

# New anatomical information on *Araripesuchus buiterraensis* with implications for the systematics of Uruguaysuchidae (Crocodyliforms, Notosuchia)

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## ABSTRACT

*Araripesuchus* (Uruguaysuchidae) is a Gondwanan mesoeucrocodylian genus that includes several species, distributed in the Cretaceous of Niger (*A. wegeneri* and *A. rattoides*), Madagascar (*A. tsangatsangana*), Brazil (*A. gomesii*), and Argentina (*A. patagonicus* and *A. buiterraensis*). The two Argentinean species came from different localities of the lower Cenomanian of Patagonia. Here, we present a complete cranial description of *A. buiterraensis* and explore its phylogenetic relationships, based on new as well as previously reported specimens. We studied the skulls of eight specimens of *A. buiterraensis*, almost all represented by partial cranium and mandible, adding new autapomorphies to the original diagnosis of this taxon. A comparison between the new specimens also reveals some discrepant features, which are interpreted as ontogeny or as intraspecific variation. We present revised scorings of several uruguaysuchid species (*A. buiterraensis*, *A. gomesii*, and *Uruguaysuchus aznarezi*) from a published morphological dataset and conduct a phylogenetic analysis to test the phylogenetic position of *A. buiterraensis*. As in recent phylogenetic proposals, this taxon was recovered as the basalmost member of a clade, which clusters all uruguaysuchids from South America. A revision of the diagnosis and a new phylogenetic definition of Uruguaysuchidae is also presented.

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## 1. Introduction

*Araripesuchus* Price, 1959 is a medium sized Gondwanan mesoeucrocodylian with terrestrial habits (Sereno and Larsson, 2009). When Price described this crocodile, he found some similarities with *Notosuchus terrestris* Woodward (1896) and include it in Notosuchidae. Gasparini (1971) noted some similarities between *Uruguaysuchus* Rusconi, 1933 and *Araripesuchus* and proposed the family Uruguaysuchidae. The first phylogenetic definition of this family was proposed by de Souza Carvalho et al. (2004) as a possible stem-based clade. Soto et al. (2011) noted this definition was incomplete and, despite being a weakly supported clade, a

node-based definition (employing *Uruguaysuchus aznarezi* and *Araripesuchus gomesii* as internal specifiers) or a stem-based definition (using *Notosuchus terrestris* as the external specifier) could be equally used. In recent studies uruguaysuchids appear in different positions, forming a paraphyletic group, with *Uruguaysuchus* closer to Ziphosuchia (Montefeltro, 2013; Turner, 2015) or a monophyletic group, including *Anatosuchus* Sereno et al., 2003 from Niger and being the sister taxon of the Peirosauridae (Pol et al. 2014; Leardi et al., 2018; Martinelli et al., 2018).

*Araripesuchus* includes several species, distributed in the Cretaceous of Niger (*A. wegeneri* Buffetaut, 1981 and *A. rattoides* Sereno and Larsson, 2009), Madagascar (*A. tsangatsangana* Turner, 2006), Brazil (*A. gomesii* Price, 1959), and Argentina (*A. patagonicus* Ortega et al., 2000 and *A. buiterraensis* Pol and Apesteguía, 2005). Both Argentinean species come from the Candeleros Formation (lower Cenomanian; Garrido, 2010), but from two different localities, one in the Neuquén Province and the other in the Río Negro Province; Fig.1).

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*A. patagonicus* was the first Patagonian species to be described. The holotype (MUCPV 269) preserves the anterior half of the skull with articulated mandible, lacking the most anterior portion of the rostrum, and also preserves part of the postcranium (Ortega et al., 2000). This specimen was found articulated and in close association with other referred specimens (MUCPV 267, 268, 268b, 270, 283; Ortega et al., 2000).

*A. buitreiraensis* was found in La Buitrera Paleontological Area (Fig. 1) and has been described only in its original description (Pol and Apesteguía, 2005). The holotype consists of an almost complete skull lacking the basicranium (Figs. 2A–B and Fig. S1). This description also includes fragmentary remains of the palate and part of the lower jaw of another specimen (MPCA PV 236) with different morphology, found at the same locality of the holotype. During the last 20 years, several new specimens have been collected, including individuals of different sizes, represented by both cranial and postcranial elements. The availability of more complete and better-preserved specimens (including skulls of different sizes) led us to redescribe the cranial anatomy of this species. The aim of this work is to increase the knowledge of the craniomandibular anatomy of *A. buitreiraensis* and to explore the implications of the new information in the phylogenetic relationships of uruguaysuchids.

## 2. Material and methods

### 2.1. Specimens of *Araripesuchus buitreiraensis*

We studied the skull of eight specimens of *A. buitreiraensis*: MPCA PV 235 (holotype), MPCA PV 242, 243, 513, 515, 583, 610 and 614 (Figs. 2, 3 and 4), all represented by partial cranium and mandible, except MPCA PV 583, which preserved only the mandible and an isolated quadrate. Most of this material was collected between 1999 and 2016 in expeditions to the Paleontological Area of La Buitrera, and they were prepared in the Fundación de Historia Natural Félix de Azara, Buenos Aires, Argentina. For comparisons, we examined other specimens and photographs of

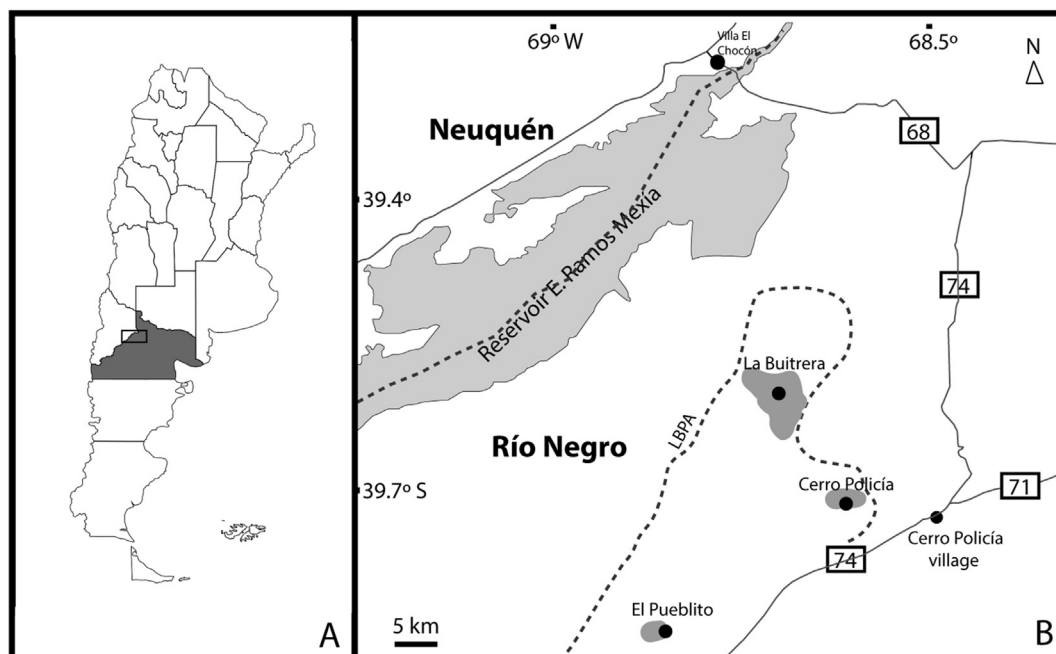
uruguaysuchids (Table S1). The measurements were collected with a Stanley electronic digital caliper and reported in the Supplementary Information (Table S2).

### 2.2. Phylogenetic analysis

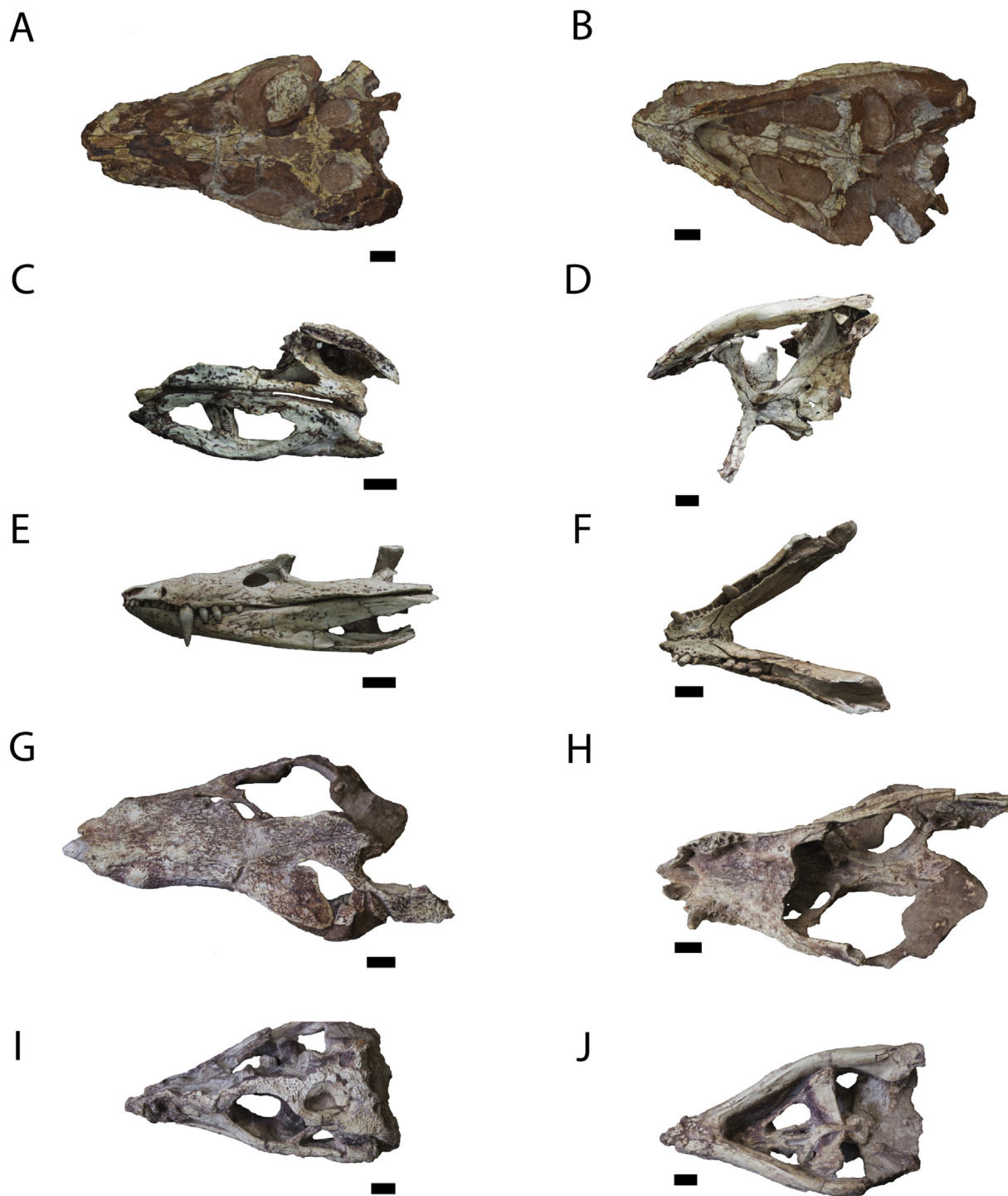
The character scorings of the species *A. buitreiraensis*, *A. gomesii*, and *Uruguaysuchus aznarezi* were revised in a recently published morphological dataset of 440 characters and 113 taxa (Martinelli et al., 2018), which constitutes an updated version of that of Fiorelli et al. (2016), Pol et al. (2012, 2014) and other sources (Clark, 1994; Ortega et al., 2000; Pol and Apesteguía, 2005; Pol, 2003; Turner and Sertich, 2010; De Andrade et al., 2011; Leardi et al., 2015a; Leardi et al., 2015b). A list of the changes introduced to the scorings of *A. gomesii*, *A. buitreiraensis*, and *U. aznarezi* is detailed in the Supplementary Information. The phylogenetic analysis was performed using the software TNT 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016) under equally weighted parsimony. The additive (=ordered) characters (a total of 43) used in previous analysis with this matrix were maintained and is detailed in the Supplementary information. The analysis consisted in using the New Technology Searches until the search produced 50 hits to minimum length. Two algorithms were employed, the sectorial search parameters (with RSS and CSS enabled) and the tree fusing (with three rounds, swap after exchanging, start from best tree and use fusing to multiply optimal trees enabled). In the general analysis we enabled driven search, replace existing trees and auto-constrain, with random seed set to 1. The most parsimonious trees (MPTs) were subjected to a round of TBR branch swapping before a strict consensus was calculated. Bremer support and Jackknife values (based on absolute frequencies) were calculated as measures of nodal support.

