

The first record of *Purussaurus* (Crocodylia, Alligatoridae) in the Late Miocene of Argentina

Paula BONA^{1,2}, Diego POL^{3,2}, Leandro M. PÉREZ^{4,2}, David E. TINEO^{5,2}, Diego BRANDONI^{6,2}
& Jorge I. NORIEGA^{6,2}

¹ División Paleontología Vertebrados, Museo de La Plata - Anexo II, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Calles 122 y 60, B1900FWA, La Plata, Buenos Aires, Argentina. paulabona26@gmail.com. ² Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Godoy Cruz 2290, C1425FQB, Ciudad Autónoma de Buenos Aires, Argentina. ³ Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, CP 9100, Trelew, Chubut, Argentina. dpol@mef.org.ar. ⁴ División Paleozoología Invertebrados, Museo de La Plata - Anexo I, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Calles 122 y 60, B1900FWA, La Plata, Buenos Aires, Argentina. pilosaperez@gmail.com. ⁵ Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. Calles 60 y 122, B1900FWA, La Plata, Buenos Aires, Argentina. tineo.d.e@gmail.com. ⁶ Laboratorio de Paleontología de Vertebrados, Centro de Investigación Científica y de Transferencia Tecnológica a la Producción - CONICET, España 149, E3105BWA Diamante, Entre Ríos, Argentina. dbrandoni@cicytpp.org.ar; cidnoriega0@gmail.com

Abstract: Herein we report the first record of *Purussaurus* Barbosa-Rodrigues, 1892 for the Neogene of Argentina. This genus is recorded in Miocene beds of different localities in Colombia, Venezuela, Brazil, and Perú, and includes at least three different species with total body lengths ranging from 8 to 13 m. The material reported here is a partially preserved tooth (MAS-PV 386) found at the locality Toma Vieja (Paraná, Entre Ríos Province, Argentina), in strata informally known as “Conglomerado osífero” or “Mesopotamiense” (Late Miocene) and traditionally regarded as the basal levels of the Ituzaingó Formation. The material corresponds to the apical portion of a conical crown, slightly compressed, lingually curved, and with a subrounded apex. The enamel is ornamented with thin apicobasal ridges that are anastomosed and separated by shallow grooves. These ridges are transversely crossed by shallow lines that give the enamel surface a crackled aspect. The crown has a continuous carina formed by the enamel that runs along the mesial and distal surface of the tooth, which divides the vestibular (or labial side of the tooth) and lingual faces of the crown that are subequal in size. The carina is ornamented with fine enamel wrinkles that are parallel to each other and perpendicular to the mesiodistal carina. This condition, known as pseudoziphodonty, together with the enamel structure and overall shape of the crown, allow referring the specimen MAS-PV 386 to *Purussaurus* sp. This finding represents the southernmost record of one of the largest predatorial neosuchian crocodylians which inhabited the wetlands that developed during the Late Miocene in South America.

Keywords: Crocodyliformes, Neogene, South American Wetlands, “Conglomerado osífero”, Entre Ríos

Resumen: Primer registro de *Purussaurus* (Crocodylia, Alligatoridae) en el Mioceno Tardío de Argentina. Damos a conocer aquí el primer registro de *Purussaurus* Barbosa-Rodrigues, 1892 para el Neógeno de Argentina. Este género está representado en el Mioceno en distintas localidades de Colombia, Venezuela, Brasil, y Perú, por al menos tres especies con tamaños corporales estimados de 8m a 13m de largo total. El material es un diente fragmentario (MAS-PV 386) procedente de estratos aflorantes en la localidad de Toma Vieja (Paraná, provincia de Entre Ríos), conocidos informalmente como “Conglomerado osífero” o “Mesopotamiense” (Mioceno Tardío) y tradicionalmente considerados como niveles basales de la Formación Ituzaingó. Corresponde al sector apical de la corona de un diente cónico, levemente comprimido, curvado lingualmente, y subredondeado en el ápice. El esmalte se encuentra ornamentado por finas crestas apicobasales, anastomosadas y separadas por suaves surcos. Estas crestas están atravesadas perpendicularmente por líneas delgadas que observadas bajo lupa le dan al esmalte un aspecto craquelado. Presenta una carena continua formada por esmalte, extendida a lo alto de las caras mesial y distal del diente, que lo divide en dos sectores vestibular y lingual, subiguales. Dicha carena se encuentra ornamentada por finas crenulaciones muy marcadas, paralelas entre sí y perpendiculares a la carina mesiodistal. Esta condición denominada pseudozifodontia, combinada con las características del esmalte y la forma general del diente, permite asignar a MAS-PV 386 a *Purussaurus* sp. Este hallazgo representa el registro más austral de uno de los depredadores de mayor tamaño de cocodrilos neosquios conocidos, que habitó en los humedales que se desarrollaron en el Mioceno Tardío de América del Sur.

Palabras clave: Crocodyliformes, Neógeno, Humedales sudamericanos, “Conglomerado osífero”, Entre Ríos

INTRODUCTION

Wetlands concentrate a large part of the continental biodiversity and therefore play a fundamental role in macroevolutionary processes (Greb *et al.*, 2006). Today, South American land ecosystems associated with the Amazon, Paraguay, and the southernmost Paraná-del Plata fluvial systems are part of the largest wetlands of the world (Orfeo & Neiff, 2008). The early history of these ecosystems dates back to the early Neogene, when they developed in tectonically controlled environments linked to the compressive Andean orogeny, which remodeled the foreland basin landscape (Wesselingh *et al.*, 2001; Hoorn *et al.*, 2010, 2022; Tineo, 2020; Tineo *et al.*, 2021). South American Neogene wetlands and associated fluvial systems are mainly known from several Miocene geological outcroppings such as the exceptional depositional and fossil records of Pebas–Solimões formations (close to the Peruvian-Colombian-Brazilian borders), the Honda Group (La Venta, Colombia), the Urumaco Formation (Urumaco, Venezuela), the Yecua Formation (Argentinian-Bolivian Sub-Andean zone) and the “Conglomerado osífero” (Ituzaingó Formation, Entre Ríos Province, Argentina) (*e.g.*, Langston, 1965; Cione *et al.*, 2000; Wesselingh *et al.*, 2001; Hoorn *et al.*, 2010, 2022; Riff *et al.*, 2010; Salas-Gismondi *et al.*, 2015, 2016, 2018; Tineo, 2020; Tineo *et al.*, 2021). These sedimentary beds had been deposited in a temporal range that goes approximately from the Early Miocene (ca. 23 Ma) to the Late Miocene (ca. 10.5–7/5 Ma) (*e.g.*, Uba *et al.*, 2009; Hoorn *et al.*, 2010, 2022), and are mostly composed of shallow aquatic settings of varying salinity and marine influence, such as lakes, swamps, and rivers, that represent different sequences of inland mega wetlands (*e.g.*, Early to Middle Miocene sections of the Peruvian Pebas Formation and Late Miocene Yecua Formation; Nutall, 1990; Wesselingh *et al.*, 2001; Boonstra *et al.*, 2015; Hoorn *et al.*, 2022; Uba *et al.*, 2009; Tineo, 2020; Tineo *et al.*, 2021), and predominantly fluvial or delta plain deposits (*e.g.*, the Late Miocene Urumaco, Tranquitas, and Ituzaingó formations; Tineo *et al.*, 2022; Quiroz & Jaramillo, 2010; Hoorn *et al.*, 2010; Brandoni *et al.*, 2019).

