Rift of Southeastern Brazil’ – CRSB (Medeiros and Bergqvist 1999a; Sant’Anna and Ricomini 2001; Sant’Anna et al. 2004). The Itaboraí Basin holds the major fossiliferous deposits of Rio de Janeiro State (southeastern Brazil) and represents the only ones that preserve vertebrates and macroinvertebrates. These fossils record one of the earliest phases of the radiation of the endemic mammalian lineages of South America after the Cretaceous–Paleogene biotic crisis (e.g. Bergqvist and Ribeiro 1998; Klein and Bergqvist 2002; Bergqvist et al. 2009).

The basin is a small depression lying over the crystalline basement of the Paraíba do Sul Group (Medeiros and Bergqvist 1999a, 1999b). The Itaboraí Basin is a small half-graben, having a rhombohedral shape with a NE–SW major axis 1.400<sup>km</sup>, and a NW–SE directed minor axis 500<sup>km</sup> wide. The sedimentary sequence reaches a maximum thickness of 125<sup>m</sup> (Rodrigues-Francisco et al. 1985). Lithologically, the calcareous sediments of the Itaboraí Basin mostly comprise limestones deposited during a hydrothermal phase (S1 layer by Medeiros and Bergqvist 1999b [Rodrigues-Francisco et al. 1985; Sant’Anna et al. 2004]). A second sedimentary cycle was deposited in fissures and is composed of lacustrine marls, karstic marls and breccias formed by freshwater and clastic flows containing plant and animal remains from the margins of the basin (S2 layer by Medeiros and Bergqvist 1999b; Figure 1). Due to strong CRSB tectonic activity, some NE-directed faults were generated in the basin (with the São José Fault being the most significant) and include an extrusive ankaramitic magmatic event that crosscut the S1 and S2 sedimentary sequences (Ferrari 2001). These extrusive rocks are absolutely K/Ar dated to 52.6 ± 2.4 Ma (early Eocene *sensu* Riccomini and Rodrigues-Francisco 1992).

The occurrence of fossils in the Itaboraí Basin has been known since the 1930s when the Portland Mauá National Company began the extraction of calcareous sediments for industrial cement production (Leinz 1938). According to Bergqvist et al. (2005, 2008), the relative fossil diversity of the Itaboraí Basin at family level consists of 44% mammals, 23% mollusks, 14% reptiles (lizards, chelonians, crocodyliforms), 7% birds, 5% amphibians and 7% plants. The crocodyliform fauna from Itaboraí includes at least four undescribed taxa. One of them has been listed as *Caiman* sp. (e.g. Price and Paula-Couto 1950; Price and Campos 1970) and is the focus of the present contribution. The other three taxa have been identified as members of Sebecidae and are much larger in body size. These include a large skull referred as a bretesuchid (Gasparini et al. 1993; Pinheiro et al. 2011a), an isolated maxilla identified as *Sebecus* indet. (Price and Paula-Couto 1946), and premaxillary–maxillary remains of a gracile form identified as *Sebecus* cf. *huilensis* (Pinheiro et al. 2011b).

The age of the Itaboraí sediments has been inferred based on biostratigraphic information of different taxonomic groups, but these inferences differ markedly depending on the group being analysed (Bergqvist et al. 2005, 2009). Early

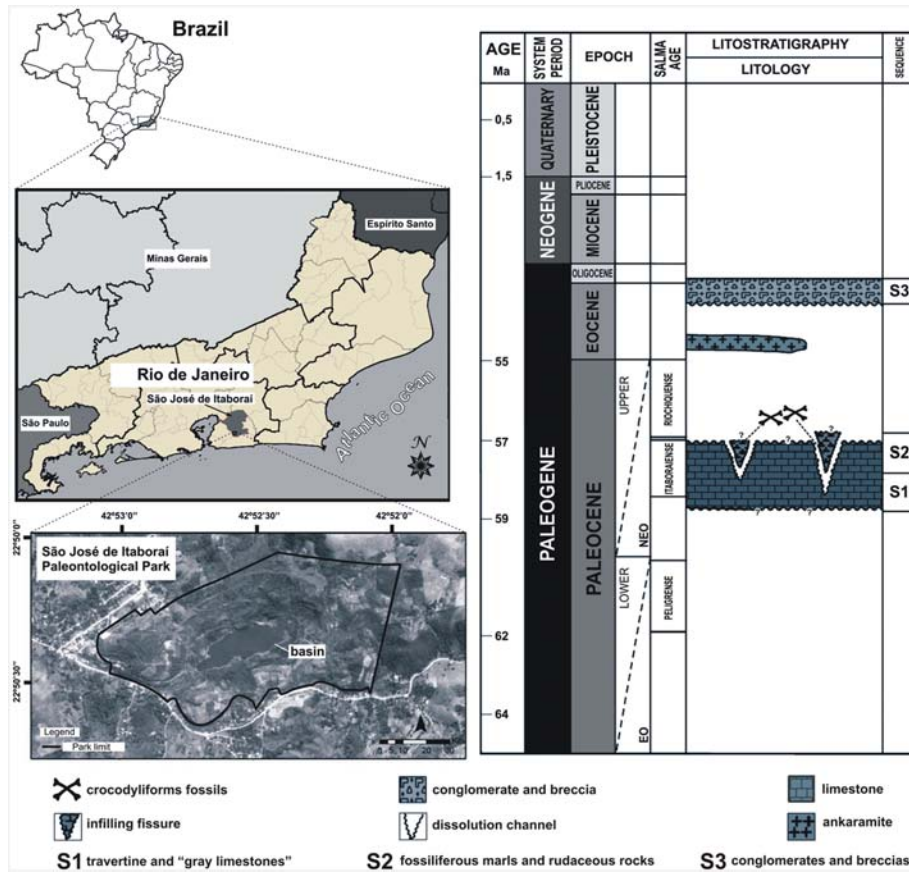


Figure 1. Location of the Itaboraí Basin and Paleontological Park with basin litostratigraphic chart on the right (modified from Bergqvist et al. 2005).