### 2.3. Institutional abbreviations

AMNH, American Museum of Natural History, New York, U.S.A.; DGM, Departamento de Produção Mineral, Rio de Janeiro, Brazil; FC,



**Fig. 1.** Location map of the fossiliferous localities of La Buitrera and Cerro Policia, Río Negro province, Argentina (A, B). In B, it is possible to identify the different localities that form the La Buitrera Paleontological Area, from La Escondida to El Pueblito. LBPA, La Buitrera Paleontological Area. Modified from Garberoglio et al. (2019).



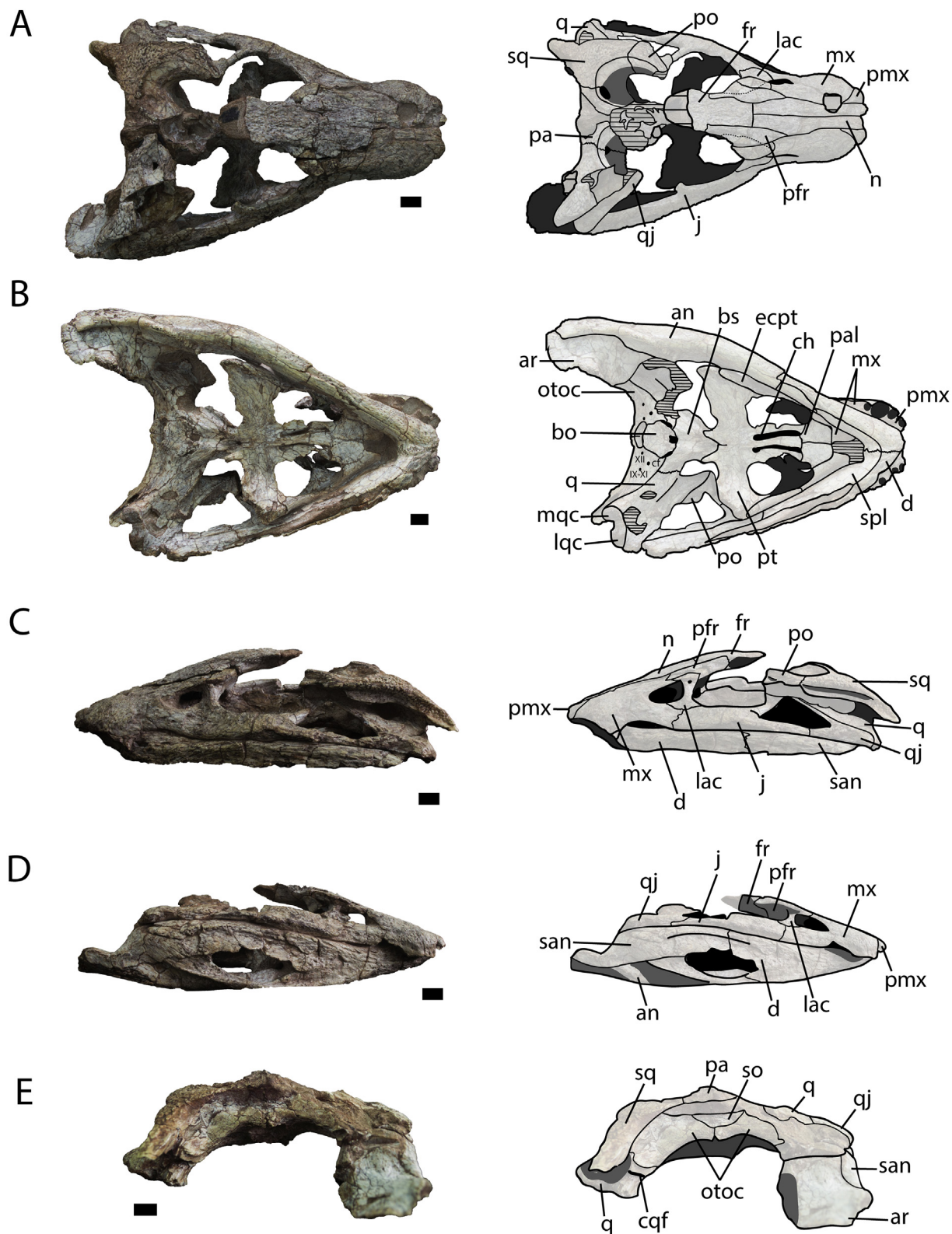
**Fig. 2.** Skull of several specimens of *Araripesuchus buiterraensis*. MPCA PV (holotype) 235 in **A**, dorsal and **B**, ventral view; MPCA PV 513 in **C**, lateral and **D**, ventral view; MPCA PV 515 in **E**, lateral view; MPCA PV 583 in **F**, dorsal view; MPCA PV 610 in **G**, dorsal and **H**, ventral view; MPCA PV 614 in **I**, dorsal and **J**, ventral view.

Facultad de Ciencias, Montevideo, Uruguay; **FMNH**, Field Museum of Natural History, Chicago, U.S.A.; **GDF**, Muséum National d'Histoire Naturelle, Paris, France; **MLP**, Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina; **MNN**, Muséum National du Niger, Niamey, Niger; **MPCA**, Museo Paleontológico Carlos Ameghino, Cipolletti, Río Negro, Argentina; **MUCPV**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; **UA**, University of Antananarivo, Madagascar. .

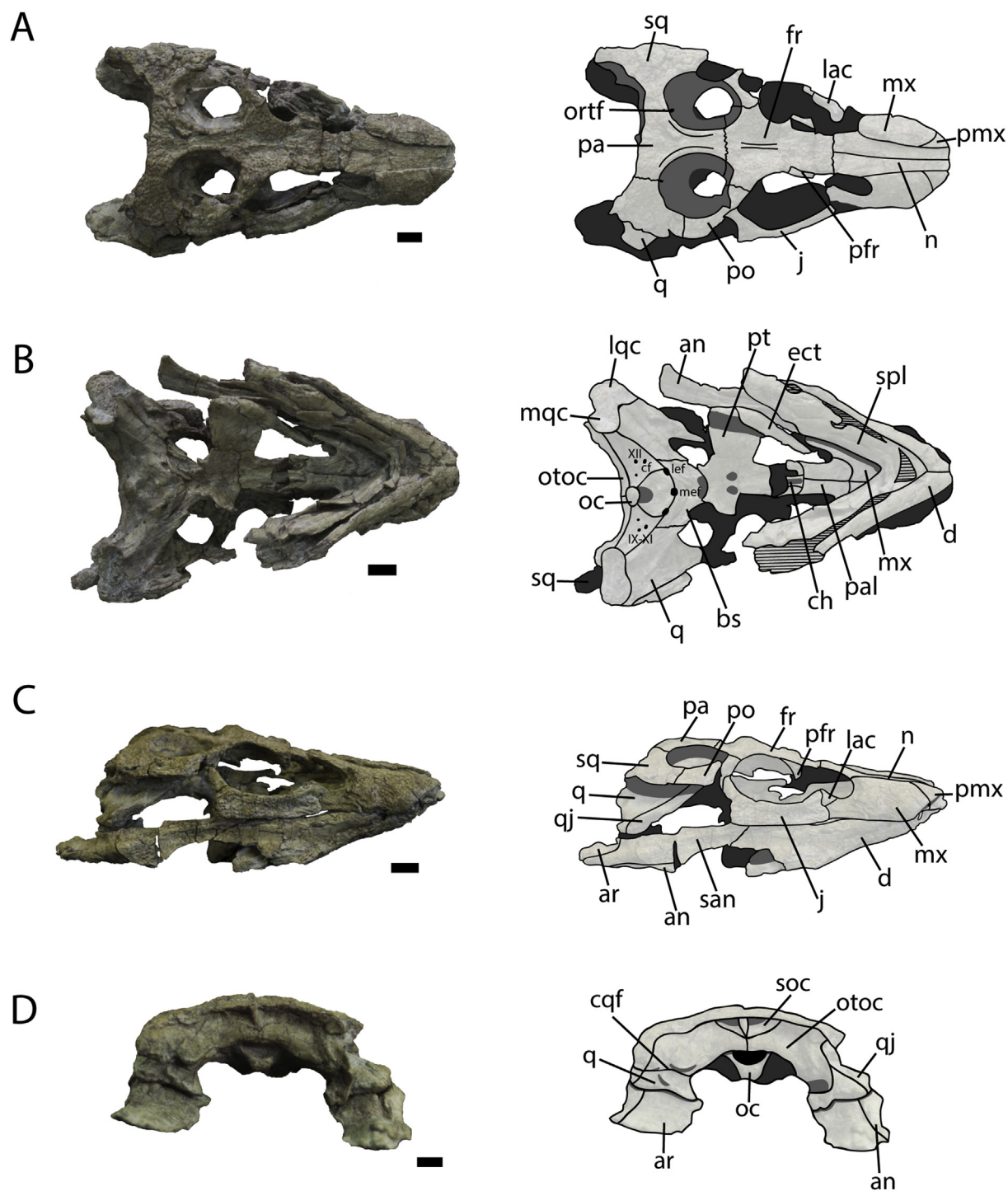
### 3. Geological setting

All known specimens of *Araripesuchus buiterraensis* were found in three paleontological localities (La Buitrera, Cerro Policía and El Pueblito) of La Buitrera Palaeontological Area (Garberoglio et al., 2019, Fig. 1), about 30 km northwest of the Cerro Policía village, in Río Negro Province (Patagonia, Argentina). The specimens were found in rocks of the upper section of the Candeleros Formation,





**Fig. 3.** *Araripesuchus buiterraensis* MPCA PV 242. Partial skull in **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, right lateral and **E**, occipital views. Abbreviations: **an**, angular; **ar**, articular; **bo**, basioccipital; **bs**, basiesphenoid; **cf**, carotid foramen; **ch**, choana; **cqf**, cranioquadrate foramen; **d**, dentary; **ecpt**, ectopterygoid; **fr**, frontal; **j**, jugal; **lac**, lacrimal; **lqc**, lateral quadrate condyle; **mef**, median Eustachian foramen; **mqc**, medial quadrate condyle; **mx**, maxilla; **n**, nasal; **otoc**, otoccipital; **pa**, parietal; **pal**, palatine; **pfr**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quatrojugal; **san**, surangular; **so**, supraoccipital; **spl**, splenial; **sq**, squamosal; **IX-XI**, opening for IX-XI cranial nerves; **XII**, opening for the XII cranial nerve. Scale bars = 1 cm.