All these Miocene deposits achieve astonishing associations of continental fossil vertebrates. Among them, Miocene crocodyliform assemblages are characterized by the presence of a great diversity of amphibian neosuchians, the Crocodylia, and the much less diverse and abundant ter-

restrial sebecosuchians, such as *Langstonia huilensis* Langston (1965) (= *Sebecus huilensis*; Paolillo & Linares, 2007) from the Middle Miocene of La Venta, Colombia. Crocodylia is the best represented group, with a large diversity of gavialoids (*e.g.*; *Siquisiquesuchus venezuelensis* Brochu & Rincón, 2004; *Aktiogavialis caribesi* Salas-Gismondi *et al.*, 2018; *Dadagavialis gunai* Salas-Gismondi *et al.*, 2018) and several species of *Gryposuchus* (Gürich, 1912) and alligatoroids (*e.g.*, *Gnatusuchus pebasensis* Salas-Gismondi *et al.*, 2015; *Kuttanacaiman iquitosensis* Salas-Gismondi *et al.*, 2015; *Globidentosuchus brachyrostris* Scheyer *et al.*, 2013; *Centenariosuchus gilmorei* Hastings *et al.*, 2013; *Culebrasuchus mesoamericanus* Hastings *et al.*, 2013; *Acresuchus pachytemporalis* Souza-Filho *et al.*, 2018; *Paleosuchus* Gray, 1862; several species of *Caiman* Spix, 1825, *Purussaurus* Barbosa-Rodrigues, 1892, and *Mourasuchus* Price, 1964). These crocodylians show a high range of morphological disparity and body sizes indicative of the ecological diversity that this group achieved during the Neogene (an event that in terms of morphological disparity and taxonomic diversity occurs for the only time during the entire evolutionary history of these lineages). Salas-Gismondi *et al.* (2015, 2016) analyzed part of these hyperdiverse crocodylian fossil records. These authors concluded that several Miocene assemblages are probably vinculated with different paleoenvironments developed in relation to the geological evolution of basins during the Neogene in Northern South America. They proposed that crocodylian associations in shallow water paleoenvironments, like lagoons, swamps, and marginal marine embayments (*e.g.*, several early Middle Miocene deposits) are characterized by a predominance of gavialoids with body morphotypes typical of shallow water piscivores forms (*e.g.*, adults with orbits not protruded such as *Gryposuchus pachakamue* Salas-Gismondi *et al.*, 2016, *Piscogavialis jugaliperforatus* and *Siquisiquesuchus venezuelensis*) and medium sized alligatoroids, including caimanines with crushing dentitions with more grinding feeding habits (*e.g.*, *Gnatusuchus pebasensis*, *Kuttanacaiman iquitosensis*, *Caiman wannlangstoni* Salas-Gismondi *et al.*, 2015). Among these assemblages, large forms of alligatoroids are less frequent, although the enigmatic but probably “gulp feeding” *Mourasuchus atopus* Langston, 1966 (Langston, 1965; Riff *et al.*, 2010; Tineo *et al.*, 2015; Cidade *et al.*, 2017), and the predator *Purussaurus neivensis* Mook (1941) are also registered in some Middle

Miocene South American localities (such as in the late Middle Miocene of La Venta, Colombia; e.g., Langston, 1965). These interpretations suggest that although most of early Middle Miocene caimanine alligatorids would have been endemic and became regionally extinct, others such as *Mourasuchus* and *Purussaurus* persisted in the Middle–Late Miocene in fluvial dominated paleoenvironments (e.g., *Mourasuchus arendsi* Bocquentin-Villanueva, 1984, from Venezuela, Brazil and Argentina; *M. amazonensis* Price, 1964, from Brazil; *M. pattersoni* Cidade et al., 2017, from Venezuela; *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892, from Brazil and *P. mirandai* Aguilera et al., 2006, from Venezuela, and *Mourasuchus* sp. from Bolivia) and would have coexisted with large specialized piscivores (e.g., *Ikanogavialis* Sill, 1970; *Hesperogavialis* Bocquentin-Villanueva & Buffetaut, 1981; *Gryposuchus colombianus* Langston, 1965; *G. croizati* Riff & Aguilera, 2008; *G. neogaeus* Burmeister, 1885). Crushing caimans, such as *Globidentosuchus brachyrostris* Scheyer et al., 2013 and *Caiman wannlangstoni* Salas-Gismondi et al., 2015, were also found in rocks of ~7–9 Ma of the Urumaco Formation, indicating that niche was also occupied by caimanines in what is believed to be the last relict of the Pebas System environments (Hoorn et al., 2010; Salas-Gismondi et al., 2016).

The southernmost record of these neogene South American crocodylians is in the Late Miocene of northeastern Argentina (see below). In general terms, this crocodylian association is taxonomically similar to that of lower latitudes, with a greater diversity of Caimaninae, dominated by medium to large sized caimans (e.g., *Caiman australis* Burmeister (1883); *C. lutescens* Rovereto (1912), *C. gasparinae* Bona & Paulina Carabajal, 2013 and *Caiman* cf. *C. latirostris*, Bona & Barrios, 2015; Bona et al., 2013) and a gavialoid, *Gryposuchus neogaeus*, that was interpreted as a highly aquatic and underwater feeding piscivorous crocodylian given its reduced skull pneumaticity (Bona et al., 2017). Among the large forms, *Mourasuchus arendsi* (= *M. nativus* Gasparini, 1985; Cidade et al., 2018) and generalist animal eating caiman like forms are also registered. Although several huge caimanine species have been described (e.g., Bravard, 1858; Burmeister, 1885; Rovereto, 1912; Rusconi, 1933; Gasparini, 1981, 1985), only *C. lutescens* and *C. gasparinae* (represented by a skull table and a partial skull, respectively) are currently recognized and the presence of the Miocene mega-

predator *Purussaurus* was never mentioned in these latitudes (e.g., Bona & Barrios, 2015; Bona et al., 2013).

We present herein the first record of *Purussaurus* in the Late Miocene of Argentina together with a detailed description of this material and a discussion of its paleogeographic and paleoenvironmental implications.