inferences were based on gastropods, plants and polymorphs, and the age varied between the lower Paleocene and Pliocene (e.g. Maury 1935; >Mezzalira 1946; Magalhães 1950; Trindade 1956; Parodiz 1969; Cunha et al. 1984a, 1984b; Lima and Cunha 1986; Mussa et al. 1987). Post-Cretaceous isolation of South America generated a strongly endemic resident mammalian fauna, complicating faunal correlation with other continents (Flynn and Swisher 1995). However, this endemism facilitated correlations within South America, and allowed the establishment of approximately 20 mammal-based ages (SALMAs) for this continent (Bergqvist et al. 2005). The inferred age of the Itaboraí Basin based on the mammalian fauna has been the matter of a recent debate, ranging from the early Paleocene (Muizon and Brito 1993) to earliest Eocene (Gelfo et al. 2009). According to Rage (1998), there may be an important problem in the ‘Itaboraí’s S2 paleofauna’, which may include, at least to some extent, a mixture of fossils of slightly different ages, a possibility given fossiliferous sediments found in multiple fissure infillings. Gayet et al. (1991) noted that deposition of S2 does not comprise a unique continuous sedimentary process; some deposits possibly formed during the middle Paleocene, while other shorter depositional events occurred during late Paleocene or even early Eocene.

Because of its paleontological importance, the Itaboraí Basin area was designated as a paleontological park in 1995 (Figure 1): ‘Parque Paleontológico de São José de Itaboraí’ (‘São José de Itaboraí Paleontological Park’, municipal law no. 1.346 [Beltrão et al. 2001]).

### 3. Systematic paleontology

- Order: Crocodylia Gmelin 1789 (*sensu* Benton & Clark 1988)
- Suborder: Brevirostres von Zittel 1890 (*sensu* Brochu 1997)
- Superfamily: Alligatoroidea Gray 1844
- Family: Alligatoridae Cuvier 1807 (*sensu* Norell et al. 1994)
- Subfamily: Caimaninae Brochu 1999 (following Norell 1988)
- Genus: Eocaiman Simpson 1933

#### Type species

*Eocaiman cavernensis* Simpson 1933

#### Taxonomic content

The genus comprises 3 species based on 20 specimens: *Eocaiman cavernensis* (AMNH 3158); *E. palaeocenicus*

(MPEF-PV 1933, 1935, 1936; MLP 90-II-12–117, 90-II-12–124, 93-XII-10–11, 93-XII-10–13, 95-XII-10–20, 95-XII-10–27; MACN-PV CH 1914, 1915, 1916, 1627); *E. itaboraiensis* sp. nov. (MCT 1791-R, 1792-R, 1793-R, 1794-R). Additionally, fragmentary materials (UCPM 38,878, 39,023) from the middle Miocene of Colombia (Villavieja Formation, La Venta) were also referred to *Eocaiman* sp. by Langston (1965), but a detailed study of these materials remain to be conducted to test their phylogenetic affinities.

### Temporal range and distribution

*Lower Paleocene to middle Miocene: Eocaiman palaeocenicus* represents the most ancient record from the lower Paleocene of Chubut Province, Argentina (El Gauchito locality, Salamanca Formation; see Bona 2007). *Eocaiman cavernensis* comes from the middle Eocene of Chubut Province, Argentina (Sarmiento Formation). The geologically youngest material referred to this genus would be from the Miocene of Colombia ('La Venta fauna' of Honda Group) if the affinities of the above-mentioned undescribed material is confirmed.

### Emended diagnosis

Caimaninae with following unique combination of characters; mandibular symphyseal region broad and shallow (with a width/height ratio of at least 1.6 at the level of the fourth dentary teeth), and extending to fifth or sixth dentary alveolus; first and fourth dentary teeth enlarged, with tenth–eleventh or twelfth–thirteenth teeth enlarged at mid-posterior region of the toothrow; dentary height at first and fourth dentary teeth lower than the height at the level of eleventh–twelfth dentary teeth; alveolar margin of dentary concave between fourth and tenth–thirteen teeth (where alveolar margin arises markedly).

### *Eocaiman itaboraiensis* sp. nov

(Figures 2–5)

#### Holotype

MCT 1791-R, a well-preserved small left anterior dentary fragment, broken at the level of the eleventh alveolus and bearing four fully preserved teeth (**d3**, **d5**, **d9** and **d10**).

