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## A new species of *Caipirasuchus* (Notosuchia, Sphagesauridae) from the Late Cretaceous of Brazil and the evolutionary history of Sphagesauria

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Sphagesauridae is a group of notosuchian crocodyliforms from the Late Cretaceous of South America characterized by highly specialized jaws and dentition. Here, we describe a new sphagesaurid from the Santo Anastácio Formation (Caiuá Group, Bauru Basin), south-east Brazil. The specimen is composed of a partial palate, neurocranium, mandible and fragmentary teeth. It represents a new species that can be assigned to *Caipirasuchus* due to the presence of a lateromedially narrow and anteroposteriorly long mandibular symphyseal region, apicobasal ridges on the posterior teeth, a diastema between D5 and D6, and a linear row of large neurovascular foramina on the lateral surface of the dentary. It differs from previously described *Caipirasuchus* species based on a ventrolaterally inclined surface of the dentaries posterior to the tooth row, a connection between the anteroventral margin of the external mandibular fenestra and the floor of the Meckelian canal, and the anterior process of the angular forming a 'V'-shaped suture in its contact with the splenial. The results of a phylogenetic analysis of notosuchians recovered the so-called 'advanced notosuchians' in a clade, for which we propose a phylogenetic definition and erect the name Sphagesauria. We also recovered two more inclusive clades encompassing an array of Mesozoic notosuchians, here named Xenodontosuchia, which includes Sphagesauria + Baurusuchia, and Eunotosuchia, including Xenodontosuchia, Uruguaysuchidae and other Cretaceous forms.

<http://zoobank.org/urn:lsid:zoobank.org:pub:FD8D706F-9E01-4C09-BE4E-DC3BEDE151DC>

**Keywords:** *Caipirasuchus*; Sphagesauridae; Santo Anastácio Formation; Bauru Basin; Notosuchia

### Introduction

Notosuchia (*sensu* Gasparini 1971) (Table 1) is a species-rich group of crocodyliforms known mainly from the Cretaceous deposits of Gondwana (Turner & Sertich 2010; Godoy *et al.* 2014; Pol *et al.* 2014; Pol & Leardi 2015). In the past three decades, several new notosuchians have been discovered from Madagascar (Buckley & Brochu 1999; Buckley *et al.* 2000; Turner 2006; Rasmussen *et al.* 2009), continental Africa (Gomani 1997; Sereno *et al.* 2003; Sereno & Larsson 2009; O'Connor *et al.* 2010) and especially South America (Ortega *et al.* 2000; Carvalho *et al.* 2005; Marinho & Carvalho 2009; Novas *et al.* 2009; Iori & Carvalho 2011; Montefeltro *et al.* 2011; Godoy *et al.* 2014; Pol *et al.* 2014; Martinelli *et al.* 2018). The diversity of Notosuchia includes mostly terrestrial forms (Ósi 2013; Pol *et al.* 2014), which have a set of uncommon morphologies among crocodyliforms,

including shortening of the rostrum and a vast array of various tooth specializations, in both size and shape, which have been related to diverse diets, including hypercarnivory, herbivory, omnivory and durophagy (Ósi 2013; Godoy *et al.* 2014; Pol *et al.* 2014; Fiorelli *et al.* 2016; Iori & Carvalho 2018; Melstrom & Irmis 2019; Montefeltro *et al.* 2020).

Sphagesauridae (Kuhn 1968) (Table 1) forms a unique group of notosuchians, with indisputable records currently restricted to the Late Cretaceous deposits of South America (Novas *et al.* 2009; Carvalho *et al.* 2010; Pol *et al.* 2014; Martinelli *et al.* 2018). They are characterized by unique jaws and dentition (Pol *et al.* 2014), including an elongated mandibular symphysis, posterior teeth with an oblique orientation in relation to the craniomandibular axis and a thick enamel coating, with apicobasal crests and distinct ridges on the posterior teeth (Pol *et al.* 2014; Martinelli *et al.* 2018). Recent works have suggested that sphagesaurids are nested within a clade informally called

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**Figure 1.** Type locality of *Caipirasuchus attenboroughi*. **A**, maps of South America, Brazil and São Paulo, showing the provenance of the fossil; **B**, the outcrop of the Santo Anastácio Formation, with the bed in which the holotype specimen LAPEISA-0001 was collected *in situ* marked by an asterisk.

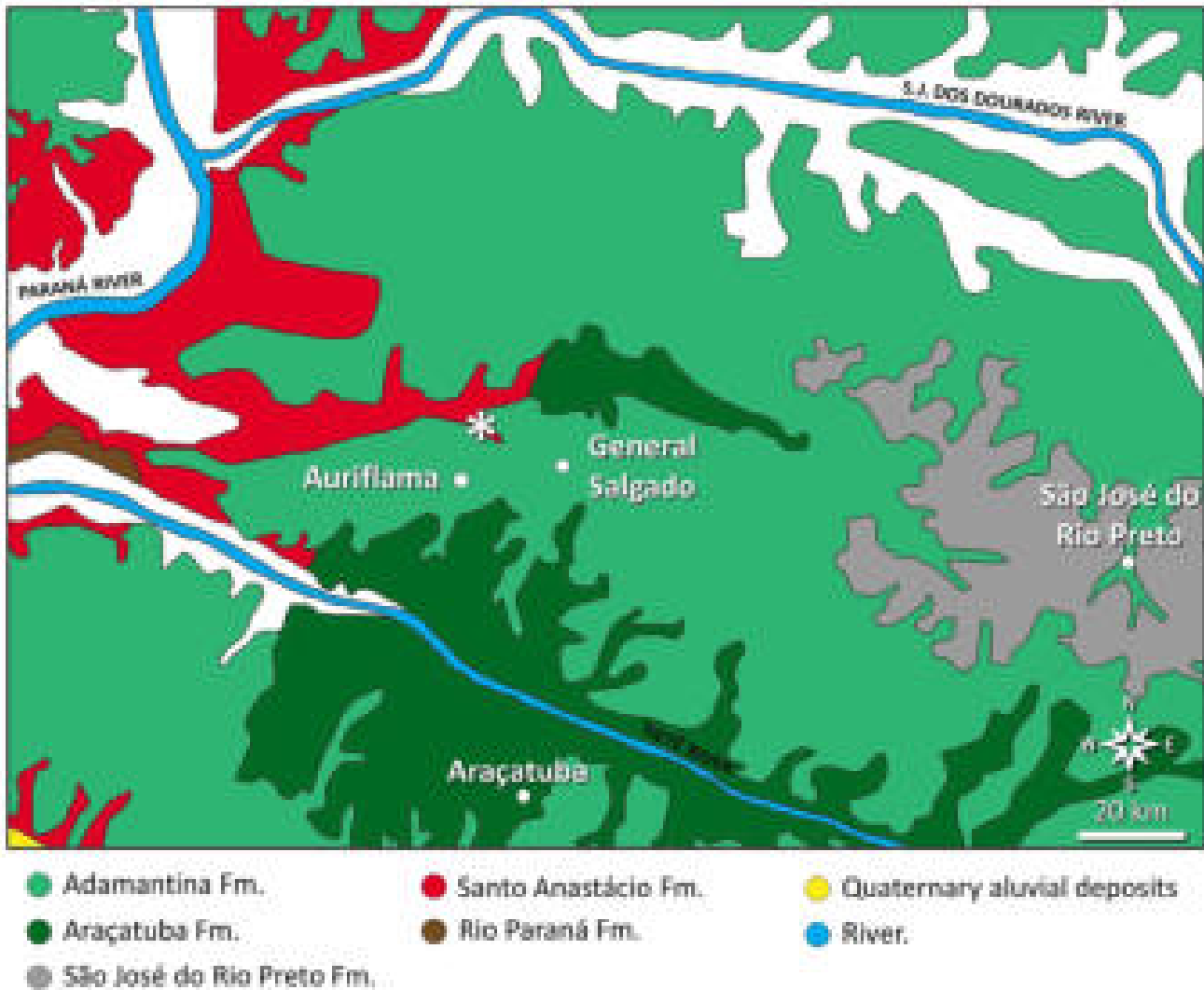
‘advanced notosuchians’ (Pol *et al.* 2014; Leardi *et al.* 2015a, b; Fiorelli *et al.* 2016; Martinelli *et al.* 2018), which also includes *Notosuchus terrestris* (Woodward 1896), *Morrinhosuchus luziae* (Iori & Carvalho 2009) and *Mariliasuchus* spp. (Carvalho & Bertini 1999; Nobre *et al.* 2007). Nevertheless, the existence of this clade remains debatable (Montefeltro *et al.* 2011, 2013; Godoy *et al.* 2014).

The past two decades witnessed a major increase in our knowledge of sphagesaurid diversity, which now encompasses at least nine species (Martinelli *et al.* 2018). Pol *et al.* (2014) revisited their phylogenetic relationships and pointed to the existence of three main subgroups: one formed by medium- to large-sized species, including *Sphagesaurus huenei* (Price 1950), *Armadillosuchus arrudai* (Marinho & Carvalho 2009) and *Caryonosuchus pricei* (Kellner *et al.* 2011a); another clade formed by the *Caipirasuchus* species *Cai. paulistanus* (Iori & Carvalho 2011), *Cai. montealtensis* (Iori *et al.* 2013), *Cai. stenognathus* (Pol *et al.* 2014), and *Cai. mineirus* (Martinelli *et al.* 2018); and a third clade composed by the smaller *Adamantinasuchus navae* (Nobre & Carvalho 2006) and *Yacarerani boliviensis* (Novas *et al.* 2009). Additionally, the puzzling *Labidiosuchus amicum* (Kellner *et al.* 2011b) might also belong to Sphagesauridae (Montefeltro *et al.* 2013; see Pol *et al.* [2014] for discussion on that topic).

Here, we describe a partial skull and lower jaws of a sphagesaurid collected in an outcrop of the Santo Anastácio Formation (Caiuá Group) in April 2016 by members of the Laboratório de Paleontologia e Evolução de Ilha Solteira (LAPEISA – FEIS/UNESP, Ilha Solteira, São Paulo), in the municipality of General Salgado, north-western São Paulo (Fig. 1). This is the first crocodyliform known from the Caiuá Group, corresponding to a new species of *Caipirasuchus*, which is closely related to *Cai. stenognathus* and *Cai. mineirus*.

### Geological setting

Much of our knowledge of notosuchian diversity comes from the Bauru Basin of south-central Brazil. The basin is divided lithostratigraphically into the Caiuá and Bauru groups (Fernandes & Coimbra 1996; Fernandes 1998), with the latter traditionally composed of the Araçatuba, Adamantina, Uberaba, Marília and Serra da Galga formations (Batezelli 2015; but see Fernandes 1998; Fernandes & Coimbra 2000; Soares *et al.* 2020). As for the Caiuá Group, it encompasses the Rio Paraná, Goio Erê and Santo Anastácio formations (Fernandes 1998; Fernandes & Coimbra 2000; Batezelli 2015), but Silva *et al.* (2005, 2009) and Meneggazo *et al.* (2015) referred the latter unit to the Bauru Group, based on the presence of a putative local discontinuity with other



**Figure 2.** Surface exposure of Bauru Basin rocks around the locality where LAPEISA-0001 was found (marked with an asterisk). Modified from Fernandes & Ribeiro (2014).

units of the Caiuá Group. The fossil record of the Bauru Group includes 20 valid notosuchian genera (Godoy *et al.* 2014; Martinelli *et al.* 2018; Pinheiro *et al.* 2018), representing the richest crocodyliform fauna known for the Cretaceous worldwide (Candeiro & Martinelli 2006; Riff *et al.* 2012). In contrast, despite its large surface exposure, vertebrate fossils are much rarer in the Caiuá Group *sensu* Fernandes (1998), and no crocodyliform has ever been formally described from this unit (Langer *et al.* 2019). For the Santo Anastácio Formation, the only vertebrate described to date is an unnamed podocmenidinuran turtle (Menegazzo *et al.* 2015).

