



PALEONTOLOGY

A new species of *Comahuesuchus* Bonaparte, 1991 (Crocodyliformes: Notosuchia) from the Upper Cretaceous of Neuquén, Lake Barreales, Patagonia, Argentina

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Abstract: Notosuchian crocodyliforms were major components of the South American Cretaceous biota and, for over 125 years, paleontological fieldwork in this continent recovered several well-preserved fossils of these animals. They are largely recognized for terrestrial life and specialized feeding habits, frequently presenting bizarre taxa such as *Comahuesuchus*. A new species, *Comahuesuchus bonapartei* n. sp. (MUCPv 597; cast MN), is described from geological strata of Sierra Barrosa Formation (Upper Turonian) and Portezuelo Formation (Lower Coniacian) of Lake Barreales, Patagonia, Argentina. The new fossil comprises a right dentary bone that shares important and unique anatomical features with specimens of *Comahuesuchus brachybuccalis*, such as the presence of a well-marked shelf on the lateral surface of the bone; a flat, low, and wide mandibular symphysis; an enlarged, labiolingually compressed caniniform tooth at caudal position in the dentary; the presence of serrated mesial and distal carinae in the caniniform with a faceted labial surface, and the absence or extremely reduction in number of the postcaniniform dentition. *C. bonapartei* differs from *C. brachybuccalis* in having individual dentary alveoli, rather a dentition set in groove. Phylogenetic analyses support a sister-relationship between both species, which are well nested within notosuchians.

Key words: Gondwana, South America, Neuquén, Upper Cretaceous, Notosuchia, Comahuesuchidae.

INTRODUCTION

South America has one of the most important fossil records of Cretaceous crocodyliforms, some groups also recorded in Africa, China and Europe (e.g., Wu et al. 1995, Sereno & Larson 2009, O'Connor et al. 2010, Rabi & Sebök 2015, Martin & De Laparent De Broin 2016, Taquet 2021), with Notosuchia being the most common clade from this period (De la Fuente et al. 2007, Pol & Gasparini 2007, Pol & Leardi 2015). The current state of knowledge about these highly specialized animals is the result of more than 125 years of paleontological fieldwork and fossil collection management in several universities

and museums, especially in Brazil and Argentina (Woodward 1896, Rusconi 1933, Price 1945, 1950, Kellner 1987, Bonaparte 1991, Gasparini et al. 1991, 1993, Carvalho & Bertini 1999, Ortega et al. 2000, Martinelli 2003, Carvalho et al. 2004, Turner & Calvo 2005, Leardi & Pol 2009, Campos et al. 2011, Kellner et al. 2014, Lio et al. 2016, Martinelli et al. 2018, Coria et al. 2019, Souza et al. 2019). The large number of new fossils unearthed and described over the last years allowed a greater understanding about these animals in areas such as anatomy (Figueiredo & Kellner 2021, Ricart et al. 2021, Nieto et al. 2022), paleobiology (Cubo et al. 2020, Fonseca et al. 2020, Fernández

Dumont et al. 2021), systematics (Ruiz et al. 2021, Pinheiro et al. 2021), and evolution (Godoy 2020, de Celis et al. 2020, Stubbs et al. 2021, Felice et al. 2021).

Since the first discoveries, back in the 19th century, when Woodward (1896) described two new species (i.e., *Notosuchus terrestris* and *Cynodontosuchus rothi*) from Neuquén, Argentina, it has been clear that the Cretaceous South American crocodyliforms were morphologically distinct from coeval fauna of Laurasia. The typical anatomical features of Notosuchia suggests a more terrestrial life (e.g., long and slender limbs), and specialized feeding habits (e.g., short snouts, complex teeth morphology). Those general traits are observed in most fossils described from the highly diversified Upper Cretaceous beds of Patagonia, which include species of Peirosauridae, Uruguaysuchidae, Sebecidae, and Baurusuchidae (Pol & Gasparini 2007, De la Fuente et al. 2007, Pol & Leardi 2015). The adaptative radiation of notosuchians during the Upper Cretaceous corresponds to about 40 to 60% of the cranial morphological disparity observed among crocodylomorphs, however

even among such divergent forms, there are bizarre outliers such as *Comahuesuchus brachybuccalis* Bonaparte, 1991 (Stubbs et al. 2021).

The species *C. brachybuccalis* was first described based on three juvenile specimens (MUCPv 202, MACN-N 30, MACN-N 31) from the Neuquén province of Argentina. The skull and mandible morphology points out small notosuchians with extremely short and wide snouts, presenting a flat and wide mandibular symphysis (Bonaparte 1991) (Figure 1). Their dentition showed unique features like the absence of postcaniniform teeth in the dentary, and the close positioning of the dentary caniniform tooth with the rostral margin of the orbits. A few years later, Martinelli (2003) described new cranial remains of *C. brachybuccalis* (MOZ 6131 P), recovered from Río Negro province, Argentina. This fossil represented the first known adult specimen, being about 25% larger than the other material (Martinelli 2003). Besides the size, other important anatomical differences were observed by Martinelli (2003), both in the