Geological and Paleontological Settings

In the Entre Ríos Province, the “Conglomerado osífero” crops out discontinuously in the river banks of the Paraná River and its tributaries, from the city of Paraná northwards to Hernandarias (Fig. 1A). The tooth here described was collected in the Toma Vieja locality (31° 42' 10" S, 60° 28' 35" W), where this conglomerate is clearly distinguished by a visible erosive unconformity from the mudstone and sandstone beds of the underlying Paraná Formation (Fig. 1B). The “Conglomerado osífero” is characterized by well consolidated levels of fine cross stratified gravel sandstone and well sorted fine to coarse grained cross stratified sandstone beds, and clayed mudstone lenses, which concentrated abundant fossil bones and teeth of fragmented and disassociated vertebrates (Brandoni & Noriega, 2013). These skeletal fragments are heavy and well mineralized and belong mostly to continental vertebrates, although a few mostly reworked marine forms can be represented (e.g., Cione et al., 2000). Traditionally, the “Conglomerado osífero” was considered as part of the fluvial system of the Ituzaingó Formation that outcrops in Entre Ríos Province (Frenguelli, 1920; Aceñolaza, 1976, 2000; Brunetto et al., 2013; Schmidt et al., 2020). Particularly, Brunetto et al. (2013) and Brandoni et al. (2019) regarded the “Conglomerado osífero” as part of the Lower Member of the Ituzaingó Formation and interpreted that it corresponds to a continental paleoenvironment dominated by a braided fluvial succession. However, Pérez (2013a) considered that these levels correspond to fluvial tide influenced channels of a marginal marine paleoenvironment and assigned them to the upper levels of the Paraná Formation.

In the absence of radiometric dating, the age of the “Conglomerado osífero” has been estimated by biostratigraphic correlation to other Neogene units, based on its mammal content and stratigraphic position. Thus, the age of the “Conglomerado osífero” is mainly interpreted to be Huayquerian (ca. 9–6.8 Ma *sensu* Cione et al., 2000), or alternatively to the Chasicoan–Huayquerian lapse (ca. 10–6.8/5.3

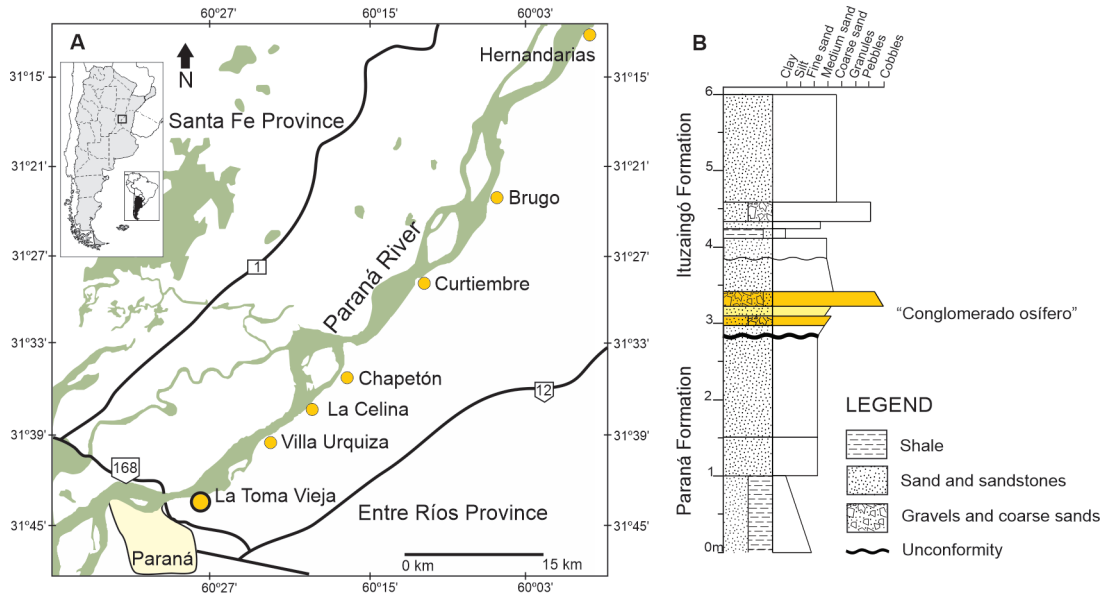


Fig. 1. Geographic and stratigraphic settings of MAS-PV 386.

Ma, Brandoni, 2013), and consequently correlated to the Tortonian–Messinian (Late Miocene) (International Chronostratigraphic Chart, 2022). $^{86}\text{Sr}/^{87}\text{Sr}$ dating of mollusks from the underlying Paraná Formation in the locality of Punta Gorda (Entre Ríos Province; Fig. 1A), indicates ages of 9.47 Ma (Tortonian; Pérez, 2013b) and 7.55–6.67 Ma (Tortonian–Messinian; del Río *et al.*, 2018). Considering the relationship between the association of vertebrates recovered from the “Conglomerado osífero” and that of other Neogene units (see Cione *et al.*, 2000; Brandoni, 2013; Schmidt *et al.*, 2020), as well as the proposed age for the Paraná Formation (Pérez, 2013b; del Río *et al.*, 2018), a Late Miocene age can be suggested for the “Conglomerado osífero”.

MATERIAL AND METHODS

MAS-PV 386 was described macro and microscopically. For the macroscopic anatomical analysis comparisons with teeth of extant and Miocene caimanines were made, with first hand materials, photographs taken from literature (Tab. 1), or own photographs. Terminology used for the spatial orientation of the tooth follows Smith & Dodson (2003); however, we decided to add the term “vestibular” as synonym of “labial”, since reptiles do not have lips. The microscopic analysis was made by the Environmental Scanning

Electron Microscope ESEM-FEI Quanta 200 of the LIMF. In addition, chemical element mapping tools (major elements) were used, and Backscattered Electrons (BE) method. The latter, based on the detection of the atomic number (Z), provides an image of the distribution of chemical elements in the material that makes up the entire piece, with the darkest areas being those with the lowest Z and the lightest and brightest ones with higher Z (Fig. 2).

Institutional Abbreviations. AMU-CURS, Alcaldía del Municipio de Urumaco, Urumaco, Venezuela; DGM, Divisão Geologia y Mineralogia, Rio de Janeiro, Brazil; MACN-PV, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Paleontología Vertebrados, Ciudad Autónoma de Buenos Aires, Argentina; MAS-PV, Museo de Ciencias Naturales y Antropológicas “Prof. Antonio Serrano”, Colección Paleontología Vertebrados, Paraná, Entre Ríos, Argentina; MCC-URU, Museo de Ciencias Naturales de Caracas-Urumaco, Caracas, Venezuela; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; LIMF, Laboratorio de Investigaciones de Metalurgia Física “Ing. Gregorio Cusminsky”, Facultad de Ingeniería, Universidad Nacional de La Plata, Buenos Aires, Argentina, UFAC, Universidade Federal do Acre, Rio Branco, Brazil.