The Santo Anastácio Formation is composed mainly of massive tabular sandy strata, intercalated with mudstone beds (Fernandes & Coimbra 1994, 2000) and bear common tubular, irregular holes that are associated with

nodules and carbonate concretions (Almeida *et al.* 1980). The unit has a maximum thickness of approximately 70–100 m (Fernandes & Coimbra 2000; Batezelli 2010) and resulted from the deposition of sand sheets that accumulated in desertic plains marginal to the sand dunes of the Caiuá Paleodesert (Fernandes & Coimbra 2000; Fernandes & Ribeiro 2014).

LAPEISA-0001 was recovered at the base of an outcrop (Fig. 1) located at the eastern limits of the Santo Anastácio Formation surface exposure, as mapped by Fernandes & Ribeiro (2014) (Fig. 2). Beyond its geographical location, the outcrop is assigned to that unit because its lithology differs markedly from that of nearby outcrops of the Adamantina Formation, but resembles that of Santo Anastácio Formation outcrops in the areas of Jales and Fernandópolis (Batezelli

2015). It is important to mention, however, that this assignment is not backed up by an extensive survey, and additional study of the local geology is necessary to position the outcrop in the stratigraphical schemes of the Bauru Basin (Fernandes 1998; Fernandes & Coimbra 2000; Silva *et al.* 2005, 2009; Batezelli 2015; Menegazzo *et al.* 2015).

The accurate dating of the Bauru Basin deposits plays a critical role in understanding notosuchian evolutionary history (Turner & Sertich 2010; Pol *et al.* 2014; Pol & Leardi 2015), but its chronostratigraphy remains under debate. An Aptian–Albian age has been inferred for the Caiuá Group, based on lithostratigraphical and palaeoclimatic data (Fulfaró *et al.* 1999; Dias-Brito *et al.* 2001), tectonic events and biostratigraphical correlation (Batezelli 2010, 2015; Menegazzo *et al.* 2016), including a record of tapejarid pterosaurs (Manzig *et al.* 2014; but see Langer *et al.* 2019). Alternatively, some authors argue for a Late Cretaceous age (Turonian–Campanian) for the Caiuá Group, based on an inferred depositional synchronicity with the best dated Bauru Group (Fernandes & Ribeiro 2014; Castro *et al.* 2018). As alternatively placed in either the Caiuá or Bauru groups, the age of the Santo Anastácio Formation is equally uncertain.

## Material and methods

### Institutional abbreviations

**ANM**, Agência Nacional de Mineração, Rio de Janeiro, Brazil; **LAPEISA**, Laboratório de Paleontologia e Evolução de de Ilha Solteira, Ilha Solteira, Brazil; **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MPMA**, Museu de Paleontologia de Monte Alto ‘Prof. Antonio Celso de Arruda Campos’, Monte Alto, Brazil; **MUCPv**, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; **MZSP**, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **UFRJ DG**, Departamento de Geologia, Universidade Federal do Rio de Janeiro no Rio de Janeiro, Rio de Janeiro, Brazil; **URC**, Museu de Paleontologia e Estratigrafia ‘Prof. Dr Paulo Milton Barbosa Landim’, Universidade Estadual Paulista, Rio Claro, Brazil.

### Collection and preparation

The specimen described here is housed in the permanent collection of LAPEISA, São Paulo State University, in Ilha Solteira-SP, Brazil. The fieldwork that resulted in its collection was communicated in advance to Agência Nacional de Mineração (ANM), as required by Brazilian

legislation (ordinance number 4.146 of 4 March 1942). The fossil was mechanically prepared using a pin vice and pneumatic tools at the Laboratório de Paleontologia, Universidade de São Paulo (Ribeirão Preto, Brazil).

### Computed tomography

Much of the palate and neurocranium of LAPEISA-0001 is covered with matrix, including the maxilla-palatine contact, the nasopharyngeal duct, the choanal region and the neurocranium. To access the anatomy of these regions, high-resolution micro-computed tomography was performed. The images were acquired at the ‘Centro para Documentação da Biodiversidade’ of the Universidade de São Paulo (Ribeirão Preto, Brazil). The scan was conducted in a GE Phoenix v | tome | x S240 Nanotom Scan machine. The material was digitized using 1000 slices at a voxel resolution of 0.1 mm. Segmentation was conducted using the software Amira v. 5.3.3. Thresholding was determined visually, using a combination of range-selection and manual operation to avoid confusing rocky matrix and bone.

### Phylogenetic analysis

LAPEISA-0001 was added to the phylogenetic data set of Montefeltro *et al.* (2013), which encompasses a high diversity of mesoeucrocodylians, including most notosuchians, and a vast sample of cranial and postcranial characters. This matrix was expanded with the inclusion of nine taxa (*Agaresuchus fortisiensis*, *Cai. stenognathus*, *Cai. mineirus*, *Caryonosuchus pricei*, *Labidiosuchus amicum*, *Lavocatchampsa sigogneaurussellae*, *Lohuecosuchus megadontos*, *Morrinhosuchus luziae* and *Pakasuchus kapilimai*) and 23 characters (485–507; see [Supplemental material](#)). Among the included characters, 14 (485–487, 489–491, 493–496, 504–507) are new and nine (488, 492, 497–503) were adapted from the data set of Pol *et al.* (2014). The final data matrix is composed of 100 taxa and 507 characters (see [Supplemental material](#)) and was analysed using equally weighted parsimony in TNT v. 1.5 (Goloboff & Catalano 2016), via a heuristic search (10,000 replicates). Tree bisection reconnection (TBR) was applied for branch swapping, saving 20 cladograms per round, and the random seed was set as ‘0’. The trees were collapsed after each replicate, and the most parsimonious trees were summarized in a strict consensus tree. *Labidiosuchus* and *Lavocatchampsa* were detected as unstable taxa in a preliminary analysis (see [Supplemental material](#), Fig. S2), likely a result of their fragmentary condition, and were excluded from the final parsimony analysis. Another factor related to the exclusion of these taxa is that they were not analysed first-hand by any of the authors of this work, hampering a more precise scoring for most of their characters.

## Systematic palaeontology

**Crocodyliformes** Hay, 1930 (*sensu* Clark  
in Benton & Clark 1988)

**Mesoeucrocodylia** Whetstone & Whybrow, 1983

**Notosuchia** Gasparini, 1971

**Eunotosuchia** taxon nov.

**Xenodontosuchia** taxon nov.

**Sphagesauria** taxon nov.

**Sphagesauridae** Khun, 1968

***Caipirasuchus*** Iori & Carvalho, 2011

***Caipirasuchus attenboroughi*** sp. nov.  
(Figs 3–5)

**Holotype.** LAPEISA-0001, including part of the secondary palate, neurocranium and an almost complete lower jaw with nine partially preserved tooth crowns (Fig. 3).

**Derivation of name.** The specific name is given in honour of Sir David Attenborough, a palaeontology enthusiast and fossil collector who sparked in many minds, including the first author of this study, an interest in life on Earth both past and present.

**Type locality.** A roadside outcrop at 111 km on SP-463 highway, General Salgado municipality, north-western São Paulo, Brazil (20°36'9.88"S, 50°30'50.19"W; Fig. 1).

**Stratigraphic horizon.** Santo Anastácio Formation, Caiuá Group, Bauru Basin (Fig. 2) Possibly Turonian–Campanian (see Geological setting and Discussion).

**Diagnosis.** A small-sized sphagesaurid that differs from other *Caipirasuchus* species by the following unique combination of characters (autapomorphies marked with an asterisk): presence of maxillopalatine fenestrae; posterior vertex of suborbital fenestra enclosed only by ectopterygoid; presence of groove in anterior portion of choanal septum; slender proximal region of pterygoids at contact with neurocranium; ventral surface of pterygoid flanges flat and smooth; basisphenoid ventral surface anteriorly continuous with choana; well-developed crest on quadrate parallel to exoccipital contact\*; absence of foramina in basioccipital ventral to the occipital condyle; hemimandibles diverging at 70° from one another at the portion between the symphyseal region and mandibular fenestra; hemimandibles continuously diverging to the level of the posterior half of the mandibular fenestra\*; lateral surface of dentaries posterior to tooth row inclined ventrolaterally\*; enlarged foramen intermandibularis oralis; anteroventral margin of external mandibular fenestra merging with floor of Meckelian canal\*; anterior process of angular contacting splenial medially and laterally\*; coronoid tuberosities placed posterior to surangular-dentary

suture; ventral coronoid tuberosities smaller than ascending medial process of angular; diastema between D5 and D6 formed by the dentary and splenial.

## Description

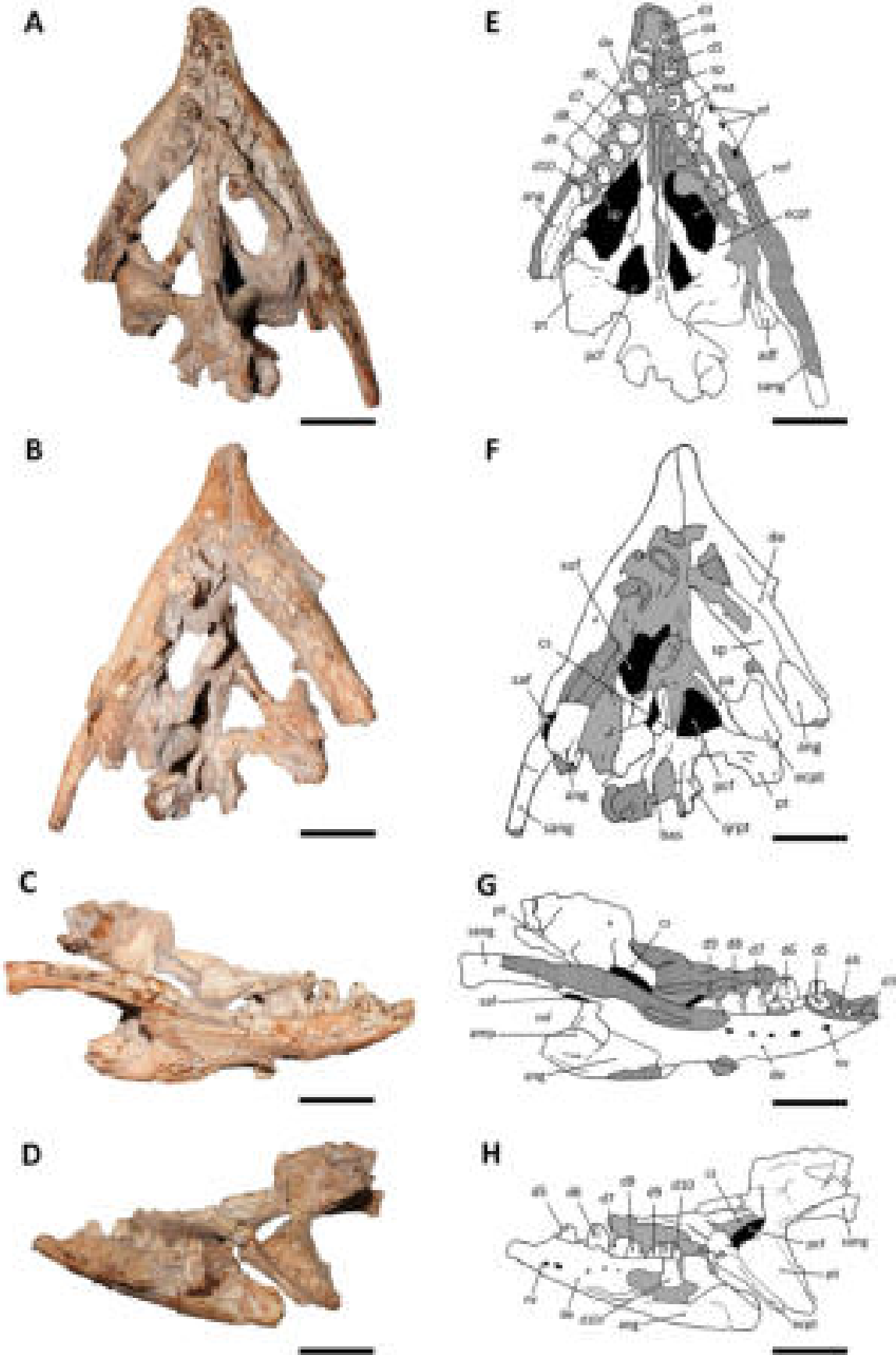
LAPEISA-001 includes a partial secondary palate, four maxillary tooth fragments, a partial neurocranium (Fig. 3) and almost complete lower jaws, with six tooth crowns preserved in the left hemimandible (Fig. 3) and four in the right. The preserved bones, although fragmented, show no signs of major deformation. However, the mandibular symphyseal region was damaged by excavation tools during road construction, obliterating most of its anterodorsal surface, including the incisiform teeth. Similar damage is also seen on the posterodorsal portion of the right mandibular ramus.