**Fig. 4.** *Araripesuchus buitreaensis* MPCA PV 243. Partial skull in **A**, dorsal; **B**, ventral; **C**, Right lateral and **D**, occipital views. Abbreviations: **an**, angular; **ar**, articular; **bo**, basioccipital; **bs**, basiesphenoid; **cf**, carotid foramen; **ch**, choana; **ccf**, cranioquadrate foramen; **d**, dentary; **ectpt**, ectopterygoid; **fr**, frontal; **j**, jugal; **lac**, lacrimal; **lef**, lateral Eustachian foramen; **lqc**, lateral quadrate condyle; **mef**, median Eustachian foramen; **mqc**, medial quadrate condyle; **mx**, maxilla; **n**, nasal; **oc**, occipital condyle; **ortf**, orbitotemporal foramen; **otoc**, otocapital; **pa**, parietal; **pal**, palatine; **pfr**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quatrojugal; **san**, surangular; **so**, supraoccipital; **spl**, splenial; **sq**, squamosal; **IX-XI**, opening for IX-XI cranial nerves; **XII**, opening for the XII cranial nerve. Scale bars = 1 cm.

the basal unit of Neuquén Group, of Cenomanian age (Leanza et al., 2004; Garrido, 2010). These deposits underlie the Huincul Formation, which was dated to 88 Ma (Corbella et al., 2004). During the Cenomanian, a desert now known as Kokorkom (Apesteguía et al., 2016) developed in this area, probably due to the aridization of the interior continental of Gondwana (Asurmendi and Sánchez, 2014;

Sánchez and Asurmendi, 2015, 2016; Sánchez et al., 2016; Candia Halupczok et al., 2017). In addition to crocodyliforms, La Buitrera Paleontological Area has produced a diverse fauna that includes rhynchocephalians (Apesteguía and Novas, 2003), squamatan lepidosaurs (Apesteguía et al., 2005), limbed snakes (Apesteguía and Zaher, 2006), dromaeosaurid (Makovicky et al., 2005) and

alvarezsaurid (Makovicky et al., 2012) theropod dinosaurs, fragmentary sauropods, dryolestoid mammals (Rougier et al., 2011), and dipnoans (Apesteguía et al., 2007).

#### 4. Systematic Paleontology

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

**Mesoeucrocodylia** Whetstone and Whybrow, 1983.

**Notosuchia** Gasparini, 1971 (*sensu* Sereno et al., 2001).

**Uruguaysuchidae** Gasparini, 1971.

Uruguaysuchidae is supported by nine unambiguous synapomorphies: vascular opening in dorsal surface of postorbital bar (27: 0→1); insertion area for *M. pterygoideus posterior* extended onto lateral surface of angular (76: 0→1); postorbital process of jugal posteriorly positioned (143: 1→2); quadratojugal not ornamented (145:1→0); dorsal edge of dentary straight with an abrupt dorsal expansion, being straight posteriorly (150: 0→1); posterior ridge on glenoid fossa of articular absent (187: 0→1); incipiently distinct development of distal quadrate body ventral to otoccipital-quadrate contact (197: 0→1); paired ridges located medially on ventral surface of basisphenoid (209: 0→1) and single or paired large neurovascular foramina on lateral surface of premaxilla (400: 0→1). And one ambiguous synapomorphy: anterior half of palatines between suborbital fenestrae with parallel lateral margins (278: 0).

**Phylogenetic definition.** We re-define Uruguaysuchidae as a stem-based group, which include all taxa more closely related to *Uruguaysuchus* than to *Lomasuchus* Gasparini et al., 1991, *Kaprosuchus* Sereno and Larsson, 2009, and *Notosuchus*.

***Araripesuchus buiterraensis*** Pol and Apesteguía (2005).

**Holotype** MPCA PV 235 (Figs. 2A–B and Fig. S1), an almost complete skull lacking most of the basicranium and in articulation with the lower jaws, which are represented by dentaries, splenials, and surangulars.

**Referred material.** MPCA PV 242, almost complete cranium, with articulated lower jaw, lacking part of the posterior skull roof (Fig. 3), postcranial elements: femur and isolated vertebrae; MPCA PV 243 an almost complete cranium, with articulated lower jaw (Fig. 4), postcranial elements: humerus, phalanges, coracoid, several vertebrae, a possible pubis, scapula, tibia, calcaneus, radial, ulnar, ilium, and the tail with articulated osteoderms; MPCA PV 513 the posterior portion of cranium, lacking part of the skull roof and with the posterior left part of the lower jaw articulated (Figs. 2C–D and Fig. S2), postcranial elements: humerus, coracoid and isolated vertebrae; MPCA PV 515 a partially complete left portion of a cranium, with part of the lower jaw articulated, lacking the basicranium and most of the skull roof (Figs. 2E and Fig. S3); MPCA PV 583 part of a lower jaw (dentaries with some teeth and splenials) and an isolated quadrate (Figs. 2F and Fig. S4); MPCA PV 610 a partially complete cranium, lacking the basicranium, and a disarticulated lower jaw with the right dentary with implanted teeth, a fragment of the left dentary and part of the splenial (Figs. 2G–H and Fig. S5); MPCA PV 614 an almost complete cranium, lacking part of the right snout and the basicranium with an articulated left lower jaw (Figs. 2I–J and Fig. S6).

**Locality and horizon.** The specimens described here come from the following sites within La Buitrera Paleontological Area: MPCA PV 235, 242, 243, 610, 614, come from the La Buitrera locality, MPCA PV 513, and 515, and from Cerro Policía locality, and 583 from El pueblito locality (Fig. 1). All the materials were collected from the upper levels of the Candeleros Formation (Keidel, in Wichmann, 1927), the basal unit of Neuquén Group, lower Cenomanian in age.

**Emended diagnosis.** This taxon is diagnosed by the combination of the following characters (autapomorphies indicated with an asterisk): maxilla with seven teeth; marked median crest at the dorsal surface of frontal; frontals extending into supratemporal fenestra, parieto-postorbital suture absent from dorsal surface of skull roof and supratemporal fossa; parietal dorsal surface narrow between supratemporal fossa; elevated rims along the medial and posterior margins of the supratemporal fenestra; vertical bone surface of squamosal for the articulation of the ear flap; supraoccipital with a vertical median crest; exposure of supraoccipital in skull roof absent; sagittal ridge on the ventral half of the posterior surface of the basioccipital absent or poorly developed; basisphenoid ventral surface wide, similar in length to basioccipital; lateral wall of the temporal region obliquely (dorsomedially) oriented; large subtymppanic foramen, about one sixth the size of the otic foramen; pterygoid flanges pneumatic; shallow and transversely elongated parachoanal fossa on the pterygoid flanges\*; choanal septum T-shaped in transversal section, completely dividing the choanal openings, the ventral surface of which is as broad anteriorly as in the midregion of the septum\*; anterior palpebral sub rectangular, remarkably broad on its anterior end and with a sinusoidal posterior margin\*; dentary with lateral concavity for the reception of the enlarged maxillary tooth; relative length and width of anterior (parallel sided) process of dentary symphysis elongated, being approximately twice as long as wide; anterior tip of the splenial U-shaped, in ventral view of the mandibular symphysis; short splenial involvement in symphysis in ventral view, forming up to 20% symphyseal length; splenial peg projected anteriorly at the ventral surface of the mandibular symphysis; surangular forming a broad dorsal shelf; dorsal margin of the external mandibular fenestra with a ventrally projected by thin lamina of the surangular\*; angular with a marked oblique crest for the insertion of the *m. pterygoideus ventralis* at maturity. Emended from Pol and Apesteguía (2005).

**Comments.** The original diagnosis included a character (caudal tip of nasal caudally separated by an acute sagittal projection of frontals) that was removed because the new material shows that this feature was incorrectly determined in the holotype by Pol and Apesteguía (2005). In the holotype, the external surface of frontal at the nasal-frontal contact is not preserved, so the anterior projection observed in this specimen corresponds to a piece of the deep (internal) surface of the frontal that was covered by nasal at the nasal-frontal suture. The referred material of *Araripesuchus* shows the nasal-frontal contact transversely oriented, as in other uruguaysuchids.

#### 5. Description

##### 5.1. General skull morphology of *Araripesuchus buiterraensis*

In dorsal view, the skull is subtriangular in shape, with a rounded snout in the holotype, MPCA PV 242 and 243 (Figs. 3 and 4), but more pointed in MPCA PV 515, 610, and 614 (Figs. 2E, G, I, S3, S5 and S6). The maxilla has its widest section at the level of the largest maxillary tooth and a constriction at the level of the antorbital fenestrae.

The external supratemporal fenestrae and fossae are partially preserved in MPCA PV 242 and 610, almost complete in MPCA PV 243, and complete in MPCA PV 515. The fenestra is large, sub-circular and as wide as the orbits. The posterior, lateral and medial walls of the fossae are oblique respect to the sagittal plane of the skull (dorsally facing) and exposed in dorsal view. In MPCA PV 242 and 243, the orbitotemporal foramen opens on the posterior wall of the supratemporal fossa, in a recess that is roofed by a bony ridge of



the parietal and the squamosal, but it is still visible in dorsal view (Figs. 3A and 4A). The posteromedial corner of the external supratemporal fenestra has a marked rim formed by the parietal. The posterior part of the dorsal surface of the interfenestral bar is lateromedially concave. The width of the interorbital bar is twice the width of the interfenestral bar and its dorsal surface is almost horizontal, with a smooth rim along the medial margin of the orbits, formed by the frontal and prefrontal.

The orbits are laterally oriented, oval, longer than wide, and anteriorly narrow. They are delimited by the lacrimal anteriorly, prefrontal and frontal dorsally, postorbital and jugal posteriorly and jugal ventrally. In MPCA PV 242, a prefrontal shelf for the articulation of the anterior palpebral bone is observed in the anterior part of the medial margin of the left orbit (Fig. 3A).

The size of the subcircular antorbital fenestrae are less than half that of the orbits; they are delimited by the maxilla anteriorly and the lacrimal dorsal and posteriorly and open at the anterior part of the oval antorbital fossae.

The preorbital region is quadrangular in transverse section (oreinirostral condition *sensu* Busbey, 1995) and wider than high (e.g., MPCA PV 515). The snout length is approximately as long as the orbitotemporal region. In lateral view, the dorsal contour of the cranium gently descends anteriorly.

The occipital condyle is posteroventrally oriented and the foramen magnum is subtriangular.

In palatal view, the secondary palate is formed by the premaxilla, maxilla and palatines. The vomers are exposed dorsally only in MPCA PV 242 through a fracture of the nasals. The subtriangular suborbital fenestrae are located lateral to the choanae and are longer than them. The choanae are oval and narrow and anteroposteriorly elongated, with lateral margins slightly obliquely oriented (anteromedially to posterolaterally). The choanae are delimited by the palatines anteriorly and the pterygoids laterally, medially and posteriorly. The interchoanal septum is formed by the pterygoids.

The lower jaw is articulated in most of the specimens here described, and it is the only preserved element in MPCA PV 583 (Figs. 2F and 54). The symphysis area is low and the dentary symphysis extends up to the seventh alveolus. In dorsal view, the splenials form less than the posterior half of the symphysis reaching the ninth mandibular alveolus. The dorsal surface of the symphysis (exposed in MPCA PV 515 and 583) is slightly concave. Both mandibular rami form an angle of approximately 70°. In lateral view, the dorsal margin of the dentary ascends abruptly at the level of the seventh tooth (approximately). The oval external mandibular fenestra is low and long, with its length less than one third of the total length of the mandible. In lateral view the external mandibular fenestra is delimited by the dentary anteriorly and anterodorsally, the angular ventrally, and the surangular posteriorly and posterodorsally.