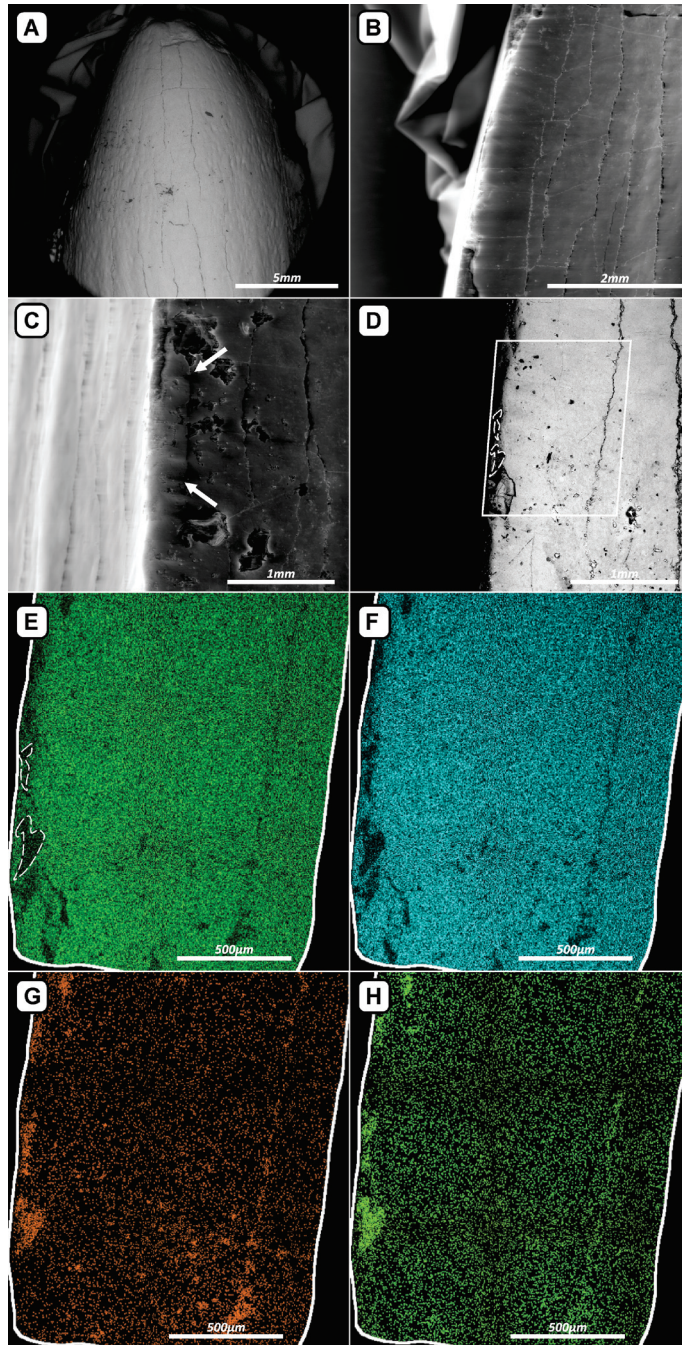


Fig. 2. Images of the tooth taken from the Environmental Scanning Electron Microscope (ESEM). (A) general view of the labial surface without metal coverage, using the low vacuum technique showing the vertical fractures and the cavities in the surface of the piece. (B) detail of the crenulated margin on the lingual aspect of the tooth, with vertical and transverse fractures. (C) detail of the mesio-distal edge of the tooth in vestibular (labial) view showing the crenulation typical of pseudozifodont teeth (indicated by arrows). (D) vestibular aspect of the tooth observed with Backscattered electrons showing fractures (in black) and positive surfaces (in white); the box delimits the area of mapping of chemical elements, carried out with EDAX. (E–H), details of the distribution of the chemical elements after the EDAX analysis: (E) phosphorus; (F) calcium; (G) iron; (H) silicon distributions. Note that the iron and the silicon are present mainly in the fractures and cavities of the tooth.

RESULTS

Systematic Paleontology

CROCODYLIFORMES Hay, 1930 (Benton & Clark, 1988)

CROCODYLIA Gmelin, 1789

ALLIGATORIDAE Gray, 1844

CAIMANINAE Brochu, 1999

Purussaurus Barbosa-Rodrigues, 1892

Purussaurus sp.

Type species. *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892.

Referred material. MAS-PV 386, incomplete tooth preserving the apex sector of an almost well preserved crown (Fig. 3).

Locality and horizon of the new specimen. Toma Vieja locality, near Paraná City (Entre Ríos Province, Argentina), “Conglomerado osífero” (traditionally considered as the base of Ituzaingó Formation, Brunetto *et al.*, 2013), Late Miocene (Brandoni, 2013; Brunetto *et al.*, 2013; Schmidt *et al.*, 2020).

Description. MAS-PV 386 consists of a fragmentary tooth that preserves most of the apical sector of the crown, which is conical but slightly compressed and lingually curved. In lingual and vestibular views, the mesial and distal margins are straight in the apical region but more curved in the base of the preserved part of the crown, where the tooth is subcircular in transverse section, with a vestibular-lingual width equal to 16.6 mm, and a mesiodistal width equal to 19.7 mm (both measured at the base of the piece). This minimal but abrupt increase in tooth width due to curving of the mesial and distal margins is present, although more marked, in other teeth assigned to *Purussaurus* (e.g., DGM 1128, Souza *et al.*, 2016, figure 3 F–H).

The tooth apex is rounded, showing a partial wear of the enamel apical surface, a condition commonly seen in worn or shed teeth of all crocodyles. The enamel of the lingual and vestibular (or labial, *sensu* Smith & Dodson, 2003) surfaces of the crown are uniformly ornamented with fine anastomosed striae or ridges separated by smooth grooves, extending from the apex to the base along the entire surface of the crown. These fine apicobasal ridges are transversely crossed by thin irregular lines, which observed under magnification give the enamel a cracked appearance.

The crown shows a conspicuous carina that extends continuously along the mesial and dis-

tal faces of the tooth dividing the crown into a vestibular and a lingual subequal sectors. This crenulated carina is preserved in several sectors of the mesial and distal margins, it is exclusively formed by the enamel and bears fine but very marked parallel crenulations, oriented perpendicularly to the carina. Under magnification (SEM) it can be verified that these crenulations are formed by rounded parallel short crests separated by a shallow valley of enamel, distributed on both the labial and lingual surfaces of the carina (Figs. 2B–C, 3C). The density of these carinae is 5 per millimeter. This condition is called pseudoziphodonty (or false ziphodonty; Prasad & de Broin, 2002) and differs from the ziphodont condition (serrated teeth) present in other archosaurs, in which the crenulations are formed by both the dentine and the enamel (Prasad & de Broin, 2002).