#### Referred specimens

MCT 1792-R, a small left anterior dentary fragment with no teeth preserved (the material lacks part of the first alveolus), is broken at the level of the thirteenth alveolus,

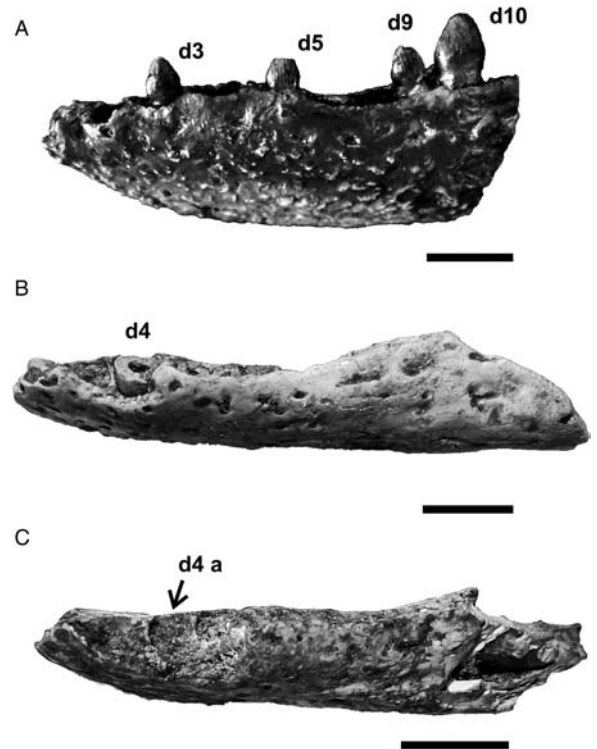


Figure 2. Left dentaries of *Eocaiman itaboraiensis* sp. nov. in left lateral view. A, MCT 1791-R; B, MCT 1792-R; C, MCT 1793-R. Scale bars equal 5<sup>mm</sup>.

and lack the mesial dentary portion from the seventh alveolus. MCT 1793-R, is a small left anterior dentary fragment with no preserved teeth; broken at ninth to tenth alveoli level and with the alveoli filled by sediment. All specimens comprise only the anterior left dentary rami and missing the splenials. An isolated small blunt tooth (root and crown), MCT 1794-R, was deposited together with the holotype and paratypes in the MCT collections. This tooth has diagnostic features of a caimanine and is clearly distinct from all other crocodyliforms known from the Itaboraí Basin; therefore, we tentatively refer this tooth to *E. itaboraiensis*.

#### Etymology

The species name, *itaboraiensis*, refers to the provenance of the material from the Itaboraí Basin.

#### Locality

Itaboraí Basin, 22°50' 20" S and 42°52' 30" W. São José Farm, São José de Itaboraí neighbourhood, ENE of the Rio de Janeiro metropolitan area (SE Brazil); 34<sup>km</sup> NE of Rio de Janeiro City; 25<sup>km</sup> ENE of Niterói City; 15.5 SE of Itaboraí City.

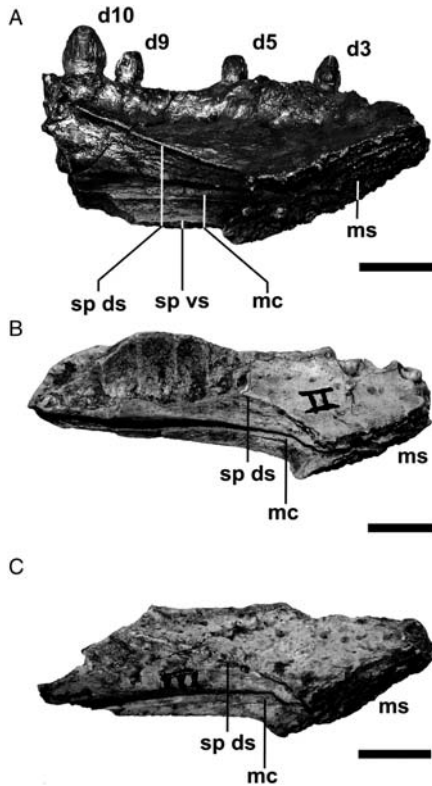


Figure 3. Left dentaries of *Eocaiman itaboraiensis* sp. nov. in medial view. **A**, MCT 1791-R; **B**, MCT 1792-R; **C**, MCT 1793-R. Scale bars equal 5 mm.

**Horizon and age**

From the fissure infilling S2 sequence of the Itaboraí Basin (Medeiros and Bergqvist 1999b), composed of marls and collapsed breccia formed by the dissolution and opening of fissures in the S1 sequence. These materials lack more precise data on the horizon or the exact fissure infilling in which it was found. Itaboraian SALMA (58–56.5 Ma, middle–upper Paleocene [Marshall 1985]).

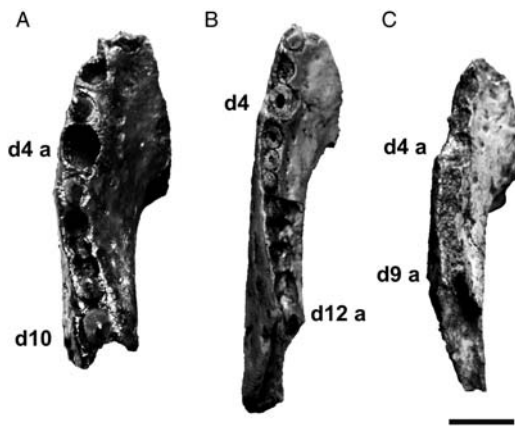


Figure 4. Left dentaries of *Eocaiman itaboraiensis* sp. nov. in occlusal (dorsal) view. **A**, MCT 1791-R; **B**, MCT 1792-R; **C**, MCT 1793-R. Scale bars equal 5 mm.