## Palate and basicranium – general morphology

The cranial bones in LAPEISA-0001 are limited to a partial secondary palate, including the right infraorbital and maxillopalatine fenestrae, the choanal groove and both pterygoid flanges (Fig. 3); the preserved neurocranium includes the quadrate ramus of the pterygoids, the basisphenoid, fragments of the basioccipital, as well as portions of the quadrate and exoccipital near the contact with the basioccipital.

## Suborbital fenestra

The general shape of the suborbital fenestra is difficult to define given the fragmentary nature of the specimen. However, its greatest mediolateral width is about two-thirds of its anteroposterior length, resembling the more elongated fenestra of *Cai. mineirus* rather than those of *Cai. paulistanus* and *Cai. montealtensis*. As in other notosuchians, such as *Comahuesuchus* and baurusuchids, the pterygoids in *Cai. attenboroughi* do not take part in the margins of the suborbital fenestra (Martinelli 2003; Montefeltro *et al.* 2011; Godoy *et al.* 2014; Pol *et al.* 2014). In ventral view, the palatine forms the medial margin of the fenestra, whereas the ectopterygoid forms the posterior margin and the posterior half of the lateral margin of the fenestra. The participation of the palatines in the posterior vertex of the suborbital fenestra is variable among baurusuchians and ‘advanced notosuchians’ (i.e. Sphagesauria). In *Cai. attenboroughi*, *Cai. mineirus*, *Cai. montealtensis*, *Mariliasuchus amarali* (UFRJ DG 106-R), *Notosuchus*, *Morrinhosuchus* and baurusuchids, the palatines do not take part in the posterior vertex of the suborbital fenestra, whereas in *Cai. paulistanus*, *Yacarerani* and *Comahuesuchus*, the vertex is located in the contact between the palatine and ectopterygoid (Martinelli 2003;



Novas *et al.* 2009; Iori *et al.* 2013). In at least one specimen of *Mariliasuchus* (MZSP-PV 50) and in *Cai. stenognathus* (MZSP-PV 139), the condition varies between the two sides of the skull (see Pterygoids, below). The nasopharyngeal duct of *Cai. attenboroughi* is proportionally wider than that of *Cai. paulistanus*, *Cai. montealtensis* and *Cai. mineirus*, but is similar to that of *Cai. stenognathus*, based on the relationship of its anteroposterior length (from the anterior vertex of the suborbital fenestra to the choanal groove) and width at its narrowest point.

### Choanal groove

*Sphagesaurus*, *Yacarerani*, *Mariliasuchus amarali*, *Notosuchus* and all *Caipirasuchus* species have a unique and complex choanal anatomy, in which the choana has a posteriorly directed opening, and is placed at the medial contact between the palatines at the posterior portion of the palatine bar. In *Cai. attenboroughi*, the same anatomical arrangement was revealed by the digital reconstructions (Fig. 4).

Posterior to the choana, *Cai. attenboroughi* has a pair of large, broad and roughly triangular openings, that are homologous with the parchoanal fenestrae (*sensu* Montefeltro *et al.* 2011), which usually appear as large, triangular apertures (Pol 2003; Andrade & Bertini 2008a; Montefeltro *et al.* 2011; Godoy *et al.* 2014). The parchoanal fenestra of *Cai. attenboroughi* faces anteroventrally along its anterior portion and posteroventrally on its posterior portion, at the level of the pterygoid flange. The anterolateral margin and the anterior portion of its medial margin are formed by the palatines, whereas it is enclosed medially by the pterygoids via the choanal septum (anteriorly) and the anterior margin of the pterygoid wings (posteriorly). The same configuration is present in *Cai. stenognathus*, *Cai. mineirus* and *Cai. montealtensis* (MPMA 68-0003 12), which is different from the large anteromedial surface of the pterygoid that almost completely surrounds the choanal groove (*sensu* Pol *et al.* 2014) in sebecids, mahajangasuchids, peirosaurids (*Montealtosuchus*, *Lomasuchus*, *Hamadasuchus*, *Barreirosuchus*), *Araripesuchus* and *Anatosuchus*.

The stout choanal septum of *Cai. attenboroughi* tapers in its posterior third and presents a longitudinal superficial groove at the anterior portion of its ventral surface. The same groove is seen in *Cai. stenognathus*

and *Cai. mineirus*, but not in *Cai. paulistanus* or *Cai. montealtensis*. As in the other *Caipirasuchus* species, the pterygoid of *Cai. attenboroughi* comprises most of the choanal septum, with the palatines participating only in the anterior portion of the choanal groove. *Cai. attenboroughi* has no sign of parchoanal fossae (*sensu* Montefeltro *et al.* 2011) on the ventral surface of the pterygoids, differing from baurusuchids, sebecids and some sphagesaurids (*Sphagesaurus* and *Cai. montealtensis* MPMA 15-0001/90; MPMA 68-0003/12).

### Maxilla

Only a small portion of the right maxilla is preserved, forming the anterior margin of the suborbital fenestra and contacting the palatine medially (Fig. 4). The contact between the maxilla and palatine is marked by an elongated maxillopalatine fenestra (*sensu* Andrade & Bertini 2008b), which is also present in *Cai. stenognathus* (Pol *et al.* 2014), *Cai. mineirus* (Martinelli *et al.* 2018), *Mariliasuchus amarali* (URC R-67, URC R-68, UFRJ 106-R; MZSP-PV 50; Andrade *et al.* 2006; Zaher *et al.* 2006; Andrade & Bertini 2008b) and *Notosuchus* (MACN-PV-RN 1038; Andrade & Bertini 2008b; Barrios *et al.* 2018). In *Cai. attenboroughi*, the maxilla forms the anterolateral margin of the maxillopalatine fenestra, enclosing most of that aperture, as in *Cai. stenognathus* and *Notosuchus*. In contrast, the maxillopalatine fenestrae of *Cai. mineirus* and *Mariliasuchus* are formed mostly by the palatine.

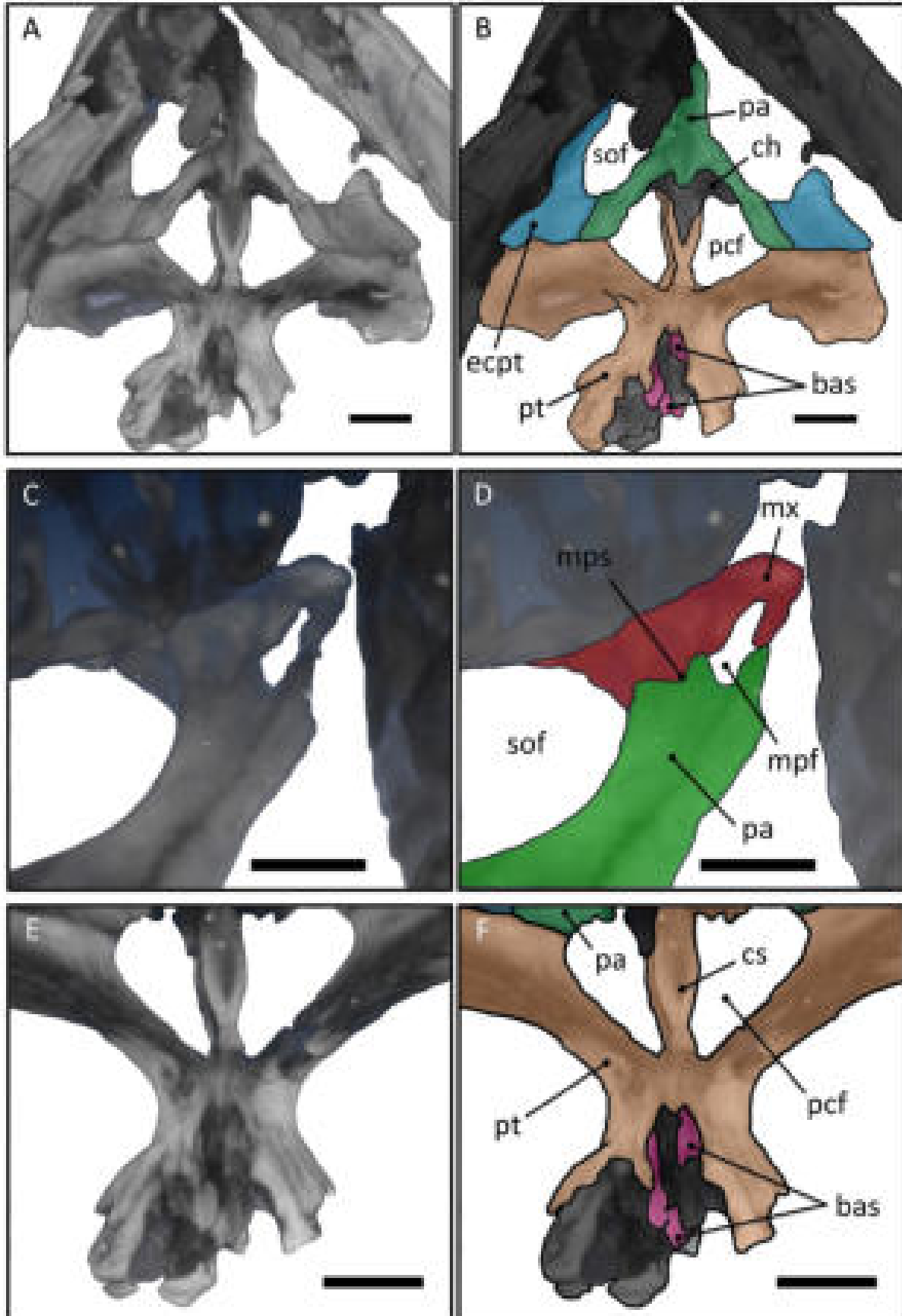
### Palatine

Both palatines are visible primarily in the digital reconstructions (Fig. 4). Each bone of the pair contacts the maxilla anteriorly, via a posterolaterally to anteromedially directed suture, forming a triangular-shaped surface in ventral view. The palatine encloses the posterior margin of the maxillopalatine fenestra.