Several features acquired during the fossilization and depositional processes of MAS-PV 386 can be observed. In a macroscopic view, damaged areas are present at the base and the mesial and distal margins of the tooth, with worn surfaces and fractures (Fig. 3). Under magnification (SEM) an evident wear can be observed at the apex of MAS-PV 386, and several excoriations associated with longitudinal microfractures running from the apex to the base and connected to each other with finer subhorizontal microfractures (Fig. 2A). The longitudinal microfractures are arranged in the smooth grooves or valleys between the apicobasal striae that constitute the general ornamentation of the crown (Figs. 2A, 3). The vestibular surface of the tooth shows a process of micro alveolarization, identified from the presence of small depressions distributed all over the surface of the enamel. Finally, the tooth is broken at the base and, given the nature of this fracture, it can be inferred that it was separated from the skull after fossilizing.

Comparisons. Teeth preserved implanted in the upper and lower jaws are scarce in the crocodylian fossil record. In the case of *Purussaurus*, few teeth were recovered *in situ* and described in the literature (e.g., Langston, 1965; Aguilera *et al.*, 2006; Aureliano *et al.*, 2015; Souza *et al.*, 2021). A gradual transition in the shape and size of teeth has also been described for this taxon, from taller and pointed anterior teeth to broader, lower, and more bulbous posterior ones (Langston, 1965; Aureliano *et al.*, 2015). The teeth of *Purussaurus* have been described as rounded in a basal section but with crowns tending to be compressed (Langston, 1965) and

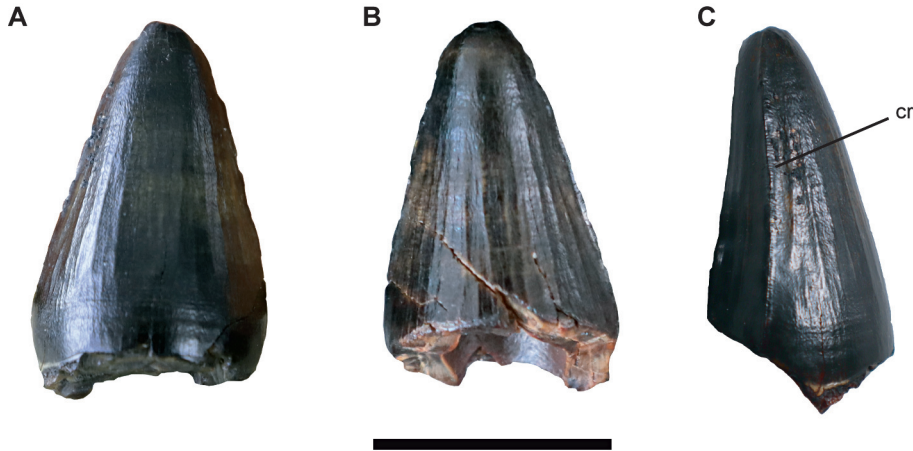


Fig. 3. Isolated tooth of *Purussaurus* sp. MAS-PV 386 in (A) vestibular; (B) lingual; and (C) mesio-distal views. Abbreviations: cr, crenulations. Scale bar = 20 mm.

bearing pseudozipodont ridges. Antermost, larger, conical and sharp teeth of both upper and mandibular series of *Purussaurus* have been described as slightly compressed and lingually and distally curved (Langston, 1965; Aguilera et al., 2006; Aureliano et al., 2015). In *P. mirandai* the premaxillary teeth are sharp, anteroposteriorly and labiolingually curved; these teeth are relatively compressed as MAS-PV 386 (with a vestibular-lingual width of 15–30 mm and a mesio-distal width of 19–39 mm, *sensu* Aguilera et al., 2006). Due to its dimensions and proportions, MAS-PV 386 is more similar to the premaxillary second tooth of *P. mirandai* (e.g., AMU-CURS-135, described by Aguilera et al., 2006), although given that MAS-PV 386 is an isolated tooth, its relative size and position in the tooth row cannot be specified since the body size of the individual is unknown. Some posterior maxillary teeth of *P. mirandai* are preserved in some specimens (e.g., AMU-CURS-135, MCC URU-115-72V) and as in most of caimanines, these teeth are blunt, more rounded and lower than the anterior ones, with a general morphology clearly different from MAS-PV 386. The dentary teeth arrangement of *P. mirandai* is similar to other caimanines with the anterior teeth larger, taller and sharper, being the mandibular tooth 4 the tallest of the first teeth preserved (e.g., AMU-CURS-135). In this species mandibular teeth are more compressed than the teeth of the upper jaw and than in MAS-PV 386. Following this reasoning, MAS-PV 386 could correspond to a tooth of the upper series.

In relation to the crown ornamentation, the teeth of *Purussaurus* have been described as pseudozipodont (see below). All these teeth pres-

ent mesiodistal carinae, sometimes incompletely preserved and with fine striations perpendicular to the surface of the crown. In *P. mirandai*, the third premaxillary teeth of MCC URU-115-72V and some isolated teeth associated with AMU-CURS-135 show a striae density of 3 per 5 mm, different from MAS-PV 386 in which the density of these striae is 5 per millimeter. Finally, the enamel of isolated teeth assigned to *Purussaurus* has been described by several authors (e.g., Langston, 1965; Aguilera et al., 2006; Aureliano et al., 2015; Souza et al., 2016, 2021) which conclude that in smaller teeth (especially in the posterior and more bulbous ones), the enamel is generally wrinkled whereas larger teeth generally show smooth enamel but with longitudinal and transverse lines along the crown, conditions similar to those of MAS-PV 386.

DISCUSSION

Among crocodyliforms, zipodont teeth are characteristic of carnivorous species with inferred terrestrial habits (as well as a few marine metriorhynchids; Gasparini et al., 2006). Zipodont teeth are common among predatory species within the diverse clade Notosuchia, such as peirosaurids (e.g., *Montealtosuchus* Carvalho et al., 2007, *Lomasuchus* Gasparini et al., 1991) and baurusuchids (e.g., *Baurusuchus* Price, 1945; e.g., Riff & Kellner, 2011) from the Cretaceous and the sebecids from the Paleogene–Neogene of South America (e.g., *Sebecus* Simpson, 1937; *Sahitysuchus* Kellner et al., 2014; e.g., Colbert, 1946). Zipodont teeth also occur in eusuchians of supposedly terrestrial habits such as the

Table 1. List of published materials used for morphological comparisons.