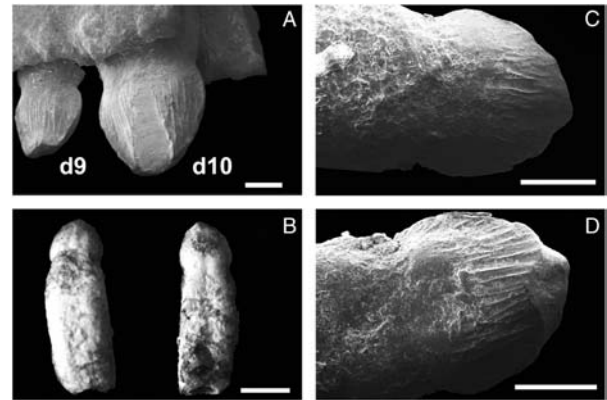


Figure 5. Select teeth of *Eocaiman itaboraiensis* sp. nov. **A**, crown surface detail of MCT 1791-R in lingual view; **B**, MCT 1794-R labial view in left, lingual view in right; **C**, MCT 1794-R labial crown surface detail; **D**, MCT 1794-R lingual crown surface detail. *Abbreviations*: **d9**, ninth dentary tooth; **d10**, tenth dentary tooth. Scales: **A**, equals 1 mm; **B**, equals 2 mm, **C** and **D**, equal 1 mm.

**Diagnosis**

*Eocaiman itaboraiensis* is a caimanine that differs from all other species in the following set of characters (autapomorphies marked with \*): dentary with slightly elevated region along symphyseal suture; reduced angle between longitudinal axes of symphysis and mandibular ramus (approximately 6°)\*; sutural facets on medial surface of dentary for splenial reaching mandibular symphysis, ventral and dorsal to Meckelian groove; first tooth procumbent; tenth and eleventh mandibular teeth enlarged\*; concave alveolar margin of dentary short and poorly developed, comprising region of **d6–d8**; dentary tooth row mesially deflected posterior to **d5** in dorsal view\*.

**Remarks**

The specimens referred to *E. itaboraiensis* sp. nov. have been kept associated in the MCT collection but lack information regarding their precise provenance. However, the different colouration of these fossils and the carbonate matrix (varying from yellowish to greyish-white) suggests these specimens were recovered from different S2 fissure infills.

**4. Description**

**4.1. General features**

The specimens of *E. itaboraiensis* are notably small, with the dentary fragment of all three specimens not exceeding 30 mm in length: MCT 1791-R measures 25 mm from the first to the tenth alveolus; 1792-R measures 29 mm from the first to the twelfth alveolus; 1793-R measures 25.5 mm

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from the first to the ninth alveolus (Figures 2–4). The similar size of the three specimens and the ornamentation of their external surfaces suggest *E. itaboraiensis* was a small-bodied taxon, and if these specimens indeed represent adult individuals it would represent the smallest caimanine taxon known to date.

The dentary of *E. itaboraiensis* is intermediate in robustness between the markedly robust dentary of *E. palaeocenicus* (MPEF-PV 1933) and the more gracile and low dentary of *E. cavernensis* (AMNH 3158). The holotype (MCT 1791-R) is 12% longer than the two referred specimens (as measured from the length of the second to the ninth alveoli) and 35.3% broader (as measured by the maximum lateromedial width of the symphyseal region), suggesting a difference in their ontogenetic stages (Figure 4). Other characters that vary among these specimens are consistent with an ontogenetic explanation, such as ornamentation and the degree of development of the enlarged dentary teeth.

The ornamentation of the holotype (MCT 1791-R) is more strongly developed than in the other specimens, with more numerous and deeper circular pits located mainly in the anteriormost portion of the dentary and more developed but irregularly shaped depressions along the posterior region of the preserved dentary (Figure 2). The ornamentation of MCT 1792-R and 1793-R is poorly developed and consists of small and well-spaced pits and shallow grooves, resembling the condition of *E. cavernensis* (AMNH 3158). The holotype (MCT 1791-R) bears seven neurovascular foramina on the lingual surface of alveolar region, whereas in MCT 1792-R there are nine neurovascular foramina located at level of **d1** and **d7**, and in MCT 1793-R there are nine foramina between **d1** and **d9** (Figures 3 and 4).

#### 4.2. Mandibular symphysis

The length of the mandibular symphysis in *E. itaboraiensis* resembles the condition of other species of *Eocaiman*, extending posteriorly to the sixth mandibular alveolus (Figures 4 and 6). In the holotype, the posterior end of the symphysis reaches the final two-third of **d6**, whereas in the MCT 1792-R and 1793-R symphysis reaches the posterior margin of the **d6** (Figure 4). The dorsal surface of the dentary at the symphyseal region is wide and low, but bears a slightly elevated area along the sutural margin of the symphysis. The low and spatulated morphology of the symphyseal region of *E. itaboraiensis* is more similar to that of *E. cavernensis* (AMNH 3158) than the rounded and ‘U’-shaped condition of *E. palaeocenicus* (MPEF-PV 1933 [Figure 6]).