## 5.2. Skull bones

### 5.2.1. Premaxilla

Fragments of both premaxillae are preserved in the holotype, MPCA PV 242, 243, 515, and 610. In dorsal view, the posterior triangular process of premaxilla wedges between the maxilla and the nasal. This process extends more posteriorly than in other uruguaysuchids like *Araripesuchus gomesii*, *A. tsangatsangana*, *A. wegneri*, *Uruguaysuchus*, and *Anatosuchus* (see MPCA PV 515 and 610; Figs. S3 and S5). The external narial openings are crushed in most specimens except for MPCA PV 515, in which the left one is better preserved and has an elongated oval contour (Figs. 2E and S3). The nares are delimited by the premaxilla posteriorly and ventrally. A slender anterior process, formed by the premaxilla,

curves dorsally at the anterior tip of the snout and reaches the nasal to form the internarial septum, as also occurs in *A. wegneri* and *peirosaurids*. Five teeth are preserved on the right premaxilla of MPCA PV 515 as in *A. wegneri* and *A. tsangatsangana*, differing from *Uruguaysuchus* and *A. gomesii*, which have four premaxillary teeth (Fig. 5A).

The premaxilla contacts the maxilla posteriorly and the nasals dorsomedially and anteriorly, at the internarial septum. The palatal contacts of this bone are not observed because this area is damaged in MPCA PV 243 and is covered by the lower jaw in the rest of the specimens. The premaxilla-maxilla suture is obliquely oriented (anteroventral to posteromedial). There are two foramina on the lateral surface of the premaxilla. The anterior one is small and located at the level of the fourth premaxillary alveolus and the posterior one is located at the premaxilla-maxilla suture. This latter is larger, oval (higher than wide) in MPCA PV 515 and circular in MPCA PV 610, delimited by the premaxilla anteriorly and the maxilla posteriorly. According to Sereno and Larsson (2009), the premaxilla-maxilla foramen appears to have an anterior diverticulum that may pneumatize the premaxilla, a condition likely present in *Araripesuchus buiterraensis*. The external surface of the premaxilla is smooth in all specimens.

### 5.2.2. Maxilla

Fragments of left and right maxillae are preserved in the holotype, MPCA PV 242, 243, 515, and 610. The maxilla has three planes: one lateral and subvertically oriented, and the other two (dorsal and palatal) horizontally oriented; as a result, the snout is trapezoidal in transverse section (oreinirostral condition *sensu* Busbey, 1995).

In dorsal view, the maxilla contacts the nasal medially along a suture that is anteroposteriorly straight and the lacrimal posteriorly by an oblique suture. The lateral edge of the maxilla is bulged at the level of the large caniniform and strongly concave near to the antorbital fossa.

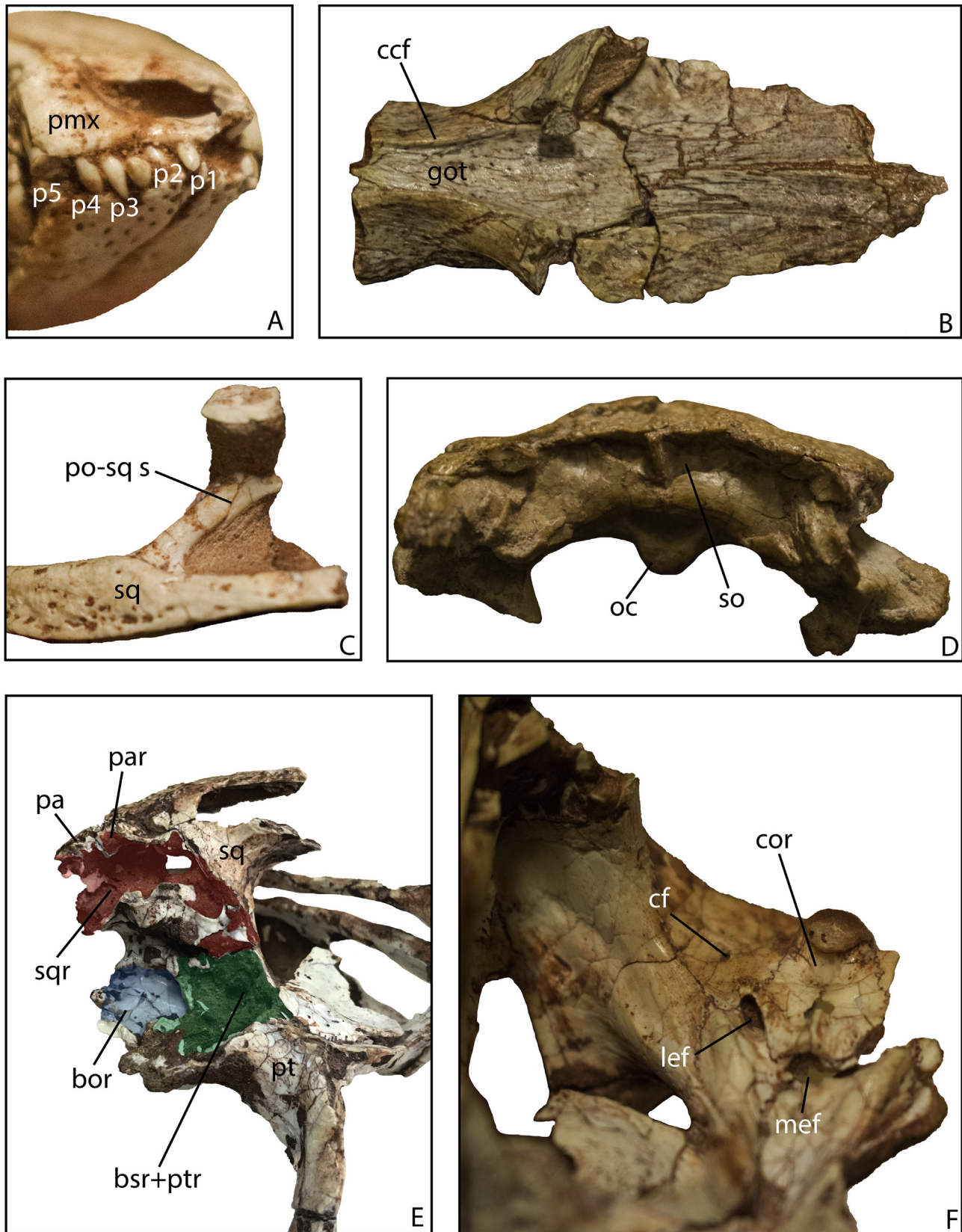
In lateral view, the maxilla forms the anterior, ventral and dorsal margins of the antorbital fenestra and fossa. It contacts the lacrimal posterodorsally and the jugal posteroventrally. Near to the alveolar margin of the lateral surface of the maxilla there are several small and aligned neurovascular foramina.

In palatal view both maxillae contacts at the midline. The posteromedial margin of the palatal branch of the maxilla contacts the palatine along a U-shaped suture, and the posterolateral margin contacts the ectopterygoid. There is a groove on the palatal surface of the maxilla running medial to the tooth row, where the inferior tooth row fit. Additionally, there are two foramina near the medial border of the caniniform alveolus. In medial view of MPCA PV 515, the maxilla contacts the lacrimal dorsally, the jugal posterodorsally, and the ectopterygoid posteroventrally.

*Araripesuchus buiterraensis* has seven maxillary teeth, differing from all other uruguaysuchids which have eight or more teeth. The external surface of the maxilla is ornamented by small pits scattered over the surface, but with a higher concentration close to the maxilla-nasal suture and close to the alveolar margin. The pitted ornamentation is absent around the antorbital fossa and only in the larger specimens (MPCA PV 242, 243, and 610) this region bears fine grooves dorsoventrally oriented.

### 5.2.3. Nasals

The nasals are well preserved in MPCA PV 243 and 610, and partially preserved in MPCA PV 235, 242, and 515. They are narrow and long, with parallel lateral margins and extend along the length of the snout. The nasals contact the frontal posteriorly along a straight and transverse suture, the prefrontals posterolaterally, the maxilla laterally, and the premaxilla anterolaterally and



**Fig. 5.** Photographs showing details of the cranial anatomy of *Araripesuchus buiterraensis*. **A**, rostrum of MPCA PV 515 in anterolateral view; **B**, frontal of MPCA PV 242 in ventral view; **C**, orbital region of MPCA PV 515 in left lateral view; **D**, skull of MPCA PV 243 in occipital view; **E**, braincase of MPCA PV 513 in anteromedial view. Abbreviations: **bor**, basioccipital diverticulum; **bsr**, basisphenoid recess; **ccf**, crista cranii frontalis; **cf**, carotid foramen; **cor**, condylar recess; **got**, groove for the olfactory tract; **lef**, lateral Eustachian foramen; **mef**, medial Eustachian foramen; **oc**, occipital condyle; **p1-p5**, premaxillary tooth 1-5; **po-sq s**, postorbital-squamosal suture; **pa**, parietal; **par**, parietal recess; **pt**, pterygoid; **ptr**, pterygoid recess; **so**, supraoccipital; **sq**, squamosal; **sqr**, squamosal recess; **F**, posteroventral view of MPCA PV 513. Abbreviations: **cor**, condylar recess; **cf**, carotid foramen; **lef**, lateral Eustachian foramen; **mef**, medial Eustachian foramen.



anteroventrally, at the joint of the internarial septum. The nasals do not contact the lacrimals, differing from *Araripesuchus gomesii* and *A. patagonicus*. Also, as in all species of *Araripesuchus*, they are excluded from the anteorbital fenestra. The dorsal surface of the nasals is ornamented with well-spaced pits and fine longitudinal grooves towards the naso-frontal suture.

#### 5.2.4. Lacrimal

The lacrimals are completely preserved in MPCA PV 242, 515 (on the left side), and 610. These elements are also partially preserved in the left side of MPCA PV 614 and 243. They contact the maxilla anteriorly, the prefrontals posteriorly, and the jugal ventrally. The lacrimals have two rami, one dorsal, oriented horizontally, and the other ventral, that is oriented vertically. The dorsal ramus of the lacrimal is ornamented with a few pits. It extends over the posterolateral surface of the snout and projects laterally, roofing the antorbital fossa and fenestra. This region also bears a shelf for the articulation of the anterior palpebral. The ventral ramus of the lacrimal has a smooth surface; it extends ventrally as a vertical pillar that divides the antorbital fenestra from the orbit. This pillar is triangular in cross section, with the major apex posteromedially oriented and a broad ventral base that contacts the jugal posteriorly and the maxilla anteriorly, along a straight suture. The anterolateral surface of this pillar forms the posterior wall of the antorbital fossa and the robust rim that delimits the orbit anteriorly. The lacrimal foramen (preserved in MPCA PV 242 and 515) opens at the dorso-lateral margin of the posterior surface of this pillar and it is enclosed entirely by the lacrimal.

As in *Araripesuchus gomesii*, *A. patagonicus*, *A. wegeneri*, and unlike *A. tsangatsangana*, the lacrimal of *A. buitreaensis* has a posterior lateral edge for the contact facet of the anterior palpebral. Also, unlike all other South American uruguaysuchids, the lacrimal, in dorsal view, do not surpass the anterior portion of the prefrontal.

#### 5.2.5. Prefrontal

The prefrontals are partially preserved in MPCA PV 242, 243, 614 and the holotype, but are completely preserved in MPCA PV 610. In dorsal view, they are elongated contacting the lacrimal laterally and the frontal medially. They extend along the anterolateral margin of the interorbital bar and have a ventrally directed pillar that contact the pterygoids posteriorly and vomers anteriorly. The prefrontals bear a shelf for the articulation of the anterior palpebral (preserved in MPCA PV 242 and 243) that is larger than the postorbital shelf. In MPCA PV 610, the left palpebral was found articulated on this shelf (Fig. S5). The dorsal surface of prefrontals is ornamented by small pits.