Taxon	Material	Provenance	Author
<i>Purussaurus mirandai</i>	AMU-CURS-135: skull with associated mandibles	Urumaco Formation (Late Miocene), El Hatillo, Falcon State, northwestern Venezuela	Aguilera <i>et al.</i> (2006)
<i>Purussaurus mirandai</i>	AMU-CURS-33: isolated posterior tooth	Urumaco Formation (Late Miocene), Tío Gregorio, Falcon State, northwestern Venezuela	Aguilera <i>et al.</i> (2006)
<i>Purussaurus mirandai</i>	MCC URU-115-72: premaxilla and maxilla in palatal view	Urumaco Formation (Late Miocene), 3.5 km northwest of El Picache, Falcon State, northwestern Venezuela	Aguilera <i>et al.</i> (2006)
<i>Purussaurus brasiliensis</i>	UFAC 1118: mandible	Solimões Formation (Late Miocene), Acre State, Brazil	Aureliano <i>et al.</i> (2015)
<i>Purussaurus brasiliensis</i>	DGM 527-R	Solimões Formation (Late Miocene; but see Souza <i>et al.</i> 2021 for other interpretations of provenance), "Petrópolis" outcrop, in the left side of the upstream Juruá River, between Porto Walter and the debouchment of Igarapé Ouro Preto (Price, 1967) Acre State, Brazil	Souza <i>et al.</i> (2021)
<i>Purussaurus</i> sp.	DGM 1128-R: isolated tooth	Solimões Formation (Late Miocene), Chapiama locality, at the right margin of a tributary of Chapiama stream, Acre State, Brazil	Souza <i>et al.</i> (2016)
<i>Purussaurus brasiliensis</i>	Isolated tooth unnumbered, figured by Aureliano <i>et al.</i> (2015), figure 5	Solimões Formation (Late Miocene), Cachoeira do Bandeira site, near the frontier with Bolivia, Acre State, Brazil	Aureliano <i>et al.</i> (2015)

planocraniids (*e.g.*, *Planocrania* Li, 1976 and *Boverisuchus* Kuhn, 1938; *e.g.*, Brochu, 2012) and mekosuchines (*e.g.*, *Quinkana* Molnar, 1981 and *Kambara* Willis *et al.*, 1993; *e.g.*, Brochu, 2001; Buchanan, 2009). Pseudoziphodont teeth are less common in non eusuchian crocodyliforms, being reported in some peirosaurids (*e.g.*, *Barcinosuchus* Leardi & Pol, 2009) and atoposaurids (Venczel & Codrea, 2019). The presence of pseudoziphodont teeth is even less frequent within Crocodylia. In particular, the only record of pseudoziphodont teeth for the Cenozoic of South America is restricted to the large caimanine *Purussaurus* and, in fact, this feature has been regarded as a diagnostic character for this genus (Souza *et al.*, 2021).

The general morphology of MAS-PV 386 is like the anterior teeth of specimens assigned to *Purussaurus* from northern regions (*e.g.*, Brazil, Colombia), in which the anterior teeth have slightly flattened crowns subcircular at their bases (Langston, 1965; Aguilera *et al.*, 2006; Aureliano *et al.*, 2015; Souza *et al.*, 2016, 2021).

Considering the general structure of the enamel of MAS-PV 386, it also resembles specimens assigned to *Purussaurus* in having longitudinal and transverse striae along the crown (*e.g.*, DGM 1128-R and DGM 1194-R, Souza *et al.*, 2016, figure 3 F-I; Aureliano *et al.*, 2015, figure 5). The pseudoziphodonty, the macro and microscopic appearance of the enamel, together with the general shape of the tooth, allows us to assign MAS-PV 386 to the genus *Purussaurus*. However, the lack of species level diagnostic features in the teeth of each species of this genus precludes assigning MAS-PV 386 to any of the known *Purussaurus* species. Furthermore, MAS-PV 386 differs from teeth assigned to *P. mirandai*, *P. neivensis*, and *P. brasiliensis*, which have been described as curving backwards and slightly inwards in these species (Langston, 1965; Aguilera *et al.*, 2006; Aureliano *et al.*, 2015; Souza *et al.*, 2021). As occur in most generalist alligatorids, the dentition of *Purussaurus* is heterodont in shape and size, showing a general transition from taller conical pointed anterior teeth (with some hypertrophied

Table 2. List of crocodylians of the “Conglomerado osífero” (Ituzaingó Formation, Paraná Province, Argentina).

Taxon	Specimens
<i>Mourasuchus arendsi</i>	MLP 73-IV-15-8: skull table; MLP 73-IV-15-9: posterior part of the skull
<i>Caiman australis</i>	MACN-PV 258, complete left maxilla (holotype)
<i>Caiman gasparinae</i>	MLP 73-IV-15-1: partial skull (holotype); MACN-PV 5555: fragment of right premaxilla
<i>Caiman lutescens</i>	MACN-PV 13551: skull table (holotype)
<i>Caiman latirostris</i>	MACN-PV 5416: left premaxilla and maxilla; MACN-PV 5576: left premaxilla; MLP 73-IV-15-16, fragment of left premaxilla; MLP 73-IV-15-12: fragment of braincase; MLP 89-XII-5-1: fragment of left dentary
<i>Caiman</i> cf. <i>C. yacare</i>	MLP 73-IV-15-5 and MLP 73-IV-15-6: right dentary fragments; MLP 73-IV-5-17 and MACN-PV 5417: fragments of right maxillae
<i>Purussaurus</i> sp.	MAS-PV 386: partial tooth
<i>Gryposuchus neogaeus</i>	MLP 68-IX-V-1: brain case; MLP 26-413: almost complete skull

teeth such as the 4th dentary tooth, 3rd/4th premaxillary teeth and 2nd/3rd maxillary teeth) to lower and rounded posterior teeth which are more button like shaped (e.g., Aguilera et al., 2006; Aureliano et al., 2015). After the anatomical comparisons here made, MAS-PV 386 is within the range of size variation of *Purussaurus* and the morphology of the crown indicates that it is probably an anterior tooth. As it is an isolated tooth, the position of MAS-PV 386 in the teeth row cannot be specified. However, compared with the proportions of the less compressed upper teeth and the relatively more compressed lower teeth of *Purussaurus mirandai*, the proportions of MAS-PV 386 indicate that it could be a tooth from the upper series (premaxillary tooth or anterior maxillary tooth).