The angle formed between the longitudinal axis of the mandibular symphysis and the longitudinal axis of the mandibular ramus of *E. itaboraiensis* is the smallest among known species of *Eocaiman*, forming an angle of

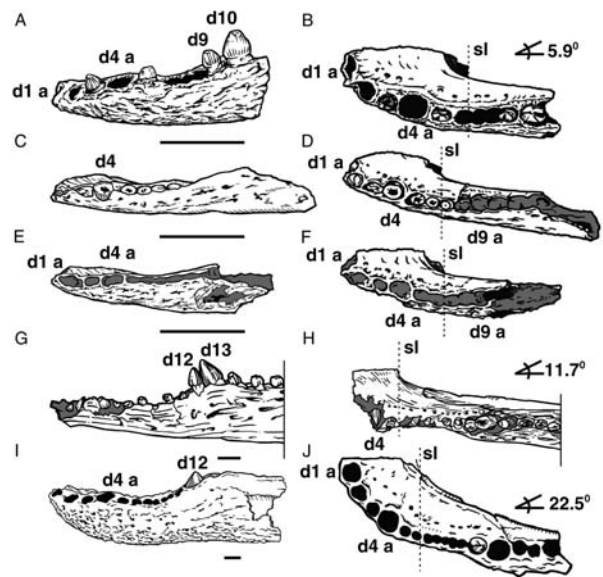


Figure 6. Outline drawings of the anterior dentaries of *Eocaiman* species in left lateral and occlusal views. **A** and **B**, *E. itaboraiensis* sp. nov. MCT 1791-R; **C** and **D**, *E. itaboraiensis* sp. nov. MCT 1792-R; **E** and **F**, *E. itaboraiensis* sp. nov. MCT 1793-R; **G** and **H**, *E. cavernensis* AMNH 3158; **I** and **J**, *E. palaeocenicus* MPEF-PV 1933. Vertical dashed lines represent the transversal axis at the level of the posterior end of the mandibular symphysis. Scale bars equal 1<sup>o</sup>cm.

approximately 6° (*E. cavernensis*, 11.7°; *E. palaeocenicus*, 22.5° [Figure 6]).

The splenials are not preserved in *E. itaboraiensis* but the sutural facets on the dentary indicate that the splenials reached the mandibular symphysis, especially dorsally. The medial surface of the dentary bears a well-marked lineation dorsal to the Meckelian groove and along its ventromedial margin; both lineations end at the mandibular symphysis (Figure 3). The sutural surface of the mandibular symphysis is dorsal to the Meckelian groove, and the posterior surface of the symphysis has an irregular outline with the ventral portion more developed, also suggesting that the splenial may cover the posterodorsal region of the symphysis. However, as the splenials are not preserved in any of the specimens of *E. itaboraiensis*, we can only determine that the splenial reached the mandibular symphysis but we cannot determine the details of its participation. In caimanines (and derived alligatorines), the splenial extends anteriorly dorsal to the Meckelian groove but does not reach the symphysis (Brochu 1999; Bona and Desojo 2011). The only possible exception has been noted for *Tsoabichi greenriverensis*, a caimanine from the Lower Eocene of Wyoming, which possibly possesses a splenial participation of the mandibular symphysis although its condition cannot be determined with certainty (Brochu 2010). Splenial participation in the mandibular symphysis is a plesio-

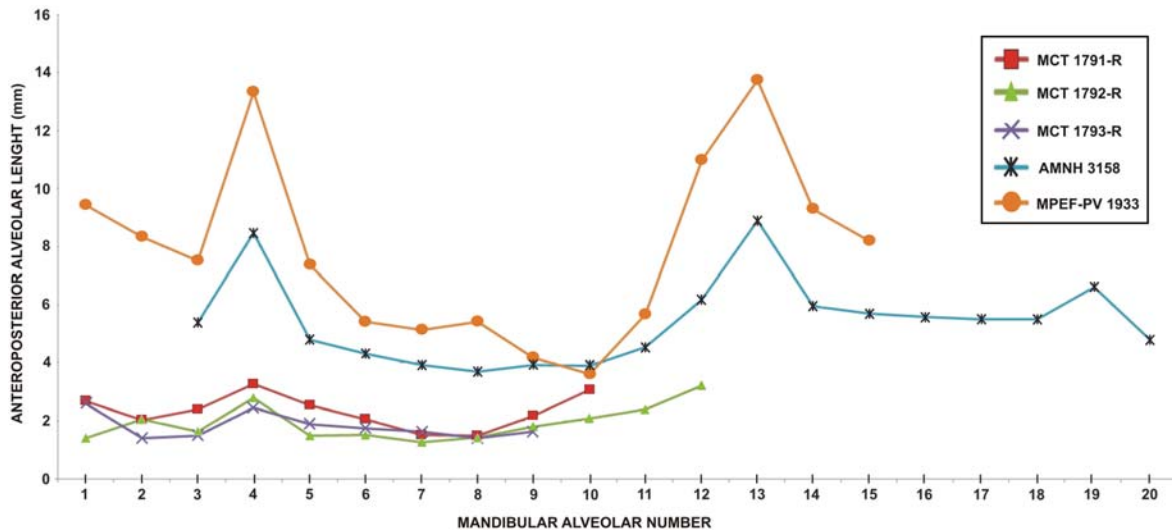


Figure 7. Comparisons of the anteroposterior length of anterior alveoli of the dentary. The left toothrow was measured for all taxa except for *E. cavernensis* (AMNH 3158) where measurements for **d3–d13** were measured from the better-preserved right mandibular ramus.