The medial surface of the palatine of *Cai. attenboroughi* is similar to the condition in other *Caipirasuchus* species, forming a long and narrow interfenestral bar between the suborbital fenestrae. The flat ventral surface of the palatine forms the floor of the nasopharyngeal duct. The longer interfenestral bar is similar to that of *Sphagesaurus huenei* (Pol 2003), whereas this structure is

←  
**Figure 3.** *Caipirasuchus attenboroughi* sp. nov. (LAPEISA-0001, holotype) and interpretative drawing. **A** and **E**, dorsal view; **B** and **F**, ventral view; **C** and **G**, right lateral view; **D** and **H**, left lateral view. The grey and hatched areas indicate the presence of matrix and broken surfaces, respectively. **Abbreviations:** **amp**, ascending medial process of the angular; **ang**, angular; **bas**, basisphenoid; **cs**, choanal septum; **de**, dentary; **ecpt**, ectopterygoid; **d3** to **d10**, dentary teeth; **d10r**, root of molariform tooth (D10); **mf**, mandibular fenestra; **mxt**, fragments of the maxillary teeth; **nf**, neurovascular foramina; **pa**, palatine; **pcf**, parchoanal fenestra; **pt**, pterygoid; **qrpt**, quadrate ramus of pterygoid; **saf**, shallow anterior fossa of the surangular; **sang**, surangular; **sof**, suborbital fenestra; **sp**, splenial. Scale bars = 2 cm.





stouter in *Yacararani* (Novas *et al.* 2009), *Mariliasuchus* (UFRJ 106-R; Zaher *et al.* 2006) and *Notosuchus* (MACN-PV-RN 1037). In baurusuchids, the ventral floor of the nasopharyngeal duct is longer and narrower than that of sphagesaurids (Montefeltro *et al.* 2011; Godoy *et al.* 2014; Pol *et al.* 2014). Although poorly preserved, the interfenestral bar in *Comahuesuchus* and *Pakasuchus* is longer and wider than in *Caipirasuchus*.

The posterior region of the palatine in *Cai. attenboroughi* diverges laterally to form the posterolaterally directed palatine bars (*sensu* Zaher *et al.* 2006), separating the suborbital fenestrae from the choanal groove. The distal portion of each diverging ramus contacts the medial edge of the ectopterygoid at the posterior corner of the suborbital fenestra but does not form its posterior vertex. Its distal tip reaches the contact between the ectopterygoid and pterygoid, forming a triple junction at the ventromedial portion of the pterygoid flange (Fig. 4). The ventral surface of the palatine, near the contact with the ectopterygoid, is similar to that of *Cai. stenognathus*, with a morphology intermediate between the broad exposition of *Cai. paulistanus* and *Cai. montealtensis* and the extremely reduced surface of *Cai. mineirus*.

The ventral surface of the posterior region of palatine of *Cai. attenboroughi* (medially in the choanal groove) is marked by a longitudinal groove that is only accessible via the digital reconstructions. At its posterior end, the palatine becomes narrower, forming the anterior margin of the choanal opening, including the anterior-most portion of the choanal septum, and attaching to the pterygoid posteriorly.

### Ectopterygoids

Only the posteroventral processes of the ectopterygoids are preserved in LAPEISA-0001, each forming a bar that encloses the posterolateral margin of the suborbital fenestra and overlying the pterygoid flange. On the right side, the participation of the bone in the lateral margin of the suborbital fenestra is preserved only on its posterior portion, so that the exact configuration of the anterior ectopterygoid process is not accessible.

The posteroventral bar of the ectopterygoid of *Cai. attenboroughi* is broad with a sub-circular cross-section. This condition is similar to that of *Cai. stenognathus*, whereas in *Cai. mineirus*, *Cai. paulistanus* (MPMA 67-0001/00) and *Cai. montealtensis* (MPMA 15-0001/90, MPMA 68-0003/12) the ectopterygoid bar is more

gracile and has a flatter ventral surface. Posterior to the bar, the ectopterygoid expands lateromedially, contacting the posterior end of the palatine bar medially and the pterygoid posteriorly. This expanded portion of the bone overlaps the pterygoid ventral surface and forms the ectopterygoid flange. The ectopterygoid-palatine contact can be seen on both sides; it includes a small anteriorly directed process of the ectopterygoid that forms the entire posterior vertex of the suborbital fenestra. This condition is also present in *Cai. mineirus*, *Cai. montealtensis* and *Mariliasuchus*, whereas this condition is seen in only on the right side of the holotype of *Cai. stenognathus*, which was regarded as a preservation artefact by Pol *et al.* (2014). In *Cai. paulistanus*, *Yacararani* and *Comahuesuchus*, the palatine also participates in the posterior vertex of the suborbital fenestra, whereas in *Mariliasuchus*, both conditions are present in different specimens. In *Notosuchus*, *Morrinhosuchus* and baurusuchids, the ectopterygoid forms a larger part of the posterior portion of the palatine bar.

### Pterygoids

The pterygoids of *Cai. attenboroughi* are fused into a single median element that, for descriptive purposes, is divided into three distinct regions: an anterior portion, a pair of lateroventrally projecting flanges and a dorsal portion. The anterior portion borders the posterior margin of the parachoanal fenestrae, the projecting flanges form the pterygoid wings, and the dorsal portion firmly attaches to the neurocranium, contacting the laterosphenoid and quadrate anteriorly and the pterygoid process of the quadrate posterolaterally.

The anterior process of the pterygoid participates extensively in the lateral and posterior edges of the parachoanal fenestrae, enclosing the structure posteriorly along the anterior margin of the pterygoid flanges, and medially through the choanal septum (see Choanal groove, above). In *Caipirasuchus* species, the separation between the parachoanal fenestrae is mostly or entirely formed by the anterior projection of pterygoid. The narrower posterior third of the choanal septum of *Cai. stenognathus* and *Cai. mineirus* is more laminar than that of *Cai. attenboroughi*, which has a wider ventral surface.

The pterygoid flanges in *Cai. attenboroughi* are lateroventrally directed, with a narrower proximal region at the contact with the neurocranium, as in *Cai. montealtensis*, *Cai. stenognathus* and *Cai. mineirus*. The base of

**Figure 4.** *Caipirasuchus attenboroughi* sp. nov. (LAPEISA-0001) digital reconstructions (left) and interpretative drawings (right). General ventral view (A, B) and details of palate (C, D) and neurocranium (E, F). **Abbreviations:** **bas**, basisphenoid; **ch**, choana (covered by matrix); **cs**, choanal septum; **ecpt**, ectopterygoid; **mpf**, maxillopalatine fenestra; **mpps**, maxilla-palatine suture; **mx**, maxila; **pa**, palatine; **pcf**, parachoanal fenestra; **pt**, pterygoid; **sof**, suborbital fenestra. Scale bars = 1 cm.

each pterygoid flange is anteroposteriorly narrow, and the flanges expand gradually from that point towards their ventral tips. Among *Caipirasuchus* species, this condition differs only from that of *Cai. paulistanus* (MPMA 67-0001/00), in which the proximal region of the flanges is stouter. *Cai. attenboroughi*, *Cai. montealtensis*, *Cai. mineirus*, *Cai. stenognathus*, *Sphagesaurus*, *Mariliasuchus* and *Notosuchus* have pterygoid flanges with restricted proximal portions and that are oriented at an angle of approximately 90° to the longitudinal axis of the skull. The flanges of *Morrinhosuchus* and *Cai. paulistanus* are similarly oriented but have a broader base. Conversely, *Yacarerani* shows more posteromedially oriented flanges, forming angles of approximately 45° to the longitudinal axis of the skull, and with the same width throughout.

The ventral surface of the pterygoid flange in *Cai. attenboroughi* is flat and smooth, lacking both the parchoanal fossae of *Cai. montealtensis* (MPMA 15-0001/90; MPMA 68-0003/12) and the slight depression seen in *Cai. stenognathus* and *Cai. mineirus*. The homogeneity (Lankester 1870) of the parchoanal fossae among sphagesaurids, baurusuchids and sebecids varies depending on the phylogenetic context. Their distribution suggests that such structures had multiple acquisitions during the evolutionary history of notosuchians (Pol *et al.* 2014), being present in Sphagesauridae, *Stratiotosuchus*, *Pissarrachamps*, *Apletosuchus*, *Sebecus querejazus* and *Lorosuchus* (Andrade *et al.* 2006; Montefeltro *et al.* 2011; Pol *et al.* 2014; Godoy *et al.* 2014). Dias *et al.* (2019) showed that the parchoanal fenestra in *Cai. montealtensis* (MPMA-68.0003/12, MPMA-68.0004/12) includes a secondary chamber connected to the internal nares. This second chamber is absent in *Cai. attenboroughi* and *Cai. paulistanus*.

Although the posterior edges of the pterygoid flanges are not completely preserved in LAPEISA-0001, they are clearly laminar in this region. On the lateral edge, the lamina becomes thicker due to the presence of pneumatic diverticula, as seen in other *Caipirasuchus* spp. and in baurusuchids (Montefeltro *et al.* 2011; Dias *et al.* 2019). In the anterior portion of the ventral surface of the flanges, the pterygoid contacts the ectopterygoids laterally and the palatines medially. A reduced platform supports the posterior end of the ectopterygoid and the palatine bars, a trait also found in all other *Caipirasuchus* species (notably enlarged in *Cai. stenognathus*), as well as in *Yacarerani*, *Mariliasuchus* and *Notosuchus* (Pol *et al.* 2014). The anterodorsal surface of each pterygoid flange bears a marked concavity at its dorsal surface, reaching ventrally about its mid-length. This crest is absent in *Mariliasuchus amarali* (UFRJ 105-R) and possibly also in *Cai. paulistanus* (MPMA 67-0001/00) and *Notosuchus* (MUCP-147, MLP-64-IV-16-5).

Posterior to the flanges, in ventral view, the pterygoid extends posterodorsally, contacting the quadrates and attaching to the basisphenoid. As in other sphagesaurids and *Mariliasuchus*, the quadrate processes of the pterygoid of *Cai. attenboroughi* are reduced due to the long pterygoid process of the quadrates. As stated by Pol *et al.* (2014), other notosuchians, such as baurusuchids, sebecids, peirosaurids, mahajangasuchids, *Araripesuchus*, *Uruguaysuchus*, *Simosuchus*, *Morrinhosuchus* and *Malawisuchus*, the quadrate processes of the pterygoid extend posteriorly to the level of the lateral pharyngotympanic tube.