As in other uruguaysuchids, except *Araripesuchus gomesii* and *A. patagonicus* (*sensu* Turner, 2006) the prefrontal prevents the contact between nasal and lacrimal.

#### 5.2.6. Frontal

The frontal is an unpaired bone, completely preserved in MPCA PV 242, 243 and 610, and partially preserved in MPCA PV 614 and in the holotype. In dorsal view, it contacts the prefrontals anterolaterally along a straight suture parallel to the sagittal plane, the nasals anteriorly, the parietal posteromedially by an interdigitated suture, and the postorbital posterolaterally. The interorbital bar is wider than the interfenestral bar. At the posterior sector of the orbits, the surface of the interorbital bar is concave, where the lateral surface of the frontal raises to form an elevated posteromedial orbital margin. At this level, the frontal also bears a marked median crest (e.g., MPCA PV 243 and 610; Figs. 2G–H, 4 and Fig. S5). This crest is also present in the African species of the clade, but absent in the other South American species. The frontal delimits the anteromedial margin of the external supratemporal fenestra and

forms the anteromedial corner of the wall of the supratemporal fossa, preventing the parietal-postorbital contact (a feature only present in *Araripesuchus wegeneri*).

The dorsal surface of the frontal is profusely ornamented, with abundant longitudinal grooves and small pits, more concentrated on the median and posterior sector of the bone. In ventral view (Fig. 5B), the *cristae cranii frontalis* are marked and curved, forming the lateral walls of the groove for the olfactory tract. At the anterior part of this groove, there are conspicuous marks for the olfactory bulbs (not visible in the larger specimen MPCA PV 242), separated by a median fine crest; these bulb marks are oval in shape and nearly as long as the tract.

#### 5.2.7. Jugal

The jugal is completely preserved in MPCA PV 242, 243 (on the right side; Figs. 3 and 4), 513, 515, 610, 614 (on the left side; Figs. S2, S3, S5 and S6), and in the holotype. Its anterior margin slightly exceeds the anterior margin of the orbit and overlaps the maxilla ventrally and the lacrimal dorsally. It contacts the quadratojugal posteriorly, anterior to the posterior corner of the laterotemporal fenestra. As in other crocodyliforms, the jugal does not form part of the antorbital fenestra. It forms the ventral and posteroventral border of the orbit, and the ventral and anteroventral margin of the infratemporal fenestra. The ascending process of the jugal forms almost the entire postorbital bar, where it laterally overlaps the descending process of the postorbital. The lateral surface of the jugal is ornamented with thin grooves and well-spaced small pits. In medial view, the jugal contacts the dorsal ramus of the ectopterygoid ventrally, the maxilla anteroventrally, and the lacrimal anterodorsally. The medial surface of the jugal is smooth and concave. On the medial surface of the jugal, there are small pits anteroposteriorly aligned.

#### 5.2.8. Parietal

The parietal is completely preserved in MPCA PV 243 and partially preserved in the holotype, MPCA PV 242, 513, and 614 (Figs. 3, 4, S2 and S6). The dorsal surface of this bone is T-shaped, with its widest portion posteriorly located, and ornamented by small pits. The fronto-parietal suture on the skull roof is interdigitated, transversely oriented, and situated at the anterior sector of the interfenestral bar. This suture extends along the medial wall of the supratemporal fossa, preventing the parietal-postorbital contact. The parietal lateral margins are slightly curved and with a narrow ridge forming the medial margin of the supratemporal fenestrae. In the posterior half of its dorsal surface, the parietal has a median longitudinal crest. The parietal extends posteriorly and reaches the posterior margin of the skull roof, which is almost transversely straight. The parietal contacts the squamosal posterolaterally along an anteroposteriorly oriented suture and the laterosphenoid ventrally. In *Araripesuchus buitreaensis*, the parietal at the level of the interfenestral bar is narrower than the parietal in *A. patagonicus*, *A. gomesii*, *A. tsangatsangana*, *Anatosuchus*, and *Uruguaysuchus*, being most similar to the parietal of *A. wegeneri*.

#### 5.2.9. Postorbital

These elements are practically complete in MPCA PV 243 (especially the right one; Fig. 4), 610, 614 (the left one in both, Figs. S5 and S6), and partially preserved in MPCA PV 242 (the left one; Fig. 3) and the holotype. In the specimen MPCA PV 515, a small portion of the left postorbital bar is preserved. The dorsal surface of the postorbital is ornamented by small pits. It forms the anterolateral margin and wall of the supratemporal fenestra and its fossa. The descending process of the postorbital forms one third of the postorbital bar and contacts the ascending process of the jugal along an oblique suture (Fig. 5C). The postorbital contacts the

frontal medially, the squamosal posteriorly, and the jugal ventrally. The postorbital-squamosal suture is located at the midpoint of the supratemporal fenestra. At the posterolateral margin of the orbits, the postorbital has an anterolaterally-projected triangular shelf for the posterior palpebral (preserved almost complete on the left side of MPCA PV 242 and partially on the left side of MPCA PV 243 and 614). In MPCA PV 610, the posterior palpebral is in articulation with its shelf (Fig. S5).

#### 5.2.10. Squamosal

Both squamosals are severely damaged in the holotype, but they are almost completely preserved in MPCA PV 242, 243, 513, and 614 (only the left one). This bone has a triangular horizontal portion in dorsal view that forms the posterolateral region of the skull table and projects laterally roofing the otic recess. The posterolateral process is slightly ventrally deflected. The occipital vertical portion of the squamosal is deeply concave and contacts ventrally with the paraoccipital process of the otoccipital. In lateral view, the squamosal bears a vertically oriented bone surface for the articulation of the ear-flap, this surface is dorsoventrally thicker than in other species of the clade, and the dorsal surface of the bone is ornamented by small pits.

#### 5.2.11. Supraoccipital

This bone is complete and exposed in occipital view in MPCA PV 242, 243, but only a left portion of this bone is preserved in MPCA PV 513. It is triangular-shaped, wider than high, and has a marked median vertical crest (Fig. 5D). It is dorsally overlapped by the parietal, and it contacts the otoccipitals ventrally, and do not forms the dorsal margin of the foramen magnum. The posttemporal openings are not observed in any specimen and may have been obliterated. In anteromedial view, MPCA PV 513 shows three recesses of the paratympanic pneumatic system exposed by a fracture (Fig. 5E). *Araripesuchus buitreaensis* is the only species of Uruguaysuchidae in which the supraoccipital is not exposed on the skull roof.

#### 5.2.12. Otoccipital

These bones are complete and exposed in occipital view in MPCA PV 243 and partially preserved in the holotype, MPCA PV 242, and 513 (only the left one; Figs. 3, 4 and Fig. S2). The posterior surface of otoccipital bears a subhorizontal crest that divides this bone in two planes, one vertical and other that faces posteroventrally. The vertical surface of the otoccipital contacts the squamosal dorsolaterally, along the paraoccipital process, and the supraoccipital medially. Below the paraoccipital process, the otoccipital forms the dorsomedial margin of the cranioquadrate passage. The posteroventral plane projects anteroventrally and contacts the basioccipital medially, the quadrate laterally, and the basisphenoid anteroventrally. Each otoccipital meets dorsal to the foramen magnum, forming its dorsal and lateral margins and the lateral portion of the neck of the occipital condyle. Lateral to the occipital condyle, there are three foramina, two dorsal ones, similar sized and horizontally aligned (one medial and the other lateral), and another ventral and larger. The ventral one is the carotid foramen, for the passage of the cerebral branch of the internal carotid artery (Porter et al., 2016). The dorsal medial foramen corresponds to the exit of the anterior and posterior branches of the cranial nerve XII and the dorsal lateral one is the metotic foramen (for the passages of the cranial nerves IX to XI). The anteroventral tip of the otoccipital forms the posterior border of the opening of the lateral Eustachian tube, which is also enclosed by the basioccipital medially and the basisphenoid laterally and anteriorly. The otoccipital do not forms a *crista tuberalis* as it does in other crocodyliforms. The otoccipital and basisphenoid separate the quadrate from the

basioccipital as in *Araripesuchus patagonicus*, but differing from *A. tsangatsangana*, in which the quadrate contacts the basioccipital (Turner, 2006).

#### 5.2.13. Basioccipital

The basioccipital is completely preserved in MPCA PV 242, 243, 513 and partially preserved in the holotype. In ventral view, this bone has an oblique orientation (posterodorsal to anteroventral) with a hexagonal shape, longer than wide. It has contacts laterally with the otoccipitals and anteroventrally with the basisphenoid. It forms the ventral portion of the occipital condyle neck and the condyle body entirely, which is ventrally oriented. Anterior to the occipital condyle, the basioccipital is markedly concave, forming a condylar recess (Fig. 5F). Anterior to this recess, the basioccipital forms a marked median crest, which reaches the posterior border of the median Eustachian tube. At this level, the external surface of the basioccipital is slightly convex because of the presence of a well-developed, U-shaped basioccipital recess, exposed dorsally by a fracture in MPCA PV 513 (Fig. 5E). The basioccipital encloses the lateral (paired) and medial (unpaired) Eustachian tubes, both medially and posteroventrally. The basioccipital tubera are not developed.

#### 5.2.14. Basisphenoid

It is complete in MPCA PV 242, 243 and 513 (Figs. 3, 4 and Fig. S2). The basisphenoid is exposed in ventral view and contacts the pterygoids both anteriorly and anterolaterally, the quadrate posterolaterally, the otoccipital posteriorly and the basioccipital posteromedially. It forms the anterodorsal borders of the median and lateral Eustachian tubes. The ventral surface of the basisphenoid is deeply concave, forming an ovoid groove delimited laterally by marked crests. These crests are also present in *Araripesuchus gomesii*, *A. patagonicus*, and *A. tsangatsangana*. These crests are formed by the basisphenoid (medially) and the pterygoids (laterally). A recess of the pneumatic paratympanic system (Dufeu and Witmer, 2015) bulges the basisphenoid at the posterior sector of these crests. This recess is exposed by a fracture in MPCA PV 513 (Fig. 5E). Dorsally and anteriorly, the basisphenoid forms a slender and elongated cultriform process (basisphenoidal rostrum), well-preserved in MPCA PV 243, that projects between the orbits and has a posterior foramen, probably for the passage of the cranial nerve VI (Fig. 6A).

#### 5.2.15. Laterosphenoid

It is exposed in MPCA PV 243 and partially in MPCA PV 242. It forms the anterolateral wall of the braincase and contacts the frontal and parietal dorsally, postorbital dorsolaterally, quadrate posterolaterally, the pterygoids anteroventrally, the epipterygoid posteroventrally, and the basisphenoid medioventrally. Both laterosphenoids approach each other in the midline anteriorly, but they do not contact (as in *A. gomesii* and *A. tsangatsangana*). The capitate process is laterally oriented and contacts the posorbital.

#### 5.2.16. Epipterygoid

The epipterygoid is preserved on the lateral wall of the braincase of MPCA PV 243 (Fig. 6B). It is a quadrangular and laminar small bone sutured to the laterosphenoid dorsally, the quadrate posteroventrally, and the pterygoid anteroventrally. Together with the laterosphenoid, the epipterygoid delimits the branches V<sub>2-3</sub> of the trigeminal nerve.