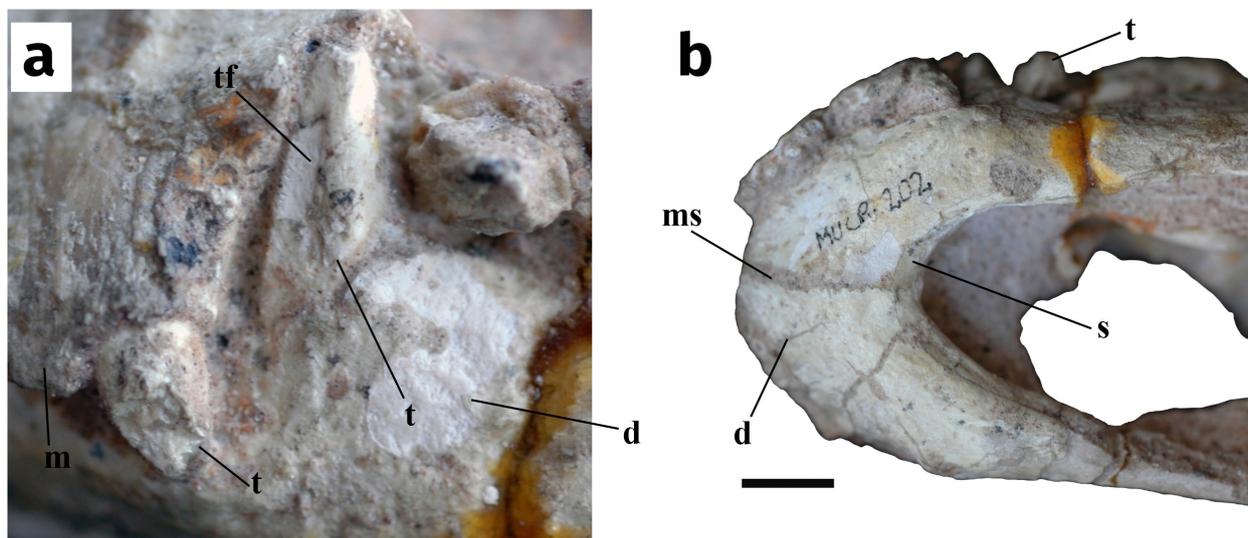


Figure 1. Holotype specimen (MUCPv 202) of *Comahuesuchus brachybuccalis*. **a**, detail of the dentary and maxillary caniniform teeth in lateral view; **b**, ventral view of the mandible. Abbreviations: **d**, dentary; **m**, mandible; **s**, splenial; **t**, tooth; **tf**, tooth facet. Scale bar: 10mm.

skull (e.g., presence of fused frontals, greater exposure of the premaxilla and supraoccipital in dorsal view, broader contact between frontals and prefrontals) and mandible (e.g., presence of a single postcaniniform tooth in the dentary, caudal divergence of the mandibular rami). Here we describe a new species, *Comahuesuchus bonapartei*, from the Futalognko quarry site, in Proyecto Dino Geo-Paleontological Park (Calvo et al. 2007a). The new fossil consists of a partially preserved right lower jaw of an adult animal (Figure 2).

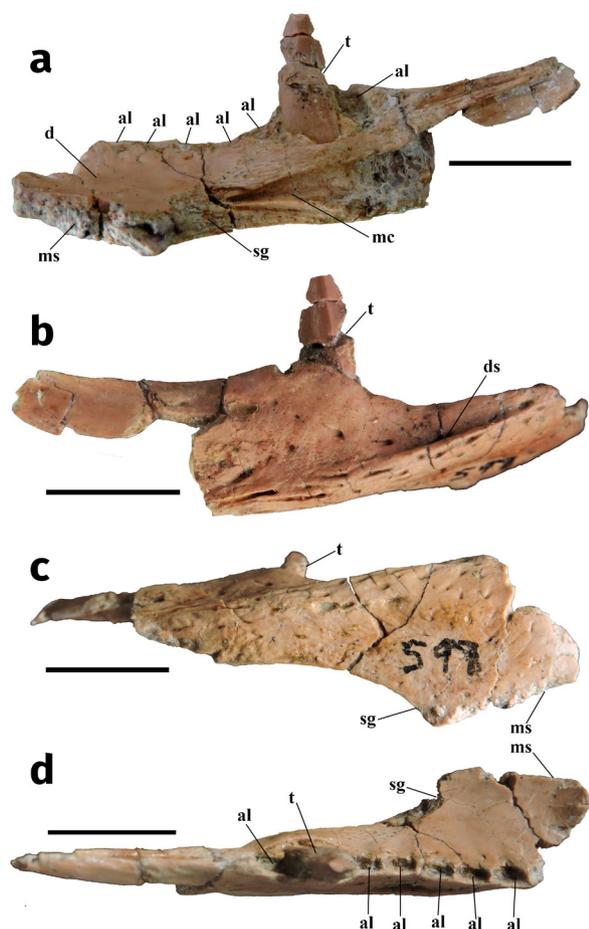


Figure 2. Holotype specimen (MUCPv 597) of *Comahuesuchus bonapartei*. Fragment of the right dentary bone in: **a**, medial view; **b**, lateral view; **c**, ventral view; **d**, dorsal view. Abbreviations: **al**, alveolus; **d**, dentary; **ds**, dentary shelf; **mc**, Meckelian Canal; **ms**, mandibular symphysis; **sg**, splenial groove; **t**, tooth. Scale bars: 10mm.

The holotype of *C. brachybuccalis* (MUCPv 202) and other referred specimens (MACN-N 30, MACN-N 31, MOZ 6131 P) were collected in Santonian strata of the Bajo de la Carpa Formation (Bonaparte 1991, Martinelli 2003). However, the new species *C. bonapartei* (MUCPv 597), comes from geological beds of the middle portion of the Sierra Barrosa Formation or the upper part of the Portezuelo Formation, which are Upper Turonian to Lower Coniacian in age (see geological background below). The new species is therefore the oldest record of the genus so far, expanding its temporal range by about 7.6 million years.