### Basisphenoid

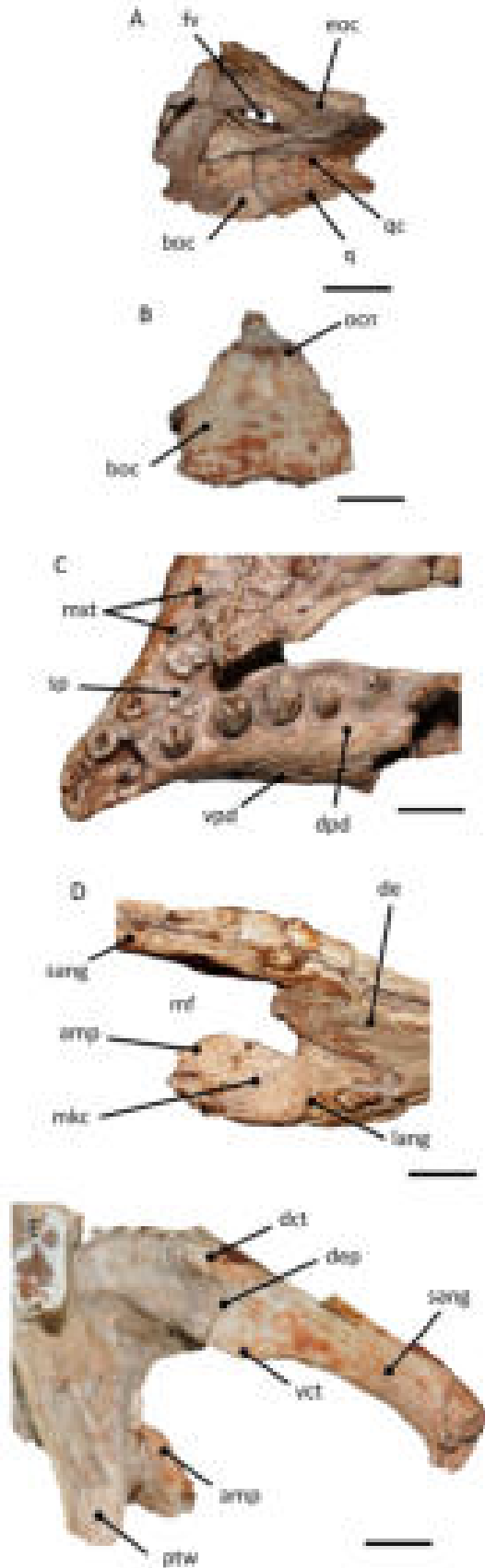
Only the anterior portion of the basisphenoid is preserved and it is covered with matrix, but its general shape is similar to that of *Cai. stenognathus*, attaching to the pterygoid anteriorly and laterally. A large ventral exposure of the basisphenoid is a common feature among notosuchians and is observed in baurusuchids, *Mariliasuchus* and sphagesaurids (Montefeltro *et al.* 2011; Pol *et al.* 2014). In *Caipirasuchus* specimens in which the region is preserved (*Cai. montealtensis*, MPMA 15-0001/90, MPMA 68-0003/12; *Cai. stenognathus* [Pol *et al.* 2014] *Cai. mineirus* [Martinelli *et al.* 2018]), the ventral surface of the basisphenoid has a trapezoidal shape, with a length equal to or longer than its width.

The basisphenoid ventral surface in *Cai. attenboroughi* is markedly recessed in its central portion between the basisphenoid crests. In a similar configuration, the openings of the medial pharyngeal tube and the pharyngotympanic tubes of *Cai. stenognathus* are within such a recess. Yet in LAPEISA-0001, the digital reconstructions reveal a collapsed basisphenoid ventral floor (Fig. 4), so those openings are not visible within the recess. In any case, the recess forms a continuous canal with the medial surface of the pterygoid anteriorly.

### Occipital surface

A fragment of the right side of the occipital region of the neurocranium of *Cai. attenboroughi* is preserved. This includes only the region of contact between exoccipital, basioccipital and quadrate (Fig. 5). It exposes a posteroventral surface, composed mostly of the ventral portion of exoccipital, with a small participation of the quadrate, and a ventral surface, composed of the quadrate and the posterior part of the basioccipital.

The exoccipital forms the main portion of the occipital fragment. Most mesoeucrocodylians have a ridge dividing the posterodorsal and posteroventral planes of the exoccipital (Pol *et al.* 2014). In LAPEISA-0001, only the portion ventral to this ridge is preserved, so the participation of the exoccipital in the occipital condyle



or in the margin of the foramen magnum cannot be determined. Dorsal to the contact with the basioccipital there is a large vagus foramen, but no further details can be assessed.

The preserved portion of the quadrate in the occipital fragment of LAPEISA-0001 corresponds to the medial-most portion of the quadrate-exoccipital suture. At this point, the quadrate bears a crest that extends parallel to the suture. This crest is absent in *Cai. stenognathus*, *Cai. mineirus* and *Yacarerani*, but an incipient similar crest is present in *Cai. montealtensis* (MPMA 15-0001/90; MPMA 68-0003/12) and *Cai. paulistanus*, and a well-developed crest is seen in *Sphagesaurus* and *Armadillosuchus* (UFRJ DG 303-R). A similar crest is found in the same region in *Simosuchus* and some peirosaurids (*Montealtosuchus*, *Stolokrosuchus*). However, in these non-sphagesaurid taxa, the crest is more ventrally positioned and farther from the quadrate-exoccipital contact. Therefore, the equivalence of these crests is not straightforward. Medial to the crest, the quadrate contacts the basioccipital.

The basioccipital portion of the occipital fragment is poorly preserved. Most of its surface is fragmented, exposing the brain cavity. A small portion of the occipital condyle neck is visible (Fig. 5) but, unlike in *Cai. stenognathus*, there is no foramen in the ventral surface beneath the occipital condyle.

### Mandible – general morphology

The mandible of LAPEISA-0001 comprises an almost complete symphyseal region and both hemimandibles are preserved posteriorly to the level of the anterior margin of the mandibular fenestra (Fig. 3). The symphyseal region is long and narrow in *Cai. attenboroughi*, reaching the level of the sixth dentary tooth (D6) (Figs 3, 5). The hemimandibles have a parallel orientation in the symphyseal region. From the posterior end of the symphysis, the hemimandibles strongly diverge posterolaterally, giving the mandible the typical ‘Y’-shape

**Figure 5.** Details of the anatomy of *Caipirasuchus attenboroughi* sp. nov. (LAPEISA-0001): **A**, posterior view of the occipital fragment (dark line indicates the contact between the bones); **B**, posterior view of the basioccipital fragment; **C**, dorsal view of the symphyseal region; **D**, medial view of the anterior right mandibular fenestra; **E**, medial view of the right mandibular ramus. Abbreviations: **amp**, ascending medial process of the angular; **boc**, basioccipital; **dct**, dorsal coronoid tuberosity; **de**, dentary; **dep**, depression between coronoid tuberosities; **dpd**, dorsal plane of the dentary; **eoc**, exoccipital; **fv**, foramen vagi; **lang**, lateral surface of the angular; **mkc**, Meckelian channel; **mxt**, fragments of the maxillary teeth; **ocn**, occipital condyle neck; **ptw**, pterygoid wing; **q**, quadrate; **qc**, quadrate crest; **sang**, surangular; **sp**, splenial; **vct**, ventral coronoid tuberosity; **vpd**, ventral plane of the dentary. Scale bars = 1 cm.

observed in sphagesaurids, *Mariliasuchus* (UFRJ DG 50-R, UFRJ DG 105-R, UFRJ DG 106-R, MZSP-PV 50), *Labidiosuchus* and *Notosuchus* (MACN-1037, MACN-1041, MUCPv-35, MUCPv-147). In other notosuchians, such as baurusuchids, sebecids, *Pakasuchus*, *Malawisuchus*, *Candidodon*, *Uruguaysuchus*, *Lybicosuchus* and *Araripesuchus*, the hemimandibles gradually diverge from one another. Pol *et al.* (2014) suggested that the holotype of *Morrinhosuchus luziae* has a ‘Y’-shaped mandible, but a newly described specimen with a more complete mandible (MPMA 12-0050/07; Iori *et al.* 2018) shows no strong curvature posterior to the symphysis. In sphagesaurids, the hemimandibles become parallel posterior to the anterior edge of the mandibular fenestra. In *Cai. attenboroughi*, the hemimandibles continue to diverge from one another at this point, resembling the condition of non-sphagesaurids such as *Mariliasuchus*, *Labidiosuchus* and *Notosuchus*.

The angle between the two hemimandibles, from the posterior end of the symphysis to the anterior margin of the mandibular fenestra, varies among *Caipirasuchus* species, being approximately 50° in *Cai. stenognathus*, 60° in *Cai. mineirus* and *Cai. montealtensis* (MPMA 68-0003/12), and 70° in *Cai. attenboroughi* and *Cai. paulistanus*. Due to the unique morphology of the mandible of sphagesaurids it is difficult to compare this particular characteristic with other notosuchians. Even among other, non-*Caipirasuchus* sphagesaurids, the scope for comparison is limited due to the few taxa for which hemimandibles are preserved.

The mandibular symphysis of *Cai. attenboroughi* is formed mostly by the dentaries, with a small participation of the dorsal portion of the splenials. It is antero-posteriorly long, tapering anteriorly in both lateral and dorsal views. The symphysis reaches the level of D6, as in the other species of *Caipirasuchus*. However, this long symphyseal region of the members of *Caipirasuchus* is further modified to be three times longer than wide. The symphysis is only twice longer than wide in larger sphagesaurids (*Sphagesaurus*, *Armadillosuchus*, *Caryonosuchus*) and is as long as it is wide in other sphagesaurids, *Mariliasuchus* and *Notosuchus* (Pol *et al.* 2014).

## Dentary

The dentary forms most of the symphysis and reaches the anterior margin of the mandibular fenestra (Fig. 3). Its lateral and ventral surfaces are weakly ornamented with shallow, irregular grooves. In lateral view, the dorsal margin of the dentary is slightly concave posterior to the symphyseal region, and then turns dorsally until the level of the last mandibular alveolus. In lateral view, the ventral margin of the dentary in *Cai. attenboroughi* is

upturned at the symphyseal region and remains roughly straight posteriorly. In ventral view, the contact between the two dentaries is marked by a slight groove at the sagittal line. The ventral surface of the dentaries is mostly preserved, but breakages at the posterior part of the symphyseal region obscure the exact course of this part of the dentary-splenic contact.

The lateral surface of the dentary of *Cai. attenboroughi* is divided into two planes (Fig. 5C). The ventral plane is ventrolaterally directed and comprises most of the lateral surface of the dentary. The dorsal plane corresponds to the alveolar shelf (*sensu* Pol *et al.* 2014), which is flat and dorsolaterally oriented and extends laterally beyond the labial margin of the alveoli. This shelf extends from between D5 and D6 to the posterior-most mandibular alveolus. As a result, this part of the tooth row is medially displaced compared to the lateral surface of the dentary. This feature is also present in other sphagesaurids, as well as in *Mariliasuchus*, *Notosuchus*, *Morrinhosuchus*, *Malawisuchus* and *Pakasuchus*, as noted by Pol *et al.* (2014).

A row of five enlarged foramina is present in the anterior portion on the alveolar shelf. The anterior two foramina are larger, being almost twice the size of the posterior three. A similar line of foramina is present in all other *Caipirasuchus*, *Yacararani* and *Mariliasuchus*, but they are not as enlarged in the latter as in sphagesaurids (Pol *et al.* 2014).