#### 5.2.17. Quadrate

It is exposed almost and complete in MPCA PV 242, 243, 513 (only the left bone) and partially complete in the holotype; an isolated left quadrate was found associated with MPCA PV 583



**Fig. 6.** Photographs showing details of the cranial anatomy of *Araripesuchus buiterraensis*. **A**, interorbital sector of the skull of MPCA PV 243 in right lateral view; **B**, detail of the braincase wall of MPCA PV 243 in right lateral view; **C**, left quadrate of MPCA PV 242 in posterior view; **D**, detail of the middle sector of palate of MPCA PV 242; **E**, posterior and middle sector of the right mandible ramus of MPCA PV 242 in lateral view. Abbreviations: **an**, angular; **ch**, choana; **cp**, cultriform process; **d**, dentary; **ept**, epityergoid; **fa**, foramen aërum; **is**, interchoanal septum; **j**, jugal; **ls**, laterosphenoid; **po**, posornital; **pch**, parchoanal fossa; **q**, quadrate; **san**, surangular; **sq**, squamosal; **pt**, pterygoid; **qj**, quadratejugal; **VI**, cranial nerve VI (abducens).



(Fig. S4C). It is a short and robust bone and firmly sutured to the braincase and palate. Its lateral portion contacts ventral and anteriorly the quadratojugal by an oblique suture, dorsal and posteriorly the squamosal, and anteriorly the postorbital (only seen in the left side of MPCA PV 243). Its medial portion contacts the laterosphenoid anteriorly, the pterygoids anteroventrally, the basisphenoid and the otoccipital posteroventrally, the prootic medially, and the parietal dorsally, at the wall of the supratemporal fossa. This bone forms the floor of the otic recess and the ventral and anterior border of the otic foramen, which is oval in shape, with the main axis orientated from dorsolateral and anterior to ventrolateral and posterior. The otic foramen in *Araripesuchus patagonicus* is smaller and more rounded. In the posteroventral border of the otic foramen there is the incisura of the otic aperture of the cranioquadrate passage (Montefeltro et al., 2016); the latter is excavated in the quadrate, near the medial contact with the otoccipital.

Anterior to the otic foramen, there is a large suboval pneumatic foramen, the subtympenic foramen (*sensu* Dufeu, 2011; Dufeu and Witmer, 2015; Montefeltro et al., 2016; = siphoneal foramen, Pol et al., 2014); this foramen is one sixth of the diameter of the otic foramen. The subtympenic foramen is present in many extant (e.g., *Osteolaemus* Cope, 1860 and *Caiman* Spix, 1825) and fossil (e.g., notosuchians, like *Caipirasuchus lori* and Carvalho, 2011) crocodyliforms. The subtympenic foramen seen in *Uruguaysuchus aznarezi*, *Araripesuchus wegeneri* and *Anatosuchus* is smaller (in comparison with the otic foramen) than that seen in *A. buitreaensis*. Also in *Uruguaysuchus* this foramen is located anterodorsally to the otic foramen and in *Notosuchus terrestris*, there are several subotic foramina anterior and ventral to the otic foramen (Barrios et al., 2018).

At the level of the floor of the otic recess, there is a depressed zone (periotic fossa *sensu* Montefeltro et al., 2016), with a bilobulated ventral margin, which is the buttress of the tympanic membrane. In occipital view, the quadrate forms the lateral border of the cranioquadrate opening. The articular ramus of the quadrate is ventrally oriented. The quadrate condyles (two) are ventrally projected from the level of the upper tooth row. The medial condyle is smaller than the half of the lateral one and is more ventrally projected. Both condyles are separated by an intercondylar groove and articulated with the glenoid fossa, formed by the articular and the surangular. The lateral condyle contacts with the articular and surangular and the medial condyle only with the articular. At the dorsal surface of the medial condyle, there is the foramen aërum just medial to a marked oblique crest, which runs dorsolaterally to ventromedially (Fig. 6C). In ventral view, the quadrate contacts medially and anteriorly the basisphenoid, medially and posteriorly the otoccipital, and anteriorly and laterally the pterygoid. At the anteroventral surface of the quadrate, there are two crests, more developed in the largest specimen (MPCA PV 242). The most anterior and marked crest corresponds topographically with the crest "A" of Iordansky (1964). This crest extends laterally to the pterygoid-basisphenoid suture at the median sector of the ventral surface of the quadrate and is almost parallel to the other crest, which corresponds topographically with the crest "B" of Iordansky (1964). This crest "B" (or *crista pseudotuberalis sensu* Barrios et al., 2018) extends from the medial condyle of the quadrate to the pterygoid and forms the lateral margins of the occiput. In MPCA PV 513 and 583 a natural fracture permits to observe that the quadrate is highly pneumatized by several cells (Fig. S4C).

#### 5.2.18. Quadratojugal

It is completely preserved in MPCA PV 513 (the left one) and partially preserved in MPCA PV 242, 243 and in the holotype. Dorsally contacts the quadrate along an oblique suture (anterodorsally to posteroventrally directed), without taking part of the

lateral articular condyle of the quadrate but reaching the lateral lobe of this bone, as in peirosaurids, sebecids (Pol et al., 2014), *Araripesuchus patagonicus*, *A. tsangatsangana*, *A. wegeneri*, and *Anatosuchus* (but unlike *A. gomesii*). Anteriorly and anteroventrally contacts the jugal by an almost horizontal suture. It forms the posterodorsal and posterior margin of the laterotemporal fenestra. The contact with the postorbital is not well-defined in any specimens, but it probably contacts the postorbital in the dorsal corner of the laterotemporal fenestra. The external surface of the bone is smooth, devoid of any ornamentation.

#### 5.2.19. Vomer

In MPCA PV 242, the posterior part of these bones are exposed by fracture. They are laminar and narrow, form the median floor of the nasal cavity and extend anteroposteriorly over the palatines, which prevent the exposure of the vomers in palatal view. Both vomers form a median groove for the support of the cartilaginous internasal septum (*sulcus septalis*). They contact posteriorly the pillar process of the prefrontals.

#### 5.2.20. Palatine

The palatines are preserved complete in MPCA PV 242 and 243 and partially in MPCA PV 515, 610, 614 and the holotype. They extend anteriorly between the maxillae contacting them through a U-shape suture. Palatines vary among different specimens, being shorter and wider in larger specimens (MPCA PV 242, Fig. 3B and 610, Fig. S5B). In MPCA PV 243 (Fig. 4B), the palatines are longer and narrow, and extend posteriorly forming the anterior half of the medial margin of the suborbital fenestrae, with the choanae in this specimen being anteroposteriorly shorter than in MPCA PV 242 and 610 (Figs. 3B and S5B). Palatines do not form part of the interchoanal septum and delimit the choanae anteriorly. Internally, palatines are pneumatized by the palatine sinus, exposed by fracture in MPCA PV 515. The palatines in the specimens MPCA PV 242 and 610 have their anterior end more quadrangular and similar to that of *Araripesuchus patagonicus* and *A. gomesii*, but in the holotype and in MPCA PV 243 they are anteriorly more rounded, resembling those of *A. wegeneri* and *Uruguaysuchus* (see discussion below).

#### 5.2.21. Pterygoid

This bone is preserved almost complete in MPCA PV 242, 243, 614 and the holotype and fragmentary in MPCA PV 513 and 515. It contacts the palatines anteriorly, the ectopterygoid laterally, the basisphenoid posteromedially, the quadrate posterolaterally, and the laterosphenoid posterodorsally. Both pterygoids are fused along the midline, except at the portion just anterior to the contact with the basisphenoid, where both pterygoids join by a short suture between the posterior median processes of the pterygoids (e.g., Fig. 3B). This condition, also seen in *Notosuchus* and in other species of *Araripesuchus* (*A. patagonicus*) differs from that of *Crocodylia* in which the interpterygoid suture persists anterior to the choanae (Iordansky, 1973; Barrios et al., 2018). Pterygoids form completely the choanal septum. This septum broadens anteriorly at its mid-region unlike, other uruguaysuchids that have an acute anterior tip. As in *Simosuchus* Buckley et al. 2000, but different from *A. gomesii*, and *A. patagonicus* (Pol and Apesteguía, 2005), it is T-shaped in transversal section and have a median groove; a groove that is also present in *Uruguaysuchus*.

Pterygoids delimit the choanae, except for the anterior margin, and the suborbital fenestrae, medially and posteriorly. The posterior margins of the choanae do not reach the pterygoid flanges. Posterior to the choanae, the pterygoids have a pair of marked depressions separated by a median crest, the parchoanal fossae (Fig. 6D). The pterygoid flanges are laminar and wide slightly inclined from anterodorsal to posteroventral, and they are bulged by

the pneumatic recesses of the pterygoid sinus (an autapomorphy of the species; Pol and Apesteguía, 2005). The anterior part (three fourth) of the lateral margin of the pterygoid flanges are sutured to the ectopterygoids. The free posteroventral apex of these flanges have a porous surface related to the contact of the transiliens cartilage, for the attachment of adductor muscles (*M. pseudotemporalis* and/or *M. intramandibularis*; Schumacher, 1973; Holliday and Witmer, 2007). The posteromedial margin of pterygoid projects posteroventrally in two conspicuous processes separated by a marked notch. The suture with the basisphenoid and the quadrate is interdigitated. Pterygoids are exposed in dorsal view by a fracture in MPCA PV 242 and 243. They extend dorso-medial and converge in the midline forming a longitudinal crest which overlaps the basisphenoid and contact the prefrontal pillars and vomers. In dorsal view, pterygoids reach posteriorly the laterosphenoid. At the posterior and medial area of the pterygoid flanges dorsal surface, there is a concave surface probably for the attachment of adductor musculature (*M. pterygoideus ventralis*).

#### 5.2.22. Ectopterygoid

Both ectopterygoids are preserved almost completely in MPCA PV 242, 243, 614 and the holotype, and only the left one in MPCA PV 513 and 515. They have two branches: a ventral one that extends like a spine lateral to the pterygoids and a dorsal one that contacts the jugal and maxilla laterally. The dorsal branch expands anteriorly, reaching the maxilla and forming most of the lateral border of the suborbital fenestra. This branch is also posteriorly projected in a short spine.

#### 5.2.23. Palpebral bones

Both (left) palpebral bones are preserved articulated in MPCA PV 610 and a fragmentary anterior palpebral bone is preserved and associated to the internal part of the orbit in MPCA PV 513 (the left one) and in the holotype (the right one). The posterior palpebral is subrectangular and approximately one sixth the size of the anterior palpebral, and it is supported by a triangular projection of the postorbital. The largest anterior palpebral is subtrapezoidal, remarkably broad on its anterior end, with a sinusoidal posterior margin. This palpebral is supported by a shelf formed by the prefrontal and lacrimal. In *Araripesuchus tsangatsangana*, the anterior palpebral does not contact the lacrimal. The contour of the anterior palpebral differs remarkably from that of the other uruguaysuchids that preserve this bone (*A. gomesii*, *A. patagonicus*, *A. tsangatsangana*, *A. wegeneri* and *Uruguaysuchus*), in which the palpebral has different sizes and a more elongated and curved contour.

#### 5.2.24. Dentary

It is preserved almost complete in MPCA PV 242, 243, 513 (the left one), 515 (the left one), 583, 610 (the right one), 614 and the holotype. In all the specimens, except MPCA PV 583 and 610, the mandible is in occlusion. In the specimen 583, it is possible to observe that the first nine alveoli are well-defined and separated, and there is an alveolar groove for four more teeth posteriorly. The dorsal surface of the dentary at the symphyseal region is planar, similar to *Araripesuchus tsangatsangana*, but different from that of *A. gomesii* and *Uruguaysuchus*. This surface has a series of foramina anteroposteriorly aligned along the medial margin of the alveoli.

The dentary symphysis reaches the level of 9th tooth and forms two thirds of the mandibular symphysis. Both dentaries contact the splenial posteromedially by a U-shaped suture. In lateral view, the dentary is anteriorly low. Its dorsal border descends from the 4th to the 7th alveoli, elevates obliquely from the 8th to the 11th alveoli and becomes posteriorly straight.