morphic condition for *Brevirostres* (Brochu 1999, 2010), maintained in basal forms of Alligatoroidea (e.g. *Leidyosuchus*, *Stangerochampsia* [Brochu 1999]) and Alligatorinae (e.g. *Navajosuchus mooki*).

#### 4.3. Tooth row morphology

The alveolar concavity at the anterior region of the dentary extending from **d5** to **d10** is only slightly developed in *E. itaboraiensis* (being more marked in MCT 1791-R than 1792-R and 1793-R [Figure 2]). This resembles the condition of *E. cavernensis* (AMNH 3158), although in the latter species it extends from **d6** to **d11**. The anterior alveolar concavity in *E. palaeocenicus* (MPEF-PV 1933) and *Eocaiman* sp. (UCPM 39,023) extends from **d6** to **d10** and is much more developed, especially in UCPM 39,023. Posterior to this region, the alveolar margin of the dentary ascends and at the level of **d10–d11** this margin is much higher than at the level of **d4** (Figure 5), a condition shared with other species of *Eocaiman* (Simpson 1933; Bona 2007). This contrasts with the condition of other members of Caimaninae (e.g. *Caiman* DGM 301-RR, 157-RR, 148-RR, and 156-RR), *Melanosuchus* (DGM 154-RR and 305-RR) and *Paleosuchus* (DGM 268-RR, 291-RR, 292-RR and 293-RR), in which the alveolar margin at the twelfth or thirteenth tooth is almost at the same level of the alveolar margin of **d4**.

The tooth row of *E. itaboraiensis* is medially deflected in dorsal view posterior to **d6** (Figure 4), as in *E. cavernensis* (AMNH 3158) but not in *E. palaeocenicus* (MPEF-PV 1933). The first twelve teeth of *E. itaboraiensis* are known – MCT 1791-R preserves the first ten alveoli, with teeth in **d3**, **d5**, **d9** and **d10**; 1792-R preserves

the first thirteen alveoli and the base and root of the first seven; 1793-R preserves the ten first alveoli. The first, fourth, tenth, and probably the eleventh alveoli of MCT 1791-R are enlarged relative to the other alveoli (Figures 4 and 7). The tooth size variation is similar in pattern to the holotype but with slightly different sizes in the two smaller referred specimens (MCT 1792-R and 1793-R), which show less enlargement of **d4**, **d10** and **d11** (Figures 4 and 7). However, in MCT 1792-R the partially preserved twelfth and thirteenth alveoli (Figure 3) are anteroposteriorly longer than the tenth and eleventh alveoli, indicating that the largest dentary teeth of *E. itaboraiensis* had not been preserved in the available specimens. This pattern of alveolar variation in the other two species of *Eocaiman* is slightly different but shares the presence of enlarged teeth in the first, fourth, twelfth and thirteenth alveoli (in *E. cavernensis* [AMNH 3158] the **d10** is also enlarged, while in *E. palaeocenicus* [MPEF-PV 1933] not the **d10**, but the **d11** is enlarged [Figure 7]).

The first dentary tooth of *E. itaboraiensis* is anteriorly procumbent, a feature shared with *E. cavernensis* (AMNH 3158) and *Eocaiman* sp. (UCPM 38,878 and 39,023); an unusual feature among crocodylians (Figure 5). *Eocaiman palaeocenicus* (MPEF-PV 1933) clearly has the generalised morphology of crocodylians with anterodorsally facing anterior alveoli. The first five dentary teeth of *E. itaboraiensis* are set in evenly spaced alveoli that are completely divided by interalveolar septa, whereas all dentary teeth posterior to **d5** or **d6** are set in a continuous alveolar groove. This condition is only present in the posteriormost teeth of the upper and lower toothrow of mature living caimanine species, although the alveolar groove is more anteriorly extensive in juvenile specimens

(e.g. *Caiman*, *Melanosuchus*; AEPP pers. obs). The presence of an anterior alveolar groove (between **d8** and **d11**) is also present in the large (almost 30cm estimated mandibular length) and presumably adult holotype of *E. palaeocenicus* (MPEF-PV 1933).

Preserved teeth possess a marked neck between the root and crown and are slightly buccolingually compressed (Figures 2, 3 and 5). They are pointed, cordiform in shape, have a slight lingual curvature, and bear many low, irregular apicobasal carinae on the outer enamel surface on both crown surfaces (Figure 5). The distal and mesial carinae are well developed in all preserved teeth and lack serrations. The tenth tooth has an extensive apicobasal wear facet (Figure 5). The isolated tooth MCT 1794-R tentatively referred to *E. itaboraiensis* is small and blunt but preserves most of the features observed in the holotype (e.g. many irregular and low apicobasal carinae on its lingual and labial surface). The distal and mesial carinae are well developed and have modestly developed enamel wrinkles but not true denticles (*sensu* Prasad and Broin 2002). In MCT 1794-R, the labial surface of the root and the base of the crown bears a slightly marked apicobasal sulcus. The sulcus divides the labial surface of the root into two lateral bulges, conferring a cordiform inverted crown shape. This condition is similar to that of posterior teeth of some extant crocodylians (e.g. *Melanosuchus niger* [DGM 154-RR, 286-RR, 305-RR]) and therefore MCT 1794-R is interpreted as a posterior tooth of *E. itaboraiensis* (Figure 5).