GEOLOGY AND PALEONTOLOGY OF LAKE BARREALES

The area where the new fossil was found comes from continental deposits of Río Neuquén Subgroup, Neuquén Group (Cazau & Uliana 1973, Leanza 1999, Garrido 2010) that it is placed subhorizontal (Rb N330°/12-14° E). The new fossil was excavated from the Futalognko site that originally was interpreted as representing the Portezuelo Formation (Calvo et al. 2007a), whose age has been interpreted as Turonian (Leanza & Hugo 2001). Recently, the Portezuelo Formation was separated into three units, named from base to top Portezuelo, Los Bastos, and Sierra Barrosa formations (Garrido 2010). Furthermore, the Portezuelo Formation (*sensu* Cazau & Uliana 1973) is covered by Plottier Formation. Leanza & Hugo (2001) support that both formations are concordant, but Danderfer & Vera (1992) argue that they are interdigitated.

A new interpretation of the local geology at Futalognko site shows that this paleontological unit is placed either in the middle part of the Sierra Barrosa Formation (*sensu* Garrido 2010) or in the upper portion of the Portezuelo Formation (*sensu* Cazau & Uliana 1973). The maximum

thickness of Sierra Barrosa Formation at the Futalognko site is just 3 meters and it is covered para-concordantly by the Plottier Formation. At this site, the upper part of the Sierra Barrosa is missing.

The new species was living in a region with a fluvial meandering river system in a flattened area of exuberant vegetation, developed in humid climate conditions (Sánchez et al. 2005). These layers were deposited by a low energy fluvial system, as part of a meandering river where the organic remains were trapped in a curve and then it was transformed in an oxbow (JOC pers. observ.). The fossil was recovered from a 50 centimeters thick brown and green claystone.

The Portezuelo Formation at Futalognko quarry, in Proyecto Dino Geo-Paleontological Park, have given an extraordinary record of a paleontological fauna including plants (Calvo et al. 2007a, Passalia et al. 2008), Osteichthyes fishes (Gallo et al. 2011), pterosaurs (Kellner et al. 2006, Kellner & Calvo 2017), turtles (Calvo et al. 2007a), titanosaur sauropods (Calvo et al. 2007b), theropods (Calvo et al. 2004a, b), and ornithopods (Calvo et al. 2007a). Among crocodyliforms the only record up to date was a single peirosaurid tooth (Calvo & Porfiri 2010), but here we describe a new fossil of this clade for the Futalognko quarry site.

On the northeast coast of Lake Barreales, several crocodyliforms were described; the Upper Turonian – Lower Coniacian *Lomasuchus palpebrosus* (Gasparini et al. 1991, Calvo & Porfiri 2010), and *Patagosuchus anielensis* (Lio et al. 2016) from the Portezuelo Formation (Wichmann 1927, De Ferrariis 1968, Cazau & Uliana 1973) or Sierra Barrosa Formation (Garrido 2010) and the Santonian age *Gasparinisuchus peirosauroides* (Martinelli et al. 2012) described previously as “*Peirosaurus tormini*” (Gasparini 1982, Gasparini et al. 1991) from the Bajo de la Carpa Formation

(Herrero Ducloux in Fossa Mancini et al. 1938). The material described here is placed 5,5 km east of the holotype site of *Lomasuchus palpebrosus*, 1,5 km east of the holotype *Patagosuchus anielensis*. The only supposed Cretaceous non-Notosuchia crocodyliform is the protosuchid *Neuquensuchus* from the Bajo de La Carpa Formation at Neuquén city (Fiorelli & Calvo 2007, Lio et al. 2018, but see Lio et al. 2018 for an alternative interpretation).

MATERIALS AND METHODS

Materials

The holotype specimen of *Comahuesuchus bonapartei* is described here and it is housed at the Museo de Ciencias Naturales de la Universidad Nacional del Comahue, Neuquén city, Argentina, under the number MUCPv-597. A cast is housed at the Paleovertebrate Section of the Departamento of Geology and Paleontology of the Museu Nacional, from the Universidade Federal do Rio de Janeiro (MN). The holotype of *C. brachybuccalis* and several fossils of different notosuchian clades were first-hand studied and used for anatomical comparisons (Table I).

Locality

The Futalognko quarry is on the north coast of Barreales lake, about 90 km northwest of Neuquén city (see Calvo et al. 2007a). The stunning fossil richness of these outcrops led to the construction of a new paleontological site for the National University of Comahue. Today, this place is named Proyecto Dino Geo-Paleontological Park, and it is the first permanent educational paleontological site in South America dedicated to field researching.

Phylogenetic analysis

The phylogenetic relationships of *Comahuesuchus bonapartei* was inferred by

Table I. Selected specimens of *Notosuchia* first-hand analysed and used for comparisons with the new species *Comahuesuchus bonapartei*.