The lateral surface of the dentary is ornamented by pits more concentrated in the anterior sector of the bone. At the posterior

part of the dentary, its lateral surface has poorly marked pits in the smaller specimens (MPCA PV 515) and deep, fine lines with no pits in the larger specimens (MPCA PV 242). In lateral view and parallel to the dorsal border of the dentary, there is a row of neurovascular foramina. The dentary delimits the external mandibular fenestra anteriorly and contacts the surangular posteriodorsally. Unlike extant crocodiles and similar to basal mesoeucrocodylians, the dentary-surangular contact is located at the middle of the dorsal border of the external mandibular fenestra (Turner, 2006). The external mandibular fenestra is oval and well-preserved in MPCA PV 242 and 614. Its posterodorsal margin is dorsoventrally wider than in *Uruguaysuchus*. The lateral wall, ventral to the external mandibular fenestra, is extremely low so the Meckelian canal is exposed in lateral view. In ventral view, the dentary symphysis is interdigitated, occupying four fifths of the mandibular symphysis. In this view, both dentaries contact the splenial by a U-shape sutured, like in *Uruguaysuchus* and different from other species of *Araripesuchus* which have a V-shaped suture. The ventral surface of these bones is ornamented by small pits.

#### 5.2.25. Splenial

It is preserved in MPCA PV 242, 243, 515, 583, 610, 614 and the holotype. In dorsal view, the splenials form one third of the mandibular symphysis and contact the dentary by a U-shaped suture. The splenial extends posteriorly forming the medial wall of the mandibular ramus, bordering the alveolar groove medially. It contacts the angular posteroventrally by an oblique suture, which reaches the anteroventral corner of the internal mandibular fenestra (see MPCA PV 515). Is not possible to observe the splenial-surangular contact in none of the specimens. In ventral view, the splenials form one fifth of the mandibular symphysis and contact anteriorly with the dentary by a U-shaped suture. The medial surface of the splenial is smooth. Just posterior to the splenial symphysis, there is a single and relative large foramen *intermandibularis oralis* for the passage of the cranial nerve V<sub>3</sub>. On the ventral surface of the mandibular symphysis there is a small peg, which also see in *Notosuchus* and *Uruguaysuchus*, but in *Araripesuchus buitreaensis* this peg projects anteriorly at the ventral surface of the mandibular symphysis.

#### 5.2.26. Surangular

The surangular is preserved almost completely in MPCA PV 242 (right one), 513 and 614 (in both the left one) and partially in 243, 515, 610 (the right one) and the holotype. The surangular has two planes (Fig. 6E): an anteroposteriorly slightly concave lateral plane that delimits the external mandibular fenestra (dorsal and posteriorly), and a shelf-like horizontal plane that is unique among uruguaysuchids. These two planes are separated to each other by a marked crest. The lateral plane is practically smooth, with some fine lines and isolated pits, and forms a thin lamina of bone ventrally projected, at the dorsal margin of the external mandibular fenestra. The surangular contacts the dentary anteriorly and the angular ventrally by oblique sutures. It forms part of the lateral border of the retroarticular process and the lateral portion of the glenoid cavity, where it articulates with the lateral condyle of the quadrate.

#### 5.2.27. Angular

The angular is preserved in MPCA PV 242, 243, 513 and 614. It forms the ventral border of the external mandibular fenestra and the floor of the Meckelian fossa, which is exposed in lateral view. At the ventral border of the external mandibular fenestra, the angular forms a thick flange with a deep sulcus, which is laterally delimited by a conspicuous crest (observed in MPCA PV 242 and 614) that extends posteriorly and anteriorly to the fenestra (Fig. 6E). The

presence of a lateral flange with a crest in the ventral border of the external mandibular fenestra and the lateral exposition of the Meckelian fossa has been mentioned in some notosuchians (e.g., *Notosuchus* and *Mariliasuchus* [Carvalho and Bertini, 1999](#)) but not in uruguaysuchids ([Pol et al., 2014](#)).

Posterior and ventral to this crest, there is a depression in the area of the attachment of the *M. pterygoideus posterior*. The angular contacts the surangular posteriorly and dorsally by an oblique, posteroventrally directed suture. It forms part of the ventrolateral portion of the retroarticular process.

In lateral view, posterior to the external mandibular fenestra, the ventral margin of the angular is straight and subhorizontal, so the ventroposterior angle of the lower jaw is of about 170°. The ornamentation is similar to that of the surangular.

#### 5.2.28. Articular

It is preserved almost complete in MPCA PV 242, 243, 513 and 614. The articular contacts the angular ventrally and the surangular laterally. It forms more than half of the glenoid fossa, where it articulates with the quadrate. The glenoid fossa is kidney-shaped with two facets separated by a longitudinal crest. The medial facet is smaller than the lateral one and articulates with the medial condyle of the quadrate. The articular forms the subrectangular retroarticular process. *Uruguaysuchus* has a process that is remarkably short anteroposteriorly, whereas *A. patagonicus* has this process dorsomedially narrow, and *A. gomesii* has it flat and quadrangular. In dorsal view, the retroarticular process is lateromedially convex, divided diagonally into two planes ([Figs. 3A and E; Figs. 4A and D](#)): one lateral and subhorizontal and the other medial and strongly oblique (facing dorsomedially). This dorsal surface of the retroarticular process is also anteroposteriorly concave, with a strongly depressed area at its anterolateral sector.

At the level of the posterior border of the glenoid fossa and on the medial surface of the articular, there is the foramen aërum. This foramen opens in a well-marked bulge and contacts a fine sulcus medial and anteriorly (probably a vascular mark). In ventral view, the articular has a strongly concave area delimited by two lateral and medial crests. In medial view, the articular anterior process is triangular, short and robust. The articular is highly pneumatized by cells, observed by fracture in MPCA PV 513.

#### 5.2.29. Dentition

Although the mandible is in occlusion in all the specimens except MPCA PV 583 and 610, the upper dentition is observed in MPCA PV 243, 515, 610, 614 and the holotype. Like in other notosuchians (e.g. *Notosuchus terrestris*, [Barrios et al., 2018](#); *Araripesuchus wegneri* and *A. tsangatsangana*) but different to *Uruguaysuchus* and *A. gomesii*, there are five premaxillary alveoli (completely observed in MPCA PV 515). Premaxillary teeth are preserved implanted in MPCA PV 243 (two teeth in the left side and one tooth in the right side) and in MPCA PV 515 (two teeth in the left side and four in the right side). The premaxillary teeth have conical, pointed crowns vertically oriented; the first three are small, the fourth is the biggest and the fifth tooth is the smallest. These teeth occluded alternatively with the lower teeth. They all have smooth enamel, without ornamentation or denticles in medial and distal margins.

There are seven maxillary teeth (see MPCA PV 610) and this is a feature unique in this species, since all other uruguaysuchids have more teeth. The first four maxillary teeth have conical, pointed crowns and are also vertically oriented. The first two teeth are smaller than the fourth (being the first the smallest of all); the third

tooth, the caniniform, is the largest of all the dental series, being three times larger than the other and surpassing the lower jaw ventrally by almost a half of its length in some specimens (MPCA PV 515; [Fig. S3B](#)). This tooth has the biggest root, which bulges the maxilla, as seen in dorsal and lateral views of the skull. Posterior to the fourth tooth, there are three teeth with slight lateral compression, rounded crowns and devoid of denticles. The reminder posterior teeth occlude more medially so they cannot be observed in lateral view. The maxillary teeth have an ornamentation given by vertical straight lines.

The dentary dentition is better observed in MPCA PV 583 and 610. As stated above, the first nine dentary teeth are implanted in complete alveoli and the posterior ones (possibly four) are implanted in a dentary groove delimited medially by the splenial. The first two alveoli are anterolaterally directed and then dorsally oriented, gradually from the second to the sixth tooth. The first nine alveoli are subquadrangular, almost equally sized except for the fourth one which is the larger tooth. MPCA PV 583 has nine implanted teeth in the left side of the dentary (three of them have lost its crowns) and three implanted teeth in the right side (one of them without its crown). MPCA PV 610 has four implanted teeth. Only one tooth of the symphyseal region of MPCA PV 583 is complete; it has a conical, slightly laterally compressed and pointed crown with a slight posterior orientation and the same ornamentation seen in the maxillary teeth. From the tenth to thirteenth teeth they are as big as the fourth, but with rounded crowns, separated from the root by a marked constriction, without denticles, smooth enamel and a slight lateral compression. The roots of those teeth are broader than the crowns.

#### 5.2.30. Hyobranchial apparatus

The right *Cornu branchiale* I (*sensu* [Schumacher, 1973](#)) is preserved and associated to the palate in MPCA PV 614 ([Fig. S6B](#)). It has a boomerang shape, with the distal end wider than the proximal. Its ventral surface is smooth without crests and its total length is almost equal to the anteroposterior length of the suborbital fenestra (almost twice the choanal length).

#### 5.3. Pneumatic sinuses

The skull of *Araripesuchus buiterraensis* is highly pneumatized, as observed by a fracture in MPCA PV 513, 515, and 583. Recesses of the median pharyngeal and pharyngotympanic systems are exposed in MPCA PV 513 including: the parietal and squamosal recesses of the pharyngotympanic sinus and the parietal diverticulum of the intertympanic diverticulum; the basioccipital recess of the basioccipital diverticulum, basisphenoid recess of the basisphenoid diverticulum, and the pterygoid recess of the pterygoid diverticulum (*sensu* [Dufeu and Witmer, 2015](#)). All these recesses are large and complex, with subdivisions that form several cells. These pneumatic systems are still present and large (i.e., pterygoid recess) in larger specimens ([Fig. 5E](#)). The pharyngotympanic system pneumatizes the quadrate to some degree, as is seen by a fracture in MPCA PV 583 that shows the quadrate diverticulum formed by several interconnected cells ([Fig. S4C](#)).

Part of the recess of the nasal cavity and paranasal sinus system are exposed by fracture in MPCA PV 515. In medial view, the maxillary (anterior and ventral) and palatine (posterior and ventral) sinuses and nasal cavity (nasopharyngeal duct, dorsal) are exposed. The maxillary and palatine sinuses are similar in size. The maxillary sinus only pneumatized the maxilla, but the palatine sinus pneumatized both the maxilla and palatine ([Fig. S3C](#)).



## 6. Discussion

### 6.1. Diagnostic features

*A. buitreaensis* is diagnosed by a combination of cranial characters, some of them autapomorphic and some shared with the other species of uruguaysuchids (see diagnosis). The supraoccipital of *A. buitreaensis* has a marked crest, which is also present in *A. tsangatsangana*, but less marked. Contrary to the other South American species, *A. buitreaensis* has a marked median crest on the frontal, which is present but lower in the African species. In *A. buitreaensis*, the prefrontal is anteroposteriorly expanded and, as in other uruguaysuchids (except for *A. gomesii*), prevents the contact between nasal and lacrimal. The retroarticular process has an equidimensional shape; this feature is different from other uruguaysuchids, which have a retroarticular process longer than wide.

Some autapomorphic characters for this species are related to the lower jaw. The unique morphology of the mandible includes the presence of a thin lamina of bone of the surangular, that projects over the external mandibular fenestra, as well as the marked crests on the posterior region of the angular and surangular. In the anterior region of the mandible, the splenial peg that continues ventrally over the symphysis also distinguishes this species from other uruguaysuchids. Other unique features of *A. buitreaensis* include the lower number of maxillary teeth in the upper jaw and the presence of teeth implanted in complete alveoli in one section of the maxilla but in a dental groove in another section.