##### 5. Phylogenetic affinities of *Eocaiman itaboraiensis*

To analyse the phylogenetic affinities of the new taxon, a cladistic analysis was conducted based on the dataset of Brochu (2010), with the addition of one character (modified from Bona 2007) and one character from Brochu (1999) (Supplementary Data). The dataset includes 3 non-alligatorid alligatoroids as successive outgroups, and 16 alligatorids in the ingroup, including all the caimanine species used by Brochu (2010) and *E. palaeocenicus*. A total of 29 taxa and 125 characters were analysed (see 1.1 and 1.2 in Supplementary data available online). Multistate characters were treated as unordered (following the original analysis of Brochu 2010) and all characters were equally weighted. The parsimony analysis was conducted using *TNT* version 1.1 (Goloboff et al. 2008). An exhaustive branch-and-bound search strategy was conducted performing the ‘implicit enumeration’ option to recover the most parsimonious trees (MPTs). Also, to avoid changes in the definition of the character states, we coded *E. itaboraiensis* and *Tsoabichi* as ‘?’ for character 40, and ‘2’ for the other caimanines.

The phylogenetic analysis recovered nine MPTs (length = 187, CI = 0.642, RI = 0.801). The number

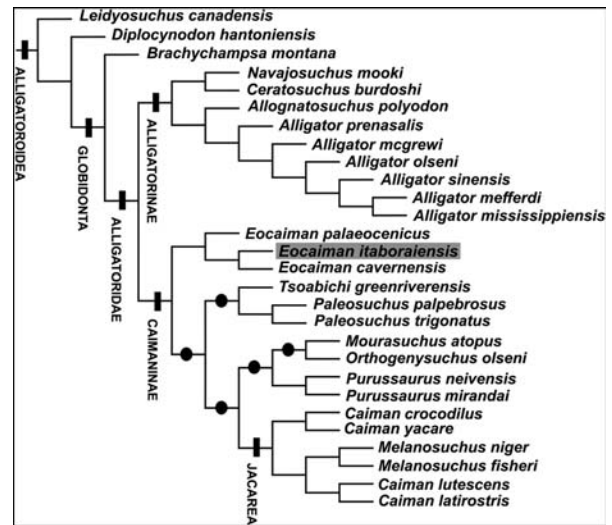


Figure 8. Phylogenetic relationships of *Eocaiman itaboraiensis* sp. nov. Reduced strict consensus of nine most parsimonious trees excluding *Necrosuchus ionensis* (solid black circles show the alternative positions of this taxon within Caimaninae clade among most parsimonious trees).

of MPTs is due to different positions for *N. ionensis*, as in the original analysis of Brochu (2010). The reduced consensus excluding *Necrosuchus* shows that the topology recovered is the same as the one obtained by Brochu (2010) with a monophyletic Caimaninae and *Eocaiman* placed as the most basal member of this clade (Figure 8). The two added taxa, *E. itaboraiensis* and *E. palaeocenicus*, form a monophyletic group with *E. cavernensis* (Figure 8), with the following internal topology: (*E. palaeocenicus* + (*E. itaboraiensis* + *E. cavernensis*)).

The *Eocaiman* clade is supported by a single unambiguous synapomorphy: dentary at level of first and fourth teeth lower than at level of eleventh–twelfth teeth (character 124 [1]); a feature retrieved as a synapomorphy of this genus in the analysis of Bona (2007). The presence of only one synapomorphy is due to the fragmentary nature of the specimens of *E. palaeocenicus* and *E. itaboraiensis*. Nevertheless, this feature distinguishes *Eocaiman* from other caimanines.

*Eocaiman cavernensis* and *E. itaboraiensis* are recovered as sister taxa given the presence of a single unambiguous synapomorphy: the presence of procumbent first dentary teeth (character 125). The anterior end of the mandibular symphysis of these two forms is dorsoventrally low and has a subhorizontal ventral margin at its anterior end. This condition contrasts with the condition of most caimanines (including *E. palaeocenicus*) in which the anterior dentary teeth project anterodorsally and the anterior margin of the dentaries is anteriorly convex and elevated.

Both *E. cavernensis* and *E. palaeocenicus* share an anteroposteriorly long symphysis with no splenial



participation, while *E. itaboraiensis* may have a short participation of the splenial in the symphysis, a plesiomorphic condition for Alligatoridae (in which the splenials are sutured under and below the Meckelian groove [Brochu 2004]). Caimanines lack splenial participation in the mandibular symphysis, with the possible exception of *Tsoabichi* (Brochu 2010), but project an anterior process dorsal to the Meckelian groove (Brochu 1999, 2010). The possible presence of the plesiomorphic participation of the splenial in the symphysis could suggest that *E. itaboraiensis* is the basalmost known caimanine, but this hypothesis requires two additional steps in the data set used here, because of the synapomorphic features of *Eocaiman* noted above, and therefore is rejected. Alternatively, if the splenial participation in *E. itaboraiensis* and *Tsoabichi* are indeed confirmed, the evolutionary history of this character in Caimaninae (and among alligatoroids in general) may have been more complex than previously thought.