Species	Specimens	References
<i>Anatosuchus minor</i>	MNN GAD 603*, MNN GAD 17, MNN GAD 18	(Sereno & Larsson 2009, Sereno et al. 2003)
<i>Araripesuchus rattoides</i>	CMN 41893*, UCRC PV3	(Sereno & Larsson 2009, Figueiredo & Kellner 2021)
<i>Araripesuchus tsangatsangana</i>	FMNH PR 2318	(Turner 2006, Figueiredo & Kellner 2021)
<i>Araripesuchus wegneri</i>	MNN GAD 20	(Sereno & Larsson 2009, Figueiredo & Kellner 2021)
<i>Comahuesuchus brachybuccalis</i>	MUCPv 202*	(Bonaparte 1991, Martinelli 2003)
<i>Mahajangasuchus insignis</i>	UA 8654*	(Turner & Buckley 2008, Buckley & Brochu 1999)
<i>Notosuchus terrestris</i>	MUCPv 137	(Andrade & Bertini 2008, Barrios et al. 2018, Fiorelli & Calvo 2007)
<i>Sebecus icaeorhinus</i>	AMNH 3160*	(Molnar 2010)
<i>Uruguaysuchus aznarezi</i>	FC-DPV 2320	(Soto et al. 2011, Figueiredo & Kellner 2021)

a traditional cladistic analysis performed in the software TNT - "Tree analysis using New Technology", version 1.6 for Microsoft Windows (Goloboff et al. 2008). The character list and data matrix used in the analysis was based on previously published authors (Pinheiro et al. 2021). The following character were treated as additive: 1, 3, 6, 9, 39, 44, 66, 72, 78, 80, 81, 86, 87, 105, 170, and 321. Heuristic searches were performed in order to explore the tree space of a set of initial Wagner trees obtained by the multiple random stepwise addition (RAS) of taxa (Wagner 1961, Farris 1970, Swofford et al. 1996). Posteriorly, the branch swapping was made using the tree bisection and reconnection (TBR) algorithm (Swofford & Olsen 1990). The total number of replicates of RAS + TBR is 5000, with 10 trees saved in each replication. The random seeds were set to zero, allowing the addition of each new taxon in several different positions during the tree search, up to the memory maximum limit. Zero-length branches were collapsed (Coddington & Scharff 1994). Consistency and retention indexes were calculated by the script "stats.run".

Institutional Abbreviations

AMNH: American Museum of Natural History, New York, USA.

CMN: Canadian Museum of Nature, Ottawa, Canada.

FC-DPV: Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

FMNH: Field Museum of Natural History, Chicago, USA.

MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

MN: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

MNN: Muséum National du Niger, Niamey, Republic of Niger.

MOZ: Museo Profesor J. Olsacher, Zapala, Argentina

MUCPv: Museo de Ciencias Naturales de la Universidad Nacional del Comahue, Neuquén, Argentina.

ROM: Royal Ontario Museum, Toronto, Canada.

UA: University of Antananarivo, Antananarivo, Madagascar.

UCRC: University of Chicago Research Collection, Chicago, USA.

Anatomical Abbreviations

Alveolous/Alveoli – al; Denticle – de; Dentary – d; Dentary Shelf – ds; Mandibular Symphysis – ms; Maxilla – m; Meckelian Canal – mc; Splenial – s; Splenial Groove – sg; Tooth/Teeth – t; Tooth/Teeth facet – tf.

RESULTS AND DISCUSSION

Nomenclatural Acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The Zoobank Life Science Identifiers (LSIDs) to the prefix <http://zoobank.org/>. The LSID for this publication is LSIDurn:lsid:zoobank.org:pub:E2725619-01C4-49B7-A4D9-C1338DA6E1CC, and the LSID for the new erected species is: urn:lsid:zoobank.org:act:AD047E50-3112-41A9-BDE1-7EAD380828C8 (*Comahuesuchus bonapartei*).

Systematic Paleontology

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone & Whybrow, 1983

Notosuchia Gasparini, 1971

Comahuesuchidae Bonaparte, 1991

Comahuesuchus Bonaparte, 1991

Comahuesuchus bonapartei

sp. nov.

Etymology: Specific name in honor of José Fernando Bonaparte (1928-2020) in recognition of his contributions to South American paleontology.

Holotype: MUCPv 597, a partially preserved (cranial-most region) of the right mandible. Cast housed at the Museu Nacional/UFRJ - MN 7831-V.

Type locality and horizon: MUCPv 597 was collected in the Fotalongko quarry situated at the northern coast of the Lake Barreales, 90 km

northwest of Neuquén City, Neuquén Province, Patagonia, Argentina. The deposits belong either the upper part of the Portezuelo Formation or the middle portion of the Sierra Barrosa Formation, which are Upper Turonian to Lower Coniacian in age.

Diagnosis: The species *Comahuesuchus bonapartei* can be distinguished from other Crocodyliformes based on the following combination of characters (unique features are marked with an asterisk): 1. short and wide snout; 2. presence of a shelf on the lateral surface of the dentary; 3. a flat, low, and wide mandibular symphysis; 4. enlarged caniniform tooth of the dentary distal to the enlarged caniniform tooth of the maxilla; 5. crown of the caniniform tooth labiolingually compressed, with serrated carinae showing five denticles per mm*; 6. caniniform tooth with three distinct facets in the labial surface; 7. presence of a single postcaniniform tooth.

Description

The holotype specimen of *C. bonapartei* (MUCPv 597) is a fragment of a right dentary bone with a maximum preserved length of 44mm (Figure 2). In lateral view it is possible to observed two very distinct regions in this bone, which are separated by a single hypertrophied mandibular tooth. The cranial region (i.e., precaniniform) comprises the mandibular symphysis, and it is dorsoventrally lower in comparison to the caudal region (i.e., postcaniniform). There is a well-marked shelf on the lateral surface of the cranial region of the dentary (Figure 2). In this surface is also possible to observe a single row of small neurovascular foramina. A few grooves and pits are present on the lateroventral border of the mandible, but besides this region, the rest of the bone surface is rather smooth. The dorsal margins, both cranial and caudal to the large caniniform tooth,

are concave, however the caudal margin has a softer curvature.