In dorsal view, the dorsal surface of the dentary of *Cai. attenboroughi* is more laterally restricted in the symphyseal region, and it gradually widens posterior to D6, where the alveolar shelf becomes more laterally developed. The area of the five posterior alveoli of the dentary possess a lingual extension that forms an incomplete alveolar septum, as in other species of *Caipirasuchus*. Yet the alveoli of D5 and D6 are completely separated from one another by a septum, as in *Cai. montealtensis*, *Cai. paulistanus* and *Cai. stenognathus* but not in *Cai. mineirus* (Martinelli *et al.* 2018).

Posterior to the tooth row, the dentaries are dorsoventrally expanded, contacting the angular, just beneath the anterior margin of the external mandibular fenestra, and the surangular, at the dorsal margin of the fenestra. The laterodorsal to medioventral inclination of the dentary is more pronounced in *Cai. attenboroughi* than in the other *Caipirasuchus* species. In lateral view, the angular-dentary contact is anteroventrally to posterodorsally inclined, so that the dentary participates only in the anterior margin of the fenestra, and it is excluded from its anteroventral margin by the angular, as in most notosuchians.

The surangular-dentary contact is not preserved in the left hemimandible of LAPEISA-0001 and is hard to

identify on the right side due to poor preservation. Yet the posterodorsal ramus of the dentary extends along the anterior portion of the dorsal margin of the mandibular fenestra. In *Yacararani*, *Adamantinasuchus*, *Labidiosuchus*, *Mariliasuchus amarali* and the other *Caipirasuchus* species, the posterodorsal ramus is divided into two processes, one dorsal and one ventral, that overlie the anterior region of the surangular, forming a ‘V’-shaped contact between the bones in lateral view (Pol *et al.* 2014).

### Splénial

The splénial of *Cai. attenboroughi* is similar to that of other sphagesaurids, covering most of the medial surface of the hemimandible, from the symphyseal region to the anterior margin of the adductor fossa. The medial surface of the splénial is flat, smooth and dorsoventrally oriented. There is an aperture at the level of the last dentary tooth, suggesting the presence of a large oval foramen intermandibularis oralis. This foramen is placed at the level of D9–10, as also seen in *Cai. paulistanus*, *Cai. montealtensis* and *Cai. stenognathus*, whereas it is more anteriorly positioned in *Cai. mineirus*, at the level of D8 (Martinelli *et al.* 2018).

The posteriorly located foramen intermandibularis oralis is a feature shared by sphagesaurids, baurusuchids and sebecids (Pol *et al.* 2014), although a larger and slot-like foramen is present only in baurusuchids and sebecids (Ortega *et al.* 1996; Sereno & Larsson 2009; Montefeltro *et al.* 2011). The foramen intermandibularis oralis is more dorsally positioned in *Morrinhosuchus*, *Notosuchus* and *Mariliasuchus* (Pol *et al.* 2014), but it is more ventrally located in sphagesaurids. Additionally, in *Cai. attenboroughi*, *Cai. montealtensis* and *Cai. paulistanus*, the foramen length is approximately 50% of the height of the splénial, whereas it is smaller in *Cai. stenognathus*, *Yacararani*, *Mariliasuchus* and *Notosuchus*.

The anterior portion of the splénial is fragmentary on both sides of LAPEISA-0001, so there is no precise information about the course of the contact with the dentary and its participation in the symphysis. However, the posterior portion of the dorsal surface of the symphysis is well preserved, and two medially displaced fragments between D5 and D6 and are interpreted as the anterior portion of the splénials (Fig. 5). Due to poor preservation, it is not possible to confirm the presence of the peg in the posterior surface of the symphyseal region, or the presence of splénial depressions (*sensu* Montefeltro *et al.* 2011).

The ventral surface of the splénial is preserved only posterior to the symphysis, where it is reduced to a thin, dorsoventrally oriented lamina covering the lingual alveolar wall, from D6 to D10, as in other species of *Caipirasuchus*. The alveolar margin of the splénial

expands labially in the form of reduced triangular processes between the alveoli, which do not contact the corresponding processes of the dentary, resulting in incomplete alveolar septa from D6 to D10, as in most notosuchians (Ortega *et al.* 1996; Pol & Apesteguía 2005; Pol *et al.* 2014). Just posterior and ventral to the last dentary tooth, the splénial contacts the angular in a ‘V’-shaped suture, but the relationship with the mandibular fenestra is not accessible.

### Angular

Only the anterior portion of the angular, forming the ventral and anteroventral margins of the mandibular fenestra, is preserved in LAPEISA-0001, showing a ‘U’-shaped cross-section, overlapped by the splénial medially and dentary laterally.

The angular of *Cai. attenboroughi* bears a distinctive shallow fossa beneath and anterior to the external mandibular fenestra. This is also present in *Cai. stenognathus*, *Cai. montealtensis*, *Adamantinasuchus*, *Yacararani*, *Mariliasuchus* and *Notosuchus*, but is absent in baurusuchids and other notosuchians (Pol *et al.* 2014). However, the condition in *Cai. attenboroughi* is unique, with the anteroventral margin of the fossa at the external mandibular fenestra gradually merging with the floor of the Meckelian canal (Fig. 5), instead of forming a prominent ridge as in the other *Caipirasuchus* species.

In medial view, the angular of *Cai. attenboroughi* has a large ascending medial process that forms the medial limit of the anterior edge of the internal mandibular fenestra (Fig. 5), as in *Mariliasuchus* (UFRJ DG 105-R; UFRJ DG 106-R) and *Adamantinasuchus* (UFRJ DG 107-R). This process is highly discrepant in size and shape among sphagesaurids and closely related notosuchians. This process is robust in *Cai. stenognathus*, with a bulbous, rugose dorsal surface (Pol *et al.* 2014), but it is less prominent in other *Caipirasuchus* species, *Yacararani* and *Notosuchus*, in which it is the same height as the angular ramus posteriorly.

In ventral view, the angular of *Cai. attenboroughi* tapers anteriorly, and the suture with the splénial has an anterior process that extends ventrally towards the anterior limit of that bone, forming a ‘V’-shaped contact. That contact is not as complex in other *Caipirasuchus* species, *Yacararani*, *Mariliasuchus* and *Notosuchus*, with little or no interdigitation between angular and splénial.

### Surangular

The surangular in LAPEISA-0001 is preserved anteriorly from the contact with the dentary and posteriorly to the posterodorsal margin of the external mandibular fenestra, forming the dorsal arch of the mandibular fenestra. The lateral contact of the surangular with the

dentary is anteroventrally positioned compared with that of other *Caipirasuchus* species, with the surangular occupying most of the dorsal margin of the mandibular fenestra. In this configuration, the surangular restricts the participation of the dentary in the fenestra. Although incomplete, the surangular does not reach the level of the last alveolus, unlike the condition in *Cai. mineirus* (Martinelli *et al.* 2018).

In medial view, the anterior portion of the surangular bears two distinct rugose protuberances, the coronoid tuberosities (*sensu* Pol *et al.* 2014) (Fig. 5), separated by a depression. These are common among notosuchians, as seen in sphagesaurids (*Caipirasuchus*, *Yacararani*, *Adamantinasuchus*), *Mariliasuchus* and *Morrinhosuchus*. In baurusuchids, *Araripesuchus gomesii*, *A. tsangatsangana* and *Simosuchus*, the tuberosities are present, but are smaller and separated by a less prominent depression (Pol *et al.* 2014). As in *Cai. paulistanus* and *Cai. montealtensis*, the dorsal coronoid tuberosity of *Cai. attenboroughi* is positioned posterior to the level of the posterior tip of the dorsal process of the dentary, whereas in *Cai. stenognathus* and *Cai. mineirus* the tuberosity is placed right below this process. The ventral coronoid tuberosity is well-developed in *Cai. attenboroughi*, facing the ascending medial process of the angular. The longitudinal depression between the coronoid processes is shallower in *Cai. attenboroughi* than in *Cai. stenognathus*, and similar to that of *Cai. paulistanus* and *Cai. montealtensis*. In the ventral surface of the surangular, just anterior to the ventral coronoid process, there is a shallow fossa, which is also present in *Cai. stenognathus* (Pol *et al.* 2014) but not possible to assess in *Cai. paulistanus*, *Cai. montealtensis* and *Cai. mineirus*. In *Cai. attenboroughi* this fossa is rounded, whereas it is more elongated and drop-shaped in *Cai. stenognathus* (Pol *et al.* 2014).

The portion of the surangular posterior to the coronoid processes becomes slightly displaced medially in relation to the rest of the bone. This orientation indicates that the main axes of the hemimandibles become parallel to one another. At the level of the mid-length of the mandibular fenestra, the surangular becomes lateromedially thinner, as in other sphagesaurids, *Mariliasuchus* and *Notosuchus*. However, *Cai. attenboroughi* shows the most extreme condition of all these taxa, in which the surangular is proportionally thinner than even those of smaller taxa, such as *Yacararani* and *Adamantinasuchus*.

### Dentition

Only two isolated tooth root fragments, both oval in cross-section, are preserved from the upper series, so most of the tooth anatomy cannot be assessed. Additionally, two small fragments preserved near the

right hemimandible, labially positioned between D6–7 and D7–8, are interpreted as maxillary tooth fragments, suggesting the presence of the characteristic occlusal pattern of sphagesaurid molariform teeth (Pol *et al.* 2014; Iori & Carvalho 2018).

The anterior-most symphyseal teeth are not preserved in the lower jaw of LAPEISA-0001, and the first preserved tooth in the right hemimandible (Fig. 3) is estimated to be D3, based on the comparison of its shape and position with better preserved *Caipirasuchus* specimens. Tooth crowns are best preserved from D5 to D10 on the left side and from D6 to D9 on the right side. Sphagesaurians have a reduced dental formula and a certain degree of heterodonty (Lecuona & Pol 2008; Montefeltro *et al.* 2009; Augusta & Zaher 2019). Based on the other species of *Caipirasuchus*, we were able to reconstruct the dental formula of *Cai. attenboroughi* as including a total of 10 lower jaw teeth, with D1–3 interpreted as incisiviforms, D4 as a transitional/caniniform tooth and D5–10 as molariforms.

In *Cai. attenboroughi*, as in most *Caipirasuchus*, the molariforms D6–10 are set in a continuous alveolar groove, whereas the first molariform (D5) is placed in an alveolus isolated from those of D4 and D6. Yet in *Cai. mineirus*, there is no diastema between D5 and D6, with all molariforms set in a continuous alveolar groove (Martinelli *et al.* 2018). In *Cai. paulistanus* and *Cai. montealtensis*, the alveolar septum is formed only by the dentary, whereas in *Cai. attenboroughi* and *Cai. stenognathus* it is formed by both the dentary labially and the splenial lingually (Pol *et al.* 2014).

The molariform teeth of sphagesaurids have a unique morphology, with deep roots, teardrop-shaped cross-sections, and laterally compressed crowns with the major axis oblique to the long axis of the hemimandible, a condition called ‘sphagesauriform’ (Iori & Carvalho 2018), but also present in the non-sphagesaurids *Mariliasuchus*, *Labidiosuchus* and *Notosuchus*. In *Cai. attenboroughi*, the molariform teeth are more oval than the typical teardrop shape seen in other *Caipirasuchus* species.