## 6. Discussion

*Eocaiman* is diagnosed by a single synapomorphy, the relative level of the mandible in the anterior (first and fourth alveoli) and mid-portion (eleventh and twelfth) of the tooth row. However, species of this genus also share a set of other common features that may diagnose *Eocaiman* (see Diagnosis), but have not been included in a phylogenetic analysis because they vary continuously in alligatoroids. These include the broad and shallow mandibular symphysis that extends to the fifth–sixth dentary alveoli and the marked concavity of the alveolar margin between the fourth and tenth–thirteen teeth (where the alveolar margin arises markedly).

Extant caimans have a strictly tropical distribution (Ross 1998), and as stated by Brochu (2010, 2011), the origin of Caimaninae suggests a dispersal event of basal alligatoroids from North America to southern South America early in the Cenozoic, with a minimum divergence time of at least 60 Ma for the two groups. This hypothesis, however, requires a dispersal event across a salt-water environment (alligatoroids are generally intolerant of salt water [Taplin et al. 1982]), as there is no strong evidence on the existence of terrestrial bridges between the Americas during the early Cenozoic. However, the fossil record of basal alligatoroids (Brochu 1999) and basal caimanines (Bona 2007; Brochu 2010, 2011) is not sufficiently complete to allow a thorough understanding of this dispersal.

*Eocaiman itaboraiensis* and the recently described *E. palaeocenicus* provides some information on the diversification pattern of Caimaninae during the Paleogene of South America, which so far is restricted to three species of *Eocaiman*, *N. ionensis* (Brochu 2011) and an additional

taxon from the Paleocene of Patagonia of uncertain phylogenetic affinities (*N. stromeri*). Despite the lack of current knowledge on the affinities of some of these forms (Figure 8; see also Brochu 2011), the Paleogene diversity of caimanines from South America appears to be restricted to basal lineages of this clade. *Eocaiman* is the basalmost Caimaninae (as suggested by Simpson [1933] and later corroborated by phylogenetic analyses [Brochu 1999, 2010, 2011; Bona 2007]). In our analysis, *Necrosuchus* is recovered in multiple positions but always basally within the lineages leading to extant caimanines (i.e. *Paleosuchus* and *Caiman* + *Melanosuchus*). The Oligocene–Miocene fossil record of Caimaninae in South America, in contrast, is dominated by more derived forms, representing early members of extant lineages (e.g. *Caiman tremembensis*, from the Oligocene of Brazil) or bizarre endemic clades such as the gigantic *Purusaurus* (Brochu 2003).

Paleoenvironmental interpretations of the Itaboraí Basin during the Paleocene suggest a semi-arid climate during the presence of plant remains (e.g. *Psidium* [Myrtaceae], *Celtis* [Ulmaceae]) with periods of high humidity (infilling fissure karst [Mussa et al. 1987; Medeiros and Bergqvist 1999b; Bergqvist et al. 2005]). The deposition of the Itaboraí sediments likely occurred during the Paleocene–Eocene Thermal Maximum (PETM), an event of increased global mean temperature from 5 to 8°C (McInerney and Wing 2011). The presence of crown-crocodylians implies a mean annual temperature equal to or higher than 14.2°C. Increasing aridity and thermal seasonality at mid-latitudes during the Cenozoic likely restricted crocodyliforms to lower latitudes (Markwick 1998).

The notably small body size of the three specimens of *E. itaboraiensis*, in comparison with other species of *Eocaiman* from the Paleocene and Eocene of Patagonia, during the PETM appears to contradict the general relationship of reptilian body size and temperature (i.e. reptilian paleothermometer [Head et al. 2009]). Several factors could explain this apparent conflict. One of them is that the Itaboraí deposits have a systematic bias favouring the fossilisation of only small-sized specimens. We found this hypothesis untenable, as there are large-bodied specimens of sebecid crocodyliforms, birds (e.g. *Diogenornis fragilis*) and mammals (e.g. *Epidolops ameghinoi* and *Carodnia vieirai*) known from these beds. Other possible explanations could be related either to some of the problems noted for this method (Denny et al. 2009; Makarieva et al. 2009; Sniderman 2009) or to physiological particularities of *E. itaboraiensis* that lived in the presumably warm and dry environment of the Itaboraí Basin. For instance, the small body size of *E. itaboraiensis* might be related to a dry climate, since miniaturisation is sometimes an evolutionary adaptation in stressful environments (Hanken and Wake 1993). An interesting parallel exists in the reduced body size of the boiid snakes

known from these sediments (Rage 2001), suggesting that the Itaboraí herpetofauna may represent an interesting case of study for testing the reptilian paleothermometer hypothesis.

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### Notes

1. Email: danielcfortier@yahoo.com.br
2. Email: dpol@mef.org.ar
3. Email: dac@abc.org.br
4. Email: bergqvist@geologia.ufjf.br

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