The medial surface of the mandible is characterized by a dorsoventrally low mandibular symphysis with a maximum preserved length of 13 mm (Figure 2). The splenial bone was not preserved, however it is possible to observe that it took part on the caudal-most border of the symphysis. This missing bone would taper cranially toward the symphysis. Also, it comprised a large part of the medial surface of the mandible, enclosing the Meckel's canal. Based on the rugose bone texture of the medial surface of the dentary close to the large tooth, it is likely that the splenial took a small part in the formation of the last mandibular alveolus. The region caudal to the caniniform tooth slopes dorsally.

The lateromedial width of the cranial-most portion of the dentary is about 10mm. The dorsal surface of the dentary at the symphyseal region is smooth, except for a series of small neurovascular foramina medial to the alveoli row (Figure 2). In dorsal view it is possible to note that the preserved portion of the right hemimandible would be approximately parallel to the left one. The contour of the dentary bone is rather straight and there are not bulges, but a shallow concavity on the dorsolateral surface, just cranial to the enlarged caniniform tooth.

There are seven preserved alveoli, and all of them can be observed in dorsal view at the lateral-most border of the dentary. As the cranial edge of the dentary is broken, it is not possible to confirm the presence of additional teeth sockets in this specimen. The five mesial-most alveoli are small and labiolingually compressed, thus showing an elliptical outline. The fifth and seventh alveoli are confluent with the very large sixth one, and all of them are placed at a slightly dorsally position compared to the others. The first three alveoli are at the same level. The only

preserved tooth is the hypertrophied caniniform tooth in the sixth alveolus. Its crown is blade-like, conical in shape with slightly convex carinae, and shows a smooth enamel surface. The tooth is missing the crown apex and shows fractures along both mesial and distal edges. Carinae margins are serrated along all their apicobasal length, with 5 denticles per mm (Figure 2). On the labial surface there is three distinct apicobasal facets, a mesiolabial, a labial, and a distolabial. The transition between each of them is smooth, but they are more evident between the mesiolabial and labial facets (Figure 2).

Comparisons

The main anatomical feature of *Comahuesuchus* is the very short and wide snout. This U-shaped morphotype is often seen as “bizarre” and sometimes is informally referred as “duck-billed” or “pug-nosed”. Species with similar snout proportions are rare among notosuchians (see Pol et al. 2014), which usually have V-shaped (e.g., *Notosuchus terrestris*) or Y-shaped rostra (e.g., Sphagesauridae) (Barrios et al. 2018, Fiorelli & Calvo 2007, Pol et al. 2014). The wider morphotype is observed in some African species like *Anatosuchus minor* (Sereno et al. 2003, Sereno & Larsson 2009), *Kaprosuchus saharicus* (Sereno & Larsson 2009), *Mahajangasuchus insignis* (Buckley & Brochu 1999, Turner & Buckley 2008), and *Simosuchus clarki* (Buckley et al. 2000, Kley et al. 2010) (Figure 3). However, there are several morphological differences between *Comahuesuchus* species and the African taxa regarding the morphology of the lower jaws, including its dentition.

The dentaries and splenial bones of *C. brachybuccalis* (MUCPv 202, MACN-N 30, MACN-N 31, MOZ 6131 P) and *C. bonapartei* (MUCPv 597) form an expanded, flat, dorsoventrally low, and lateromedially wide mandibular symphysis, regardless of specimen size (Bonaparte 1991,

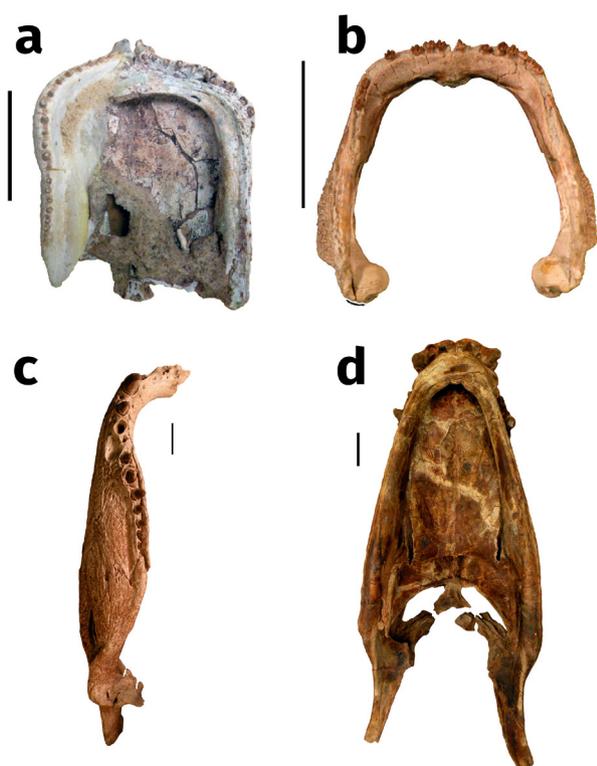


Figure 3. Notosuchian species showing a wider cranium morphotype (i.e., “duckbilled”). a *Anatosuchus minor* (MNN GAD17), skull and mandible in ventral view; b *Simosuchus clarki* (UA 8679), mandible in dorsal view. c *Mahajangasuchus insignis* (UA 9737), left mandibular rami in dorsal view; d *Kaprosuchus saharicus* (MNN IGU12), skull and mandible in ventral view. Scale bars: 50mm.