In addition to the anatomical features, the preservation traits observed in MAS-PV 386 allow us to recognize the effects of the taphonomic processes that affected the material. From the BE analysis of the SEM, differences in the chemical elements and density of the materials that compose the surface of the tooth are identified (Fig. 2 EH). By mapping the chemical elements that conform the surface of the tooth, it was possible to verify the typical presence of calcium (Ca²⁺) and phosphorus (P⁵⁺), which constitute the original components of the tooth (hydroxyapatite), but also the presence of silicon (Si) and iron (Fe). In MAS-PV 386, Si and Fe fill the fractures and probably come from the silicoclastic sediment of the conglomerate (terrigenous material) and from authigenic precipitation as ferruginous cement (hematite, Fe₂O₃), respectively, during the fossil-diagenetic processes (Figs. 2G–H). The

presence of longitudinal, transverse, and perpendicular fractures (respect of the apicobasal axis of the tooth) (Fig. 2AD) is characteristic of a fragile tooth that loses the organic component that gives it the resistance of the structure. These fractures together with the small depressions distributed all over the vestibular surface of the enamel (micro alveolarization) would indicate that the piece suffered some abrasion by roll of little magnitude generated by the silicoclastic granular sediment of the bottom of the fluvial channel where it was accumulated.

Analyzing crocodylian assemblages from other contemporary South American localities, such as Solimões and Urumaco formations, *Purussaurus* is one of the taxa that cohabited in the Late Miocene mega wetland systems. Within these associations, caimanines (such as *Mourasuchus* and different *Caiman* species) and gavialoids (such as *Gryposuchus*) are always registered showing differences in their sizes and snout, jaws and teeth shapes. This morphological variability has been interpreted as evidence of niche partitioning, which results in optimizing the availability of resources and avoiding competition (Aureliano et al., 2015). In addition to the large size of *Purussaurus* species, the pseudozipodont teeth suggest that they would have been active predators that included large vertebrates in their diets (e.g., Pujos & Salas-Gismondí, 2020). This study confirms that *Purussaurus* would have been a component of the Late Miocene Argentinian crocodylofauna occupying a separate niche from piscivorous gavialoids, animalivore caimans and *Mourasuchus* (Tab. 2).

The sedimentological characteristics observed in the “Conglomerado osífero” in the Toma Vieja locality are mainly given by channel fill deposits interpreted as a braided fluvial system (e.g., Brunetto *et al.*, 2013; Brandoni *et al.*, 2019). As mentioned above, these levels rest unconformably on the shallow marginal marine deposits of the Paraná Formation through an erosive boundary, interpreted by some authors as a regional erosive surface related to the basal section of the Ituzaingó Formation (Brunetto *et al.*, 2013; Brandoni *et al.*, 2019). The erosive coarse-grained deposits of the “Conglomerado osífero”, together with the taphonomic characteristics of most of its fossils (which are disarticulated, fragmentary, and with evidence of transport) suggest that this association represents a mixture of faunas, mainly continental with few marine taxa of different ages (Cione *et al.*, 2000; Schmidt *et al.*, 2020). Beyond this scenario, the now documented presence of *Purussaurus* in the “Conglomerado osífero” suggests that ecosystems associated with the southernmost South American Miocene wetlands would have been taxonomically similar to those of lower latitudes (e.g., Hoorn *et al.*, 2010, 2022; Tineo *et al.*, 2015; Tineo, 2020). Particularly the presence of *Gryposuchus neogaeus* and caimanines such as *Mourasuchus arndsi*, *Purussaurus*, and several species for the moment assigned to *Caiman* (Bona & Barrios, 2015; Bona *et al.*, 2013) in the Late Miocene of Paraná (Tab. 2) proposes a wide geographic distribution of these Neogene fluvial systems with a similar ecological complexity for the entire region in South America. Among the fossil material of crocodylians of the “Conglomerado osífero”, *Gryposuchus neogaeus* is the most complete specimen recovered so far (i.e., MLP 26-413, an almost complete skull; Gasparini, 1968). Caimanines, on the other hand, are represented by isolated skulls and postcranial fragments which would indicate that most of these specimens will have been transported from their source area. In this scenario, MAS-PV 386 is another example of this taphonomical features. Although a regional environmental reconstruction is necessary to interpret the different continental sub-environments that would have developed in this part of the basin, the taxonomic diversity of crocodylians recognized in the “Conglomerado osífero” indicates the presence of warm humid environments with large amounts of water, capable of to withstand large piscivores gavialoids and huge caimanines along the megapredator *Purussaurus*.

CONCLUSIONS

The record of the tooth MAS-PV 386 in the “Conglomerado osífero” in Entre Ríos Province allows us to propose for the first time the presence of *Purussaurus* in the Late Miocene of Argentina. Although isolated indeterminate remains of large crocodylians have been described in the “Conglomerado osífero” (such as cranial and postcranial fragments of vertebrae, ribs, long bones, and osteoderms; Bravard, 1858; Burmeister 1883, 1885; Rovereto, 1912; Rusconi, 1933), at the moment this genus was geographically restricted to Miocene beds of Brazil, Colombia, Perú, and Venezuela (Aguilera *et al.*, 2006; Aureliano *et al.*, 2015).

This new finding represents the southernmost record of one of the largest known predators of neosuchian crocodiles. The presence of this mega carnivore alligatorid suggests a greater taxonomic diversity for the huge caimanines in Late Miocene wetlands in northeast Argentina. The potential faunistic association of large crocodylians such as *Gryposuchus*, *Purussaurus*, and giant caimans allows to explore the hypothesis of a niche partitioning already inferred for other Miocene northernmost South American localities given by the coexistence of piscivorous and other animal eating crocodylians. This possible setting proposes the existence of more complex environments capable of sustaining all this crocodylian fauna and therefore a more complex scenario for inland wetland and fluvial ecosystems developed in the Late Miocene in the South American Chaco Parana Basin.

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REFERENCES

- Aceñolaza, F.G. 1976. Consideraciones bioestratigráficas sobre el Terciario marino de Paraná y alrededores. *Acta Geológica Lilloana* 13: 91–107.
- Aceñolaza, F.G. 2000. La Formación Paraná (Mioceno medio): estratigrafía, distribución regional y unida-