The molariform teeth of *Cai. attenboroughi* show a faint constriction between the bulbous crown and the root, as in other *Caipirasuchus* species (MPMA 67-0001/00, MPMA 15-0001/90, MPMA 68-0003/12), *Armadillosuchus* (UFRJ DG 303-R), *Adamantinasuchus* and *Mariliasuchus* (UFRJ DG 105-R, UFRJ DG 106-R). The typical carinae present in *Caipirasuchus*, *Armadillosuchus* and *Sphagesaurus* cannot be assessed in detail, because most of the enamel and dentine is absent in LAPEISA-0001. However, the few patches of preserved dentine seem to point to a less developed

dentine coating in the new taxon. Even so, it is possible to recognize the typical apicobasal ridges in D5–7 and D9.

In the posterior part of the tooth row, the teeth decrease in size along with an increase in the size of the alveolar septa. As such, D10 is much smaller than D6, a condition that resembles that of *Cai. montealtensis*. Still, the molariform teeth of *Cai. attenboroughi* appear to be larger than those of the other *Caipirasuchus* in relation to the hemimandible, in dorsal view. The ratio between the mesiodistal axis of D7 and the width of the hemimandible at the same level (from the dorsal surface of the splenial to the lateral margin of the alveolar shelf of the dentary) is relatively similar in most *Caipirasuchus* (0.42 for *Cai. montealtensis* MPMA 68-0003/12 and *Cai. mineirus*, 0.47 for *Cai. paulistanus* and 0.49 for *Cai. stenognathus*). However, it is different in *Cai. attenboroughi* (0.75 in LAPEISA-0001).

### Phylogenetic relationships

Our updated parsimony analysis resulted in eight most parsimonious trees of 2300 steps each. An excerpt focused on notosuchian relationships from the strict consensus is shown in [Figure 6](#) (see the [Supplemental material](#) for the complete topology). We highlight three main results: (1) the nesting of *Cai. attenboroughi* within *Caipirasuchus*; (2) the sister-group relationship between Baurusuchia and the newly named Sphagesauria (previously known as ‘advanced notosuchians’), forming the clade Xenodontosuchia, named herein; and (3) the identification of a clade, here named Eunotosuchia, encompassing Uruguaysuchidae and Xenodontosuchia as well as *Simosuchus*, *Libycosuchus*, *Malawisuchus* and *Morrinhosuchus* ([Fig. 6](#)).

*Caipirasuchus attenboroughi* can be assigned to that genus based on the presence of the following synapomorphies: a lateromedially narrow and anteroposteriorly long symphyseal region of the mandible (three times longer than wide), posterior teeth with apicobasal crests and rugose enamel surfaces, a diastema between alveoli D5 and D6, a linear row of large neurovascular foramina in the lateral surface of the dentary, an anteriorly pointed palatine, and a broad nasopharyngeal duct. The first four synapomorphies of this list were previously considered diagnostic of *Caipirasuchus* (Iori & Carvalho 2011; Pol *et al.* 2014), whereas the last two traits are recognized for the first time here.

Our phylogenetic analysis recovered a monophyletic Sphagesauridae based on eight unambiguous synapomorphies: the absence of a foramen in the postnarial depression in the premaxilla; a line of foramina in the lateral surface of the maxillary interrupted by a gap; an elongated prefrontal anterior to the orbits and aligned

with the longitudinal axis of the skull; a dorsal exposure of the supraoccipital in dorsal view; a convex post-orbital-squamosal suture; the infraorbital portion of the jugal deeper than the infratemporal portion; a continuous lacrimal-jugal contact; and a poorly developed quadrate process of the pterygoid.

The term ‘advanced notosuchians’ was introduced by Pol *et al.* (2014) to encompass a clade deeply nested within Notosuchia that included *Notosuchus*, *Mariliasuchus*, *Labidiosuchus* and Sphagesauridae. The term was then applied to clades with slightly variable contents in recent analyses, including studies based on independent data matrices (Learidi *et al.* 2015a, b, 2018; Fiorelli *et al.* 2016; Martin & de Broin 2016; Iori *et al.* 2018; Pinheiro *et al.* 2018; Coria *et al.* 2019). The identification of a clade with similar inclusivity in our analysis, which is also mostly independent from the data matrix of Pol *et al.* (2014), compelled us to provide a name, Sphagesauria, and a formal phylogenetic definition (see [Table 1](#)). The choice of internal and external specifiers was based on the original content of ‘advanced notosuchians’ (Pol *et al.* 2014) and the general consensus on their position in relation to other notosuchians.

The Sphagesauria clade is supported by six unambiguous synapomorphies: the distal hemimandible’s strong curvature (‘Y’-shaped mandible); the oblique disposition of the posterior teeth in relation to the cranio-mandibular axis; the lateral asymmetry of tooth crowns; the presence of ridged ornamentation and apicobasal ridges on the enamel surface of the middle to posterior teeth; and the presence of a transitional tooth in the premaxilla-maxilla contact.

Xenodontosuchia is supported by one synapomorphy, the presence of strongly laterally compressed teeth. The name Xenodontosuchia (from ancient Greek ξένος/*xénos* – ‘strange’, ὀδούς/*odoús* – ‘tooth’ and Σοῦχος/*Soukhos* – the Egyptian crocodile god Sobek) refers to the bizarre dentition of Sphagesauria and Baurusuchia.

Our phylogenetic analysis places *Pakasuchus* as the sister taxon of all other baurusuchians. This contrasts with its more usual position, in which *Pakasuchus* forms a clade with *Malawisuchus* (Pol *et al.* 2014; Martin & de Broin 2016; Pinheiro *et al.* 2018). In fact, the choanal region of *Pakasuchus* is much more similar to that of non-xenodontosuchian eunotosuchians, such as uruguaysuchids and *Malawisuchus*, than to the modified choana of other Xenodontosuchia. However, *Pakasuchus* shares a mandibular and cranial morphology similar to that of Baurusuchidae, including sculptured dentaries and splenials, a posterolateral process of the squamosal at the same level as the skull roof, a rod-shaped infratemporal bar of the jugal, and the great expansion of the ectopterygoid over the pterygoid wing, reaching its distal tip. Indeed, a few previous analyses nested *Pakasuchus* within South American forms



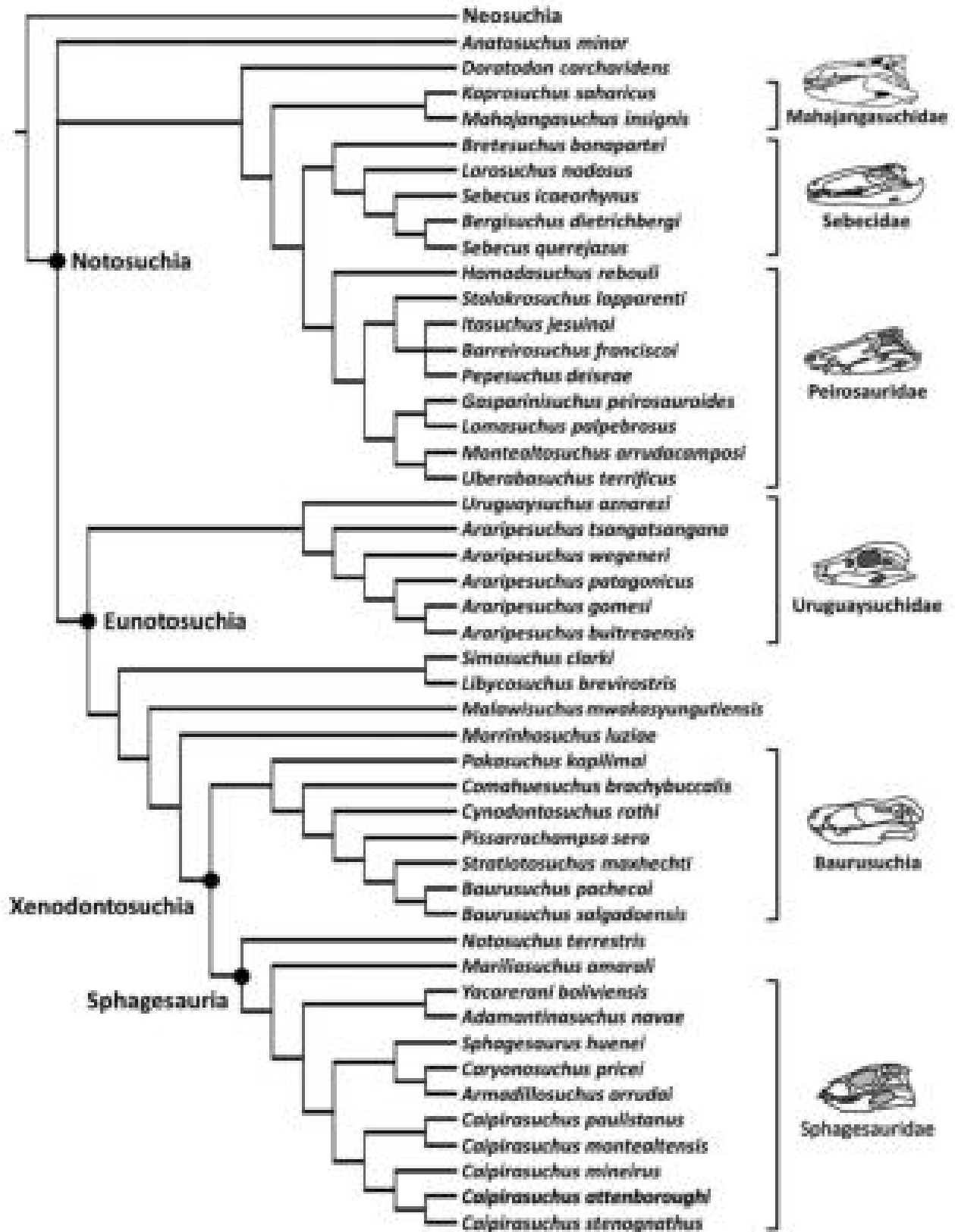


Figure 6. Excerpt of the strict consensus tree depicting the phylogenetic relationships among Notosuchia.