Martinelli 2003). The symphyseal regions of *A. minor*, *M. insignis*, and *S. clarki* are extremely short in craniocaudal length in comparison to their lateral width. They do not form an expanded bony platform as observed in *C. bonapartei*, *C. brachybuccalis* and *K. saharicus*. In comparative terms, the symphyseal shelf of *Comahuesuchus* is much wider when compared to *K. saharicus* and both differ from other species by also being longer. The development of wide symphyseal platforms are also present in some Peirosauridae, such as *Montealtosuchus arrudacamposi*, *Gasparinisuchus peirosauroides*, and *Barrosasuchus neuquenianus* (Carvalho et al. 2007, Martinelli et al. 2012, Coria et al. 2019), and Uruguaysuchidae (Pol & Apesteguía 2005,

Turner 2006, Sereno & Larsson 2009, Soto et al. 2011). However, in these later taxa the mandibular symphysis is longer than wider, which is not the case in *C. bonapartei*, *C. brachybuccalis* and *K. saharicus*.

The lateral profile of the symphyseal region is much more slender and dorsoventrally lower in *C. bonapartei* and *C. brachybuccalis* than in *K. saharicus*. The robust morphology is observed in Baurusuchidae (Price 1945, Carvalho et al. 2005, Marinho et al. 2013, Godoy et al. 2014) and large sebecians like *Barinasuchus arveloi* (Paolillo & Linares 2007). The dentary of *Comahuesuchus* species has a unique uneven lateral profile that is cranially low and caudally high, as it slopes dorsally toward the enlarged caniniform tooth. Few other notosuchians show such abrupt slope separating cranial and caudal regions of the dentary, which is the case of *Arapesuchus wegneri* and *Sebecus icaeorhinus* (Figure 3). However, in *S. icaeorhinus* the cranial-most region of the symphysis is shorter.

The lateral surface of the dentary of *C. bonapartei* bears a small shelf, ventral to the alveolar margin (Figure 2). This shelf is also present in *C. brachybuccalis*, being well developed in MOZ 6131 P (see Pol et al. 2014), but tenuous in MUCPc 202. Most taxa with enlarged maxillary caniniforms, like baurusuchids and sebecids, have a deep lateral concavity on the dentary for reception of such teeth (Riff & Kellner 2001, Kellner et al. 2014, Bravo et al. 2021). The lateral concavity is extremely reduced in both *Comahuesuchus* species. It is important to note that such feature differs from the broad shelf observed in the mandible of some “advanced” notosuchians (e.g., *Mariliasuchus amarali*, *N. terrestris*), which separates the posterior teeth from the lateral border of the dentary (Pol et al. 2014).

The major morphological difference between *C. bonapartei* and *C. brachybuccalis* is that in

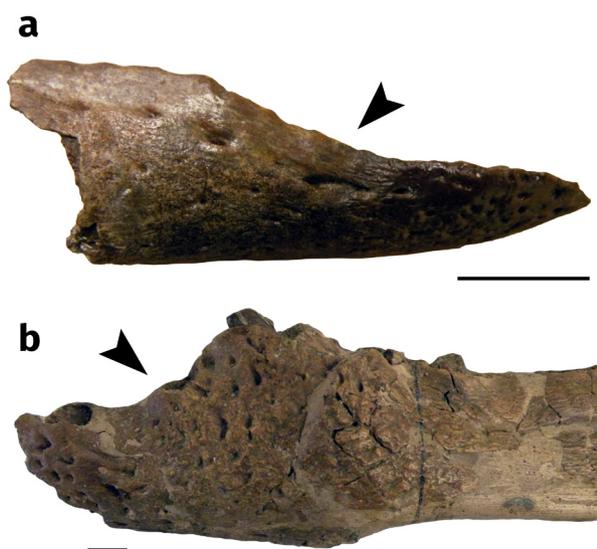


Figure 4. Notosuchians species with an abrupt slope separating the cranial and caudal regions of the dentary bones, as indicated by the arrowhead. **a**, *Araripesuchus wegeneri* (MNN GAD 26), **b**, Holotype of *Sebecus icaeorhinus* (AMNH 3162). Scale bars: 10mm.

the former species the teeth at the mandibular symphysis were set in individual alveoli, and in the latter species they were in a dentary groove. In general, *Comahuesuchus* have a reduction in the number of teeth. The most complete series is observed in *C. brachybuccalis* (MOZ 6131 P) with 11 dentary teeth and alveoli (Martinelli 2003). *Comahuesuchus bonapartei* (MUCPv 597) also shows well-preserved distal alveoli, which would bear the seven distal-most teeth. An important feature of this species is the extreme decrease in number of the postcaniniform dentition. The holotype of *C. bonapartei* (MUCPv 597) has no preserved postcaniniform tooth, however there is an alveolus distal to the enlarged caniniform tooth. The holotype of *C. brachybuccalis* (MUCPV 202) has no teeth distal to the caniniform (Bonaparte 1991), but one single postcaniniform tooth is also observed in MOZ 6131 P (Martinelli 2003). Notosuchia shows a trend for reduction of tooth count, especially in highly heterodont taxa (Riff & Kellner 2001, Ósi 2014, Figueiredo & Kellner 2021). The absence

of distal-most post-caniniform teeth in the dentary is, however, an exclusive feature of the genus *Comahuesuchus*.