Some other morphological characteristics of the species are mostly concentrated in the posterior region of the skull, such as the presence of rims at the margins of supratemporal fenestra, a vertical bony surface for the articulation of the ear-flap at the squamosal and a more dorsomedially-inclined lateral wall of the temporal region (particularly the jugal and the quadratojugal). The shape of the anterior palpebral of *A. buitreaensis* is unique among uruguaysuchids and similar to that of some peirosaurids (e.g., *Lomasuchus*, *Montealtosuchus* [Carvalho et al., 2007](#)) and other notosuchians (e.g., *Simosuchus*).

### 6.2. Ontogeny and individual variability

The difference in size between specimens may reflect different ontogenetic stages. Among these specimens, there is a notable change in the ornamentation of the cranial bones, mainly in the depth of the pits and grooves. In extant crocodiles, the dimensions of the pits increase during ontogeny and seem proportional to the size of the animal ([de Buffrénil, 1982](#)). The contour of the snout also varies among different specimens, becoming more lateromedially expanded and convex in larger specimens. This is evident in the largest specimen (MPCA PV 242) when compared with the pointed snout present in MPCA PV 515. The expansion at the anterior region of the snout in larger specimens is related to the development of a bulged area of the lateral margin of maxilla, at the level of the caniniform tooth (which seems to increase in relative size during ontogeny). This tooth is preserved in a few specimens, like MPCA PV 515 and 610, where it is pointed, almost straight and exceeds the ventral margin of the dentary in occlusion. This tooth in MPCA PV 610 is shorter and posteriorly curved.

Another feature that varies among differently sized specimens is the development of crests for muscle attachments, such as the crest of the ventral surface of the quadrate (crests “A” and “B” or *crista pseudotuberalis*) and the mandibular crest for the insertion of the *m. pterygoideus ventralis*, which are more marked in the largest specimen (MPCA PV 242). [Iordansky \(1973\)](#) noted that the development of the crests of the quadrate in extant crocodiles varies

ontogenetically, being more developed in older specimens and smoother or absent in younger and smaller specimens.

The premaxilla-maxilla foramen is elongated with a straight anterior margin in smaller specimens (like MPCA PV 515), but it is circular in larger specimens, such as MPCA PV 610 (a condition also found in other uruguaysuchids).

Some features show intraspecific (individual) variability that is not related to size or ontogeny, like the shape of maxilla-palatine suture in ventral view. In MPCA PV 242 and MPCA PV 610, this contact is quadrangular and the palatine anterior process is broad; conversely, in MPCA PV 243 and the holotype the anterior process of the palatine is heart-shaped and proportionately narrower. The concavity of the choanal septum also varies individually. In MPCA PV 242 and the holotype, this septum is less concave than in MPCA PV 243. The foramen *intermandibularis oralis* is more posteriorly placed in MPCA PV 515, but in the other specimens (and other uruguaysuchids) it is located closer to the splenial peg of the symphysis.

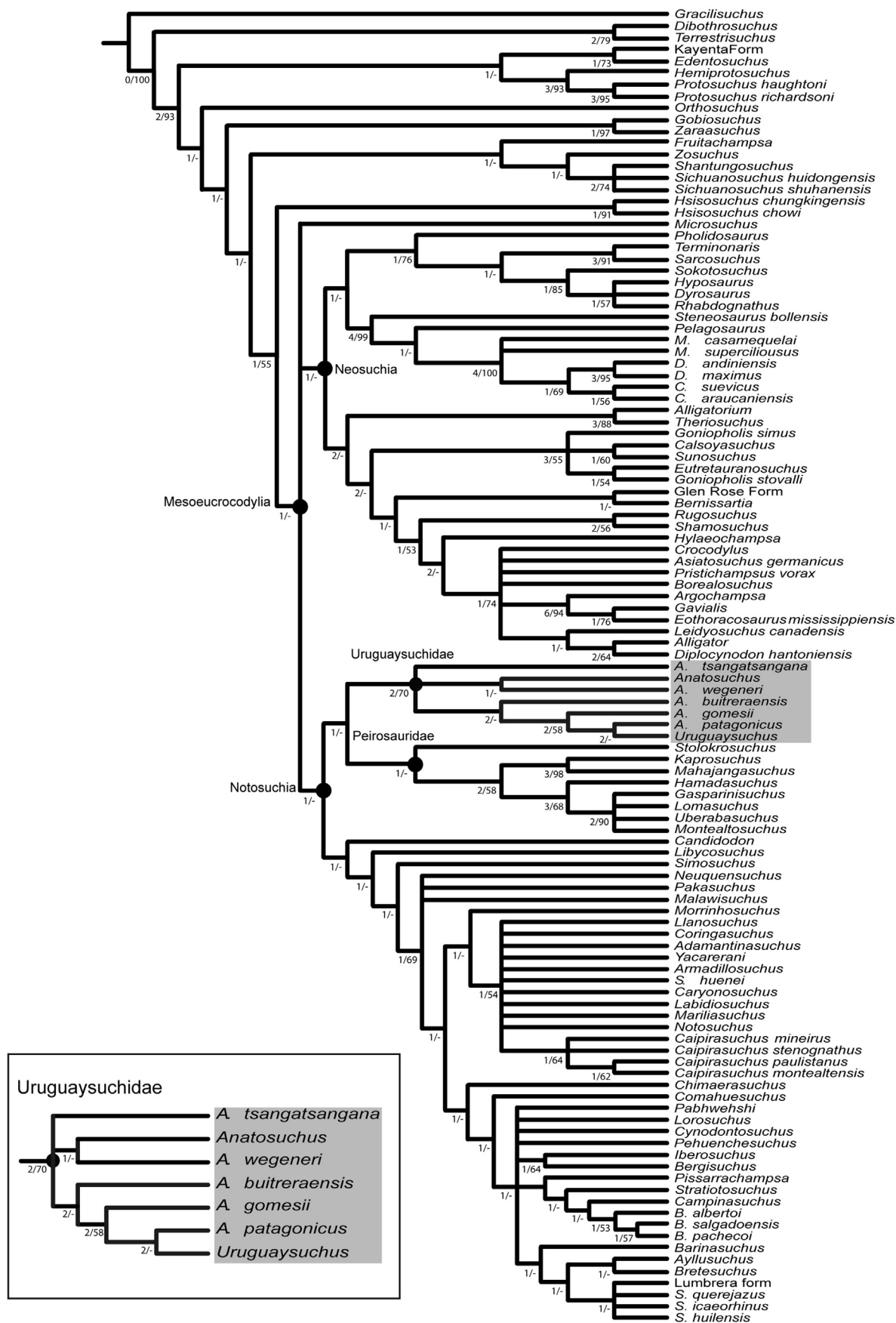
### 6.3. Phylogenetic analysis and the affinities of *A. buitreaensis*

The analysis of the data matrix found 215 MPTs of 1726 steps, with a consistency index (CI) of 0.12 and a retention index (RI) of 0.21. The topology of the strict consensus tree is generally consistent with the results of previous versions of this dataset ([Pol et al. 2014](#), [Leardi et al. 2018](#) and [Martinelli et al., 2018](#), [Fig. 7](#)) although uruguaysuchids are better resolved. Uruguaysuchidae is recovered as monophyletic, with moderate support values (Bremer = 2, Jackknife = 70; see [Supplementary Information](#) and synapomorphies listed in Systematic Paleontology) and placed within Notosuchia, as the sister clade of Peirosauridae ([Fig. 7](#)).

*Aaripesuchus wegeneri* and *Anatosuchus minor* form a clade supported unambiguously by two synapomorphies: basisphenoid hidden from ventral surface by pterygoid flanges that extend posteriorly up to the level of the basioccipital-basisphenoid suture (56: 0→1) and choanal groove partially stated with parts of the septum located dorsal to the lateral choanal margins (69: 2→1). This clade has minimal Bremer support and jackknife values of less than 50% (see [Fig. 7](#)). *A. tsangatsangana* is recovered as part of the basal polytomy of Uruguaysuchidae along with the branches that lead to the African (*A. wegeneri* and *Anatosuchus*) and the South American clades.

Within uruguaysuchids, a South American clade is recovered in all MPTs, composed by *A. buitreaensis*, *A. gomesii*, *A. patagonicus*, and *Uruguaysuchus aznarezi*. This clade is supported unambiguously by the following synapomorphies: choanal septum bar T-shaped expanded ventrally (191: 0→1), ventral surface of choanal septum marked by an acute groove (271: 0→1), frontal along its suture with the prefrontal broad and tabular shaped, with lateral sutures with prefrontals parallel to each other (353: 0→1). This clade has a Bremer support of 2, but it has jackknife frequencies lower than 50%.

*A. buitreaensis* is recovered as the sister taxon to the clade composed of all the other South American species of the family. This clade is unambiguously supported by a narrow bar between orbits and supratemporal fossa, with a sculpting restricted to anterior surface (31: 0→1), four premaxillary teeth (106: 0→1); Tooth margins in posterior region of the tooth row with denticulate carinae formed by homogeneous and symmetrical denticles with a sharp cutting edge (120: 1→0); dorsal surface of mandibular symphysis strongly concave and narrow, trough shaped (189: 0→1); and flat ventral surface of internal nares septum tapering anteriorly (225: 2→1). It also has moderate support, with Bremer values of 2 and appearing in 58% of the jackknife replicates.



**Fig. 7.** Strict consensus of 215MPTs found in the phylogenetic analysis showing the position of *A. buiterraensis*. Support measures are placed next to the nodes (Bremner/Jackknife support).

### 6.3.1. Specimen level analysis of *A. buitreaensis*

Each of the seven specimens referred here to *A. buitreaensis* were included as a separate terminal in the same data matrix. A parsimony analysis of this dataset was performed (using the same settings as before) in order to test the referral of the specimens to *A. buitreaensis* based on their position in the optimal trees. The analysis resulted in 229 MPTs of 1724 steps (CI = 0.240 and RI = 0.652). The strict consensus obtained (see Fig. S7) shows a monophyletic group clustering the holotype and all the referred specimens of *A. buitreaensis*, supporting their referral to this taxon. This clade is unresolved and ambiguously supported by the following characters: dorsal surface of frontal and parietal with midline ridge (22: 0→1); parieto-postorbital suture absent from dorsal surface of skull roof and supratemporal fossa (23: 1→0); ventral surface of basisphenoid wide and similar to in length than basioccipital (55: 0→1); one large palpebral (65: 3→2); slightly splenial involvement in symphysis in ventral view forming up to 20% symphyseal length (77: 2→1); maxilla with seven teeth (108: 0→1); U-shaped dentary symphysis in ventral view (154: 0→1); absent of exposure of supraoccipital in skull roof (171: 1→0); posterior margin of pterygoid flanges dorsoventrally thick, with pneumatic spaces (198: 0→1); orientation of quadrate body distal to otoccipital-quadrate contact in posterior view ventrolaterally (212: 0→1); pterygoid ventral surface at the origin of the pterygoid flanges bearing a pterygoid parachoanal fossa (293: 0→1); absent or poorly developed sagittal ridge on the ventral half of the posterior surface of the basioccipital (360: 1→0) and relative length and width of anterior (parallel sided) process of dentary symphysis elongated, being approximately twice as long as wide (364: 0→1).

## 7. Conclusions

Here, we present a complete cranial description of *A. buitreaensis*, together with a phylogenetic analysis and a revision of the diagnosis of Uruguaysuchidae. New autapomorphies are added to the original diagnosis of Pol and Apesteguiá (2005). The phylogenetic analysis supports *A. buitreaensis* within a clade of South American species of uruguaysuchids. A comparative analysis of the multiple specimens of *A. buitreaensis* reveals features (e.g., ornamentation, snout shape, bony crest for muscular attachment, maxilla-palatine suture, concavity of the choanal septum, etc.) that show ontogenetic and individual variation.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2020.104494>.