**Table 1** New phylogenetic definitions proposed for the main clades discussed in this study.

Clade name and registration	Phylogenetic definition, reference phylogeny and composition
<b>Notosuchia</b> Z. B. Gasparini, 1971 [this work], converted clade name <b>Registration Number:</b> 417	<b>Phylogenetic definition:</b> The most inclusive clade containing <i>Notosuchus terrestris</i> Woodward, 1896, but not <i>Crocodylus niloticus</i> Laurenti, 1768 (Crocodylia). This is a maximum clade definition. <b>Reference phylogeny:</b> Phylogenetic hypothesis depicted in Figure 6 of this work. <i>Crocodylus niloticus</i> nests within Neosuchia. <b>Composition:</b> Based on the reference phylogeny, Notosuchia includes Peirosauridae Gasparini, 1982, Sebecidae Simpson, 1937, Mahajangasuchidae Sereno & Larsson, 2009, Uruguaysuchidae Gasparini, 1971, Baurusuchia <i>sensu</i> Montefeltro <i>et al.</i> , 2011, and Sphagesauria (this work), plus some species-level taxa not nested within those groups.
<b>Eunotosuchia</b> this work [this work], new clade name <b>Registration Number:</b> 418	<b>Phylogenetic definition:</b> The least inclusive clade containing <i>Notosuchus terrestris</i> Woodward, 1896, <i>Uruguaysuchus aznarezi</i> Rusconi, 1933, and <i>Araripesuchus gomesi</i> Price, 1959, but not <i>Crocodylus niloticus</i> Laurenti, 1768 (Crocodylia). This is a minimum-clade definition. <b>Reference phylogeny:</b> Phylogenetic hypothesis depicted in Figure 6 of this work. <i>Crocodylus niloticus</i> nests within Neosuchia. <b>Composition:</b> Based on the reference phylogeny, Eunotosuchia includes Baurusuchia <i>sensu</i> Montefeltro <i>et al.</i> , 2011, Sphagesauria (this work), and Uruguaysuchidae Gasparini, 1971, plus some species-level taxa not nested within those groups.
<b>Xenodontosuchia</b> this work [this work], new clade name <b>Registration Number:</b> 556	<b>Phylogenetic definition:</b> The least inclusive clade containing <i>Sphagesaurus huenei</i> Price, 1950, and <i>Baurusuchus pachecoi</i> Price, 1945, but not <i>Uruguaysuchus aznarezi</i> Rusconi, 1933, <i>Araripesuchus gomesi</i> Price, 1959, <i>Montealtosuchus arrudacamposi</i> Carvalho <i>et al.</i> , 2007, <i>Sebecus icaeorhinus</i> Simpson, 1937 and <i>Crocodylus niloticus</i> Laurenti, 1768 (Crocodylia). This is a minimum-clade definition. <b>Reference phylogeny:</b> Phylogenetic hypothesis depicted in Figure 6 of this work. <i>Crocodylus niloticus</i> nests within Neosuchia. <b>Composition:</b> Based on the reference phylogeny, Xenodontosuchia includes Sphagesauria (this work) and Baurusuchia <i>sensu</i> Montefeltro <i>et al.</i> 2011.
<b>Sphagesauria</b> this work [this work], new clade name <b>Registration Number:</b> 419	<b>Phylogenetic definition:</b> The most inclusive clade containing <i>Sphagesaurus huenei</i> Price, 1950, but not <i>Baurusuchus pachecoi</i> Price, 1945, <i>Araripesuchus gomesi</i> Price, 1959, <i>Montealtosuchus arrudacamposi</i> Carvalho <i>et al.</i> , 2007, <i>Sebecus icaeorhinus</i> Simpson, 1937 or <i>Crocodylus niloticus</i> Laurenti, 1768 (Crocodylia). This is a maximum clade definition. <b>Reference phylogeny:</b> Phylogenetic hypothesis depicted in Figure 6 of this work. <i>Crocodylus niloticus</i> nests within Neosuchia. <b>Composition:</b> Based on the reference phylogeny, Sphagesauria includes <i>Notosuchus terrestris</i> Woodward, 1896, <i>Marillasuchus amarali</i> Carvalho & Bertini, 1999 and Sphagesauridae Kuhn, 1968.
<b>Sphagesauridae</b> O. Kuhn, 1968 [this work], converted clade name <b>Registration Number:</b> 420	<b>Phylogenetic definition:</b> The least inclusive clade containing <i>Sphagesaurus huenei</i> Price, 1950, <i>Caipirasuchus</i> (originally <i>Sphagesaurus</i> ) <i>montealtensis</i> Andrade & Bertini, 2008a and <i>Yacarerani boliviensis</i> Novas <i>et al.</i> , 2009. This is a minimum-clade definition. <b>Reference phylogeny:</b> Phylogenetic hypothesis depicted in Figure 6 of this work. <b>Composition:</b> Based on the reference phylogeny, Sphagesauria includes <i>Sphagesaurus</i> Price, 1950, <i>Caipirasuchus</i> Iori & Carvalho, 2011, <i>Yacarerani boliviensis</i> Novas <i>et al.</i> , 2009 and <i>Adamantinasuchus navae</i> Nobre & Carvalho, 2006.

(O'Connor *et al.* 2010) and it is sometimes placed as the sister group of the clade here named Xenodontosuchia (Sertich & O'Connor 2014; Meunier & Larsson 2017).

Seven synapomorphies support Eunotosuchia: external antorbital fenestra about half the diameter of the orbit; a loosely sutured premaxilla anterior to the nares; the absence of dermal bone overhanging the supratemporal fenestra; the presence of a peg in the posterior end of the mandibular symphysis; the absence of a crest and poorly delimited posterior margin on the glenoid fossa of the articular; maxillary teeth located in a groove; and

cheek tooth bases constricted. For a complete list of the synapomorphies recovered by our analysis, see the [Supplemental material](#).

## Discussion

Apart from *Yacarerani*, from the Cajones Formation of Bolivia (Novas *et al.* 2009), all indisputable sphagesaurids come from the Adamantina Formation, Bauru Basin, Brazil (Pol 2003; Nobre & Carvalho 2006; Iori &

Carvalho 2009; Marinho & Carvalho 2009; Kellner *et al.* 2011a; Iori & Carvalho 2013; Pol *et al.* 2014; Martinelli *et al.* 2018). *Caipirasuchus attenboroughi* represents the first evidence of a sphagesaurid from the Santo Anastácio Formation, expanding our knowledge of the fauna from the more poorly known deposits of the Bauru Basin.

The lack of a more precise age inference for the Santo Anastácio Formation hampers the chronological placement of *Cai. attenboroughi* (see Geological setting, above). To date, there are three possible scenarios: (1) the Santo Anastácio Formation is the youngest unit of the older Caiuá Group (Fulfaro *et al.* 1999; Dias-Brito *et al.* 2001; Batezelli 2010, 2015; Menegazzo *et al.* 2016); (2) the Santo Anastácio Formation is the oldest unit of the younger Bauru Group (Silva *et al.* 2005, 2009); or (3) the Caiuá and Bauru groups are coeval units (Fernandes & Ribeiro 2014). If placed in an older Caiuá Group, the Santo Anastácio Formation could be assigned an Aptian–Albian age, in which case *Cai. attenboroughi* would represent the oldest sphagesaurid and sphagesaurian, expanding the temporal range of both clades to the Early Cretaceous. On the other hand, if the Santo Anastácio Formation corresponds to the lowest beds of the Bauru Group, the range of Sphagesauria is less likely to be extended to the Early Cretaceous by the record of *Cai. attenboroughi*, although the taxon would remain older than the other sphagesaurids. In the third scenario, if the Santo Anastácio and Adamantina formations are time equivalent, *Cai. attenboroughi* would be contemporary with other sphagesaurids.

Given the lack of detail on local geology and the uncertainties about the chronostratigraphy of the Bauru Basin, we assume a conservative age estimate, in which the Santo Anastácio Formation is correlated with the Adamantina Formation. This hypothesis implies less ‘stratigraphic debt’ (*sensu* Fox *et al.* 1999) between the occurrences of *Cai. attenboroughi* and other sphagesaurids, sphagesaurians and baurusuchians. Therefore, our approach implies fewer *ad hoc* hypotheses about notosuchian ghost lineages. This is a strictly methodological decision and does not necessarily reflect our opinion about the chronostratigraphy of the Bauru Basin.

As for the Adamantina Formation, which contains all other Brazilian sphagesaurids, three main interpretations have been presented. The first establishes a Turonian–Santonian age, based on ostracods and charophytes (Dias-Brito *et al.* 2001; Martinelli *et al.* 2011). The second proposes a Campanian–Maastrichtian age, also based on ostracods and charophytes, as well as sauropods (Gobbo-Rodrigues *et al.* 1999; Fernandes & Coimbra 2000; Batezelli *et al.* 2003; Silva *et al.* 2003; Santucci & Bertini 2017). A third hypothesis supports a Cenomanian–Campanian age, based on a broader comparison of fossil

assemblages (Menegazzo *et al.* 2016). The first radioisotopic dating for the Adamantina Formation and the Bauru Group indicates a post-Turonian maximal age ( $\leq 87.8$  Ma) and a Coniacian–Campanian range (Castro *et al.* 2018). However, this dating was done in a single outcrop, and correlations with other outcrops of the same unit are tentative (see Montefeltro *et al.* 2011; Martinelli & Teixeira 2015; Martinelli *et al.* 2018). The Cajones Formation, which yielded *Yacarerani*, was first placed in the Maastrichtian based on the presence of fish remains (López 1975; Aguilera *et al.* 1989; Pol *et al.* 2014) and posteriorly considered to be Turonian–Santonian, due to the similarities of *Yacarerani* with sphagesaurids of the supposedly Turonian–Santonian (Dias-Brito *et al.* 2001) Adamantina Formation (Novas *et al.* 2009; Pol *et al.* 2014).

Two other fragmentary taxa were included in Sphagesauridae by Pol *et al.* (2014): *Labidiosuchus*, originally associated to the Serra da Galga Member of the Marília Formation, Bauru Group (Kellner *et al.* 2011b), and recently assigned to the Serra da Galga Formation (Soares *et al.* 2020); and *Coringasuchus*, from the Alcântara Formation, Itapecuru Group, north-east Brazil. The Serra da Galga Formation is regarded as Campanian–Maastrichtian in age, based on faunal correlations and because it overlays the Adamantina Formation (Pol *et al.* 2014; Castro *et al.* 2018; Soares *et al.* 2020). The Alcântara Formation is estimated to be of early Cenomanian age, based on its palaeovertebrate fauna (Kellner *et al.* 2009). If that is the case, *Coringasuchus* would be one of the oldest sphagesaurids. However, the fragmentary nature of the two taxa precludes their scoring in our phylogenetic data matrix.

The temporal ranges of the non-sphagesaurid sphagesaurians, *Mariliasuchus*, *Adamantinasuchus* and *Notosuchus*, are also within the Late Cretaceous. *Mariliasuchus amarali*, *M. robustus* and *Adamantinasuchus* are all from the Adamantina Formation (Carvalho & Bertini 1999; Zaher *et al.* 2006; Nobre *et al.* 2007), and *Notosuchus* comes from the Bajo de La Carpa Formation, Neuquén Group (Fiorelli & Calvo 2008; Lecuona & Pol 2008). A Santonian age is proposed for the latter unit, based on its palaeovertebrate fauna (Garrido 2010; Pol *et al.* 2014), which is concordant with the early Campanian magnetostratigraphy dating of the overlapping Anacleto Formation (Dingus *et al.* 2000; Pol *et al.* 2014). The recently described *Llanosuchus tamaensis* (Fiorelli *et al.* 2016), recovered as the sister taxon of *Notosuchus* (Fiorelli *et al.* 2016; Martinelli *et al.* 2018), comes from the Los Llanos Formation (western Argentina). A Campanian age has been suggested for this stratigraphic unit based on ostracods and charophytes (Carignano *et al.* 2013; Hechenleitner *et al.* 2014). Thus, a Turonian–Campanian range is inferred for the majority of the sphagesaurians in our analysis (Fig. 6).

## Conclusions

*Caipirasuchus attenboroughi* is the first crocodyliform recorded from the Santo Anastácio Formation, expanding the presence of notosuchians and Sphagesauridae in the Bauru Basin to that unit. *Cai. attenboroughi* represents the fifth species of the genus, making *Caipirasuchus* one of the richest notosuchian genera, outnumbered only by *Araripesuchus*. Our phylogenetic analysis recovered a topology in which three clades are named herein: Sphagesauria, including Sphagesauridae, *Mariliasuchus* and *Notosuchus*; Xenodontosuchia, formed by Sphagesauria + Baurusuchia; and Eunotosuchia, which includes uruguaysuchids, *Simosuchus*, *Libycosuchus*, *Malawisuchus*, *Morrinhosuchus* and Xenodontosuchia.

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## Supplemental material

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