The only preserved tooth of *C. bonapartei* (MUCPv 597) is enlarged caniniform in the dentary. The size of the alveoli suggests it would be at least twice as large as other neighboring teeth. A similar condition is observed in *C. brachybuccalis* MUCPv 202 (Figure 1) and MOZ 6131 P (Martinelli 2003, Pol et al. 2014). The presence of an enlarged caniniform tooth in the dentary is common among crocodyliforms, usually the fourth element in the series (Ósi 2014, D'Amore et al. 2019). In baurusuchids, sebecians, and peirosaurids the fourth dentary teeth are particularly developed as hypertrophied caniniforms (Riff & Kellner 2001, 2011, Carvalho et al. 2004, 2007, Martinelli et al. 2012). The absence of an enlarged caniniform in a more anterior position in the mandible is an uncommon feature of both *C. bonapartei* and *C. brachybuccalis*. In *C. bonapartei*, the caniniform occupies at least the sixth alveolus in the row, but possible even in further mesial alveolus, as the tip of the dentary is missing. Other species that show large caniniforms at mesial positions are the Uruguaysuchidae *Araripesuchus wegeneri* (4th and 11th) and *Araripesuchus tsangatsangana* (10th only), and the Mahajangasuchidae, *Kaprosuchus saharicus* (3rd and 8th) and *Mahajangasuchus insignis* (4th and 8th) (Buckley & Brochu 1999, Sereno & Larsson 2009, Figueiredo & Kellner 2021). Notosuchians with highly specialized dentition, sometimes including molarization of the distal-most series, lack enlarged caniniform. This is the case of the Candidodontidae (Martin & De Lapparent De Broin 2016), except for *Pakasuchus pakilimai* (O'Connor et al. 2010), Notosuchidae (Zaher et al. 2006, Fiorelli & Calvo 2007, Barrios et al. 2018), and Sphagesauridae (Pol et al. 2014, Martinelli et al. 2018).

The caniniform tooth in *Comahuesuchus* species are labiolingually compressed and shows symmetrical serrated mesial and distal carinae. In the new species, *C. bonapartei*, it is possible to observe a density of five denticles per mm, a unique feature of this species. The number of denticles per millimeter is highly variable among notosuchians (Table II), and density depends mostly on the size of the denticles and the shape of the teeth. There is no clear taxonomic pattern regarding denticle density in Notosuchia, with variation between species inside the same clade, which is the case of Sebecidae (Pol et al. 2012, Kellner et al. 2014) Peirosauridae (Leardi & Pol 2009, Barrios et al. 2016). Another important feature observed in the dentition of *C. bonapartei* MUCPv 597 (Figure 1) and in *C. brachybuccalis* MUCPv 202 (Figure 2) is the presence of faceted labial surface. Tri-faceted crowns are typical of teeth morphotypes observed in some *Geosaurus* species (Andrade et al. 2010). However, there are clear morphological differences observed in the marine *Geosaurus*, like the presence of labiolingual enamel bands, and a density of nine denticles per mm (Andrade et al. 2010). Faceted crowns are rare among Notosuchia, but it also noted in isolated tooth (MPCM 11720) from the Upper Cretaceous of Italy

(Dalla Vecchia & Cau 2011). The Italian species differs from *Comahuesuchus* species in having asymmetrical carinae and density of 5.5 to 6.5 denticles per mm (Dalla Vecchia & Cau 2011).

Phylogenetic Relationships

The cladistic analysis (traditional search, all taxa, additive characters) resulted in 3790 most parsimonious trees, each of them with 1636 steps. Our results show phylogenetic relationships inside Mesoeucrocodylia poorly resolved; however, a clade was recovered in this analysis comprising Comahuesuchidae as the sister-taxon of Sphagesauria (Figure 5). The sister relationship between *C. brachybuccalis* and *C. bonapartei* is supported by two synapomorphies, the platyrostral rostrum (char. 3), and the U-shaped dentary symphysis (char. 143), which are hallmark features of the genus. Sphagesaurians are, in turn, oreinirostral animals with broad snouts that taper cranially.

There are two main hypotheses for the higher affinities of *Comahuesuchus* in the literature, the first one favors a closer relationship with *Notosuchus terrestris* and *Mariliasuchus amarali*, i.e., Notosuchidae (Soto et al. 2011, Kellner et al. 2014, Sertich & O'Connor 2014), and the other recover it closer to Sebecosuchia (Pol et al. 2014,

Table II. Variation of average denticle density, per millimetre, in the carinae of different notosuchian species.

Species	Density of denticles	References
<i>Razanandrongobe sakalavae</i>	1 per mm	(Dal Sasso et al. 2017)
<i>Stratiosuchus maxhechti</i>	2.5 to 3.5 per mm	(Pinheiro et al. 2008)
<i>Sahitisuchus fluminensis</i>	3 to 3.5 per mm	(Kellner et al. 2014)
<i>Bayomesasuchus hernandezi</i>	3 to 4 per mm	(Barrios et al. 2016)
<i>Hamadasuchus rebouli</i>	3 to 5 per mm	(Larsson & Sidor 1999)
<i>Colhuehuapisuchus lunai</i>	4 to 6 per mm	(Lamanna et al. 2019)
<i>Comahuesuchus bonapartei</i>	5 per mm	This paper.
<i>Doratodon carcharidens</i>	6 per mm	(Dalla Vecchia & Cau 2011)
<i>Araripesuchus wegneri</i>	6 to 8 per mm	(Serenio & Larsson 2009, Dalla Vecchia & Cau 2011)
<i>Sebecus icaeorhinus</i>	6 to 9 per mm	(Pol et al. 2012)
<i>Barcosuchus gradilis</i>	11 to 12 per mm	(Leardi & Pol 2009)

Barrios et al. 2018) or at least to Baurusuchidae (O'Connor et al. 2010). However, the current analysis supports a third hypothesis that was recently proposed, *Comahuesuchus* as the sister taxon of the Sphagesauria (Pinheiro et al. 2021), a taxon that was informally known as “advanced notosuchians” (Pol et al. 2014). Interestingly, *Notosuchus terrestris* and *Mariliasuchus amarali* are recovered as sphagesaurians, thus more close-related to Sphagesauridae than to *Comahuesuchus*.

Most synapomorphies that support the taxon formed by Comahuesuchidae and Sphagesauria

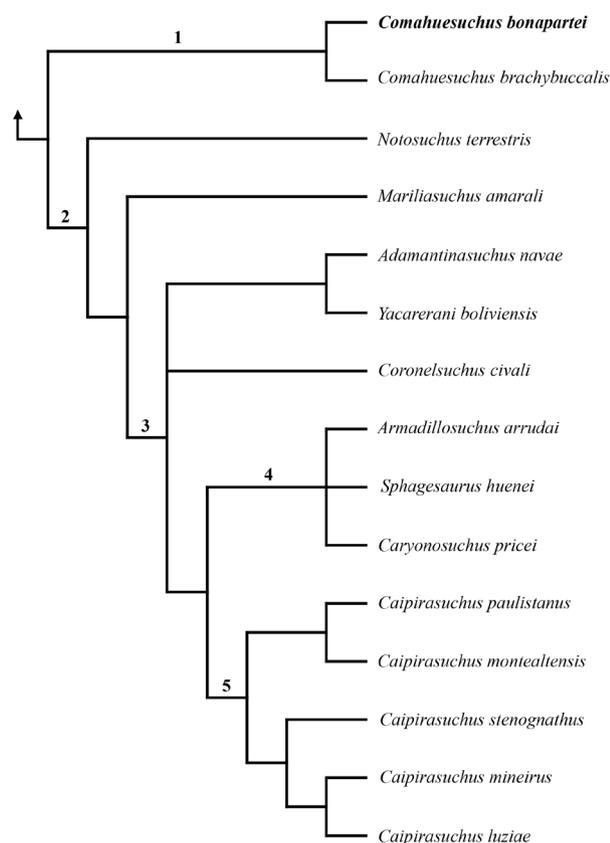


Figure 5. Detail of the strict consensus of 3790 most parsimonious trees (1636 steps) showing the phylogenetic relationships of the new species *Comahuesuchus bonapartei*, within an unnamed taxon of Mesoeucrocodylia. Arrowhead indicates the continuation of Mesoeucrocodylia. Clades are labeled as 1. Comahuesuchidae, 2. Sphagesauria, 3. Sphagesauridae, 4. Sphagesaurinae, 5. Caipirasuchinae.

can be only inferred for *C. bonapartei*, as the holotype specimen is rather fragmentary. Nevertheless, the new species shares some general features with these animals, such as the slight involvement of the splenial in the mandibular symphysis (char. 70), the shallow profile of the mandibular symphysis (char. 93), teeth that are slightly compressed laterally (char. 129), the presence of a unsculpted region in the dentary below the tooth row (char. 144), teeth with subequal root and crown width (char. 164), sculptured external surface of rostrum (char. 238), teeth without keels bearing cusps or tuberos denticles (char. 365), and absence of cingula in the teeth.

CONCLUSIONS

The specimen MUCPv 597 represents a new notosuchian species, *Comahuesuchus bonapartei*. The fossil comprises a partially preserved dentary bone that shows important anatomical features, such as the presence of a single postcaniniform tooth that is shared by both species of *Comahuesuchus* and regarded as a synapomorph of the genus. The characteristics that support this specimen as a new *Comahuesuchus* species are: the presence of serrations on the caniniforme carinae, mandibular teeth insert in isolated alveoli (compared to *C. brachybuccalis*), and the fact that it is found in a different and older geological unit, the latter often used into consideration for the consideration of a new taxon (e.g., Kellner 2010). These traits are only observed in the new species. Phylogenetic analyses support a sister-relationship with *Comahuesuchus brachybuccalis*, comprising the Comahuesuchidae family, which is well nested within advanced notosuchians. Finally, the new species expands the temporal range of the genus in about 7.6 million years, as far

as the Upper Turonian to Lower Coniacian. This represents the oldest record of *Comahuesuchus* so far.

Acknowledgments

Funding for this project was provided by the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ, E-26/201.095/2022 to AWAK) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, #313461/2018-0, #406779/2021-0, and 406902/2022-4 to AWAK).

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How to cite

KELLNER AWA, FIGUEIREDO RG & CALVO JO. 2023. A new species of *Comahuesuchus* Bonaparte, 1991 (Crocodyliformes: Notosuchia) from the Upper Cretaceous of Neuquén, Lake Barreales, Patagonia, Argentina. *An Acad Bras Cienc* 95: e20230179. DOI 10.1590/0001-3765202320230179.

Manuscript received on February 18, 2023;
accepted for publication on June 30, 2023

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#In memoriam

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#In memoriam

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AWAK, RGF and JOC wrote and reviewed the manuscript. JOC conducted fieldwork and fossil collection. JOC and RGF organized and prepared the figures.