- des equivalentes. In: F.G. Aceñolaza, & R. Herbst (eds.), *El Neógeno de Argentina*, pp. 191–238. Serie de Correlación geológica del Instituto Superior de Correlación Geológica, San Miguel de Tucumán.
- Aguilera, O.A., D. Riff & J. Bocquentin-Villanueva. 2006. A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the upper Miocene Urumaco Formation, Venezuela. *Journal of Systematic Palaeontology* 4(3): 221–232.
- Aureliano, T., A.M. Ghilardi, E. Guilherme, J.P. Souza-Filho, M. Cavalcanti & D. Riff. 2015. Morphometry, bite-force, and paleobiology of the Late Miocene Caiman *Purussaurus brasiliensis*. *PLoS One* 10(2): e0117944. doi:10.1371/journal.pone.0117944.
- Barbosa-Rodrigues, J.B. 1892. Les reptiles fossils de la Vallée de L'Amazone. *Vellosia Contribuições do Museu Botânico de Amazonas* 2: 41–60.
- Benton M.J. & J.M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton M.J. (ed), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*, pp. 295–338. Clarendon Press, Oxford.
- Bocquentin-Villanueva, J. 1984. Um nuevo Nettosuchidae (Crocodylia, Eusuchia) proveniente de la Formación Urumaco (Mioceno Superior), Venezuela. *Ameghiniana* 21: 1–8.
- Bocquentin-Villanueva J., & E. Buffetaut. 1981. *Hesperogavialis cruxenti* n. gen., n. sp., nouveau gavialide (Crocodylia, Eusuchia) du Miocène Supérieur (Huayquerien) d'Urumaco (Venezuela). *Geobios* 14: 415–419.
- Bona, P. & F. Barrios. 2015. The Alligatoroidea of Argentina: an update of its fossil record. In: M. Fernández & Y. Herrera (eds.), *Reptiles Extintos - Volumen en Homenaje a Zulma Gasparini*, pp. 143–158. Publicación Electrónica de la Asociación Paleontológica Argentina, Ciudad Autónoma de Buenos Aires.
- Bona, P. & A. Paulina Carabajal. 2013. *Caiman gasparinae* sp. nov., a huge alligatorid (Caimaninae) from the late Miocene of Paraná, Argentina. *Alcheringa: An Australasian Journal of Palaeontology* : 1–12. doi:10.1080/03115518.2013.785335
- Bona, P., A. Paulina Carabajal & Z. Gasparini. 2017. Neuroanatomy of *Gryposuchus neogaeus* (Crocodylia, Gavialoidea): a first integral description of the braincase and endocranial morphological variation in extinct and extant gavialoids. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 106: 235–246.
- Bona, P., D. Riff & Z. Gasparini. 2013. Late Miocene crocodylians from northeast Argentina: new approaches about the austral components of the Neogene South American crocodylian fauna. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103: 1–20.
- Boonstra, M., M.I.F. Ramos, E.I. Lammerts, P.O. Antoine & C. Hoorn. 2015. Marine connections of Amazonia: Evidence from foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). *Palaeogeography Palaeoclimatology Palaeoecology*. 417: 176–194, doi: 10.1016/j.palaeo.2014.10.032.
- Brandoni, D. 2013. Los mamíferos continentales del “Mesopotamiense” (Mioceno Tardío) de Entre Ríos, Argentina. Diversidad, edad y paleobiogeografía. In: D. Brandoni & J. I. Noriega (eds.), *El Neógeno de la Mesopotamia argentina*, pp. 179–191. Asociación Paleontológica Argentina, Publicación Especial, Ciudad Autónoma de Buenos Aires.
- Brandoni, D. & J.I. Noriega (eds.). 2013. *El Neógeno de la Mesopotamia argentina. Asociación Paleontológica Argentina*, Publicación Especial 14, 221 pp.
- Brandoni, D., M. Brea, E. Brunetto, J.M. Diederle, M.J. Franco, F. Gois Lima, A.I. Lutz, J.I. Noriega, L.M. Pérez, G. Schmidt & A.F. Zucol. 2019. Paleontología del Mioceno tardío de la región Noreste de Argentina. In: N. Nasif, G. Esteban, J. Chiesa, A. Zurita & S. Zurita (eds.), *Mioceno al Pleistoceno del centro y norte de Argentina*, pp. 131–162. Opera Lilloana, San Miguel de Tucumán.
- Bravard, A. 1858. Monografía de los terrenos terciarios del Paraná. Reimpresión facsimilar, Imprenta del Congreso de la Nación, Buenos Aires, 1995, V-XII + 107p.
- Brochu, C.A. 1999. Phylogenetics, taxonomy and historical biogeography of Alligatoroidea. In: T. Rowe, C.A. Brochu & K. Kishi (eds.), *Cranial morphology of Alligator mississippiensis and phylogeny of Alligatoroidea*, pp. 9–100. Society of Vertebrate Paleontology, Memoir 6, Washington.
- Brochu, C.A. 2001. Crocodylian snouts in space and time: phylogenetic approaches toward adaptive radiation. *American Zoologist* 41(3): 564–585.
- Brochu, C.A. & A.D. Rincon. 2004. A gavialoid crocodylian from the Lower Miocene of Venezuela. *Special Papers in Palaeontology* 71: 61–78.
- Brochu, C.A. 2012. Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103(3–4): 521–550.
- Brunetto, E., J.I. Noriega & D. Brandoni. 2013. Sedimentología, estratigrafía y edad de la Formación Ituzzaingó en la provincia de Entre Ríos, Argentina. In: D. Brandoni & J. I. Noriega (eds.), *El Neógeno de la Mesopotamia argentina*, pp. 13–27., Asociación Paleontológica Argentina, Publicación Especial, Ciudad Autónoma de Buenos Aires.
- Buchanan, L.A. 2009. *Kambara taraina* sp. nov. (Crocodylia, Crocodyloidea), a new Eocene mekosuchine from Queensland, Australia, and a revision of the genus. *Journal of Vertebrate Paleontology* 29 (2): 473–486.
- Burmeister, G. 1883. Reprint of Bravard, 1858: Monografía de los terrenos marinos terciarios del Paraná. *Anales del Museo Público de Buenos Aires* 3: 45–94.
- Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por Don Augusto Bravard y mencionados en su obra precedente. *Annales del Museo Nacional de Buenos Aires* 3: 95–173.
- Carvalho I.S., F.M. de Vasconcellos & S.A. Simionato

- Tavares. 2007. *Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. *Zootaxa* 1607: 35–46.
- Cidade G.M., A. Solórzano, A.D. Rincón, D. Riff & A.S. Hsiou. 2017. A new *Mourasuchus* (Alligatoroidea, Caimaninae) from the late Miocene of Venezuela, the phylogeny of Caimaninae and considerations on the feeding habits of *Mourasuchus*. *PeerJ*. 5: e3056.
- Cidade, G.M., A. Solórzano, A.D. Rincón, D. Riff & A.S. Hsiou. 2018. Redescription of the holotype of the Miocene crocodylian *Mourasuchus arendsi* (Alligatoroidea, Caimaninae) and perspectives on the taxonomy of the species. *Historical Biology* 1–17. doi: 10.1080/08912963.2018.1528246.
- Cione, A.L., M.M. Azpelicueta, M. Bond, A. Carlini, J. Casciotta, M.A. Cozzuol, M. de la Fuente, Z. Gasparini, F. Goin, J. Noriega, G. Scillato-Yané, L. Soibelzon, E. Tonni, D. Verzi & G. Vucetich. 2000. Miocene vertebrates from Entre Ríos Province, Argentina. In: F.G. Aceñolaza, & R. Herbst (eds.), *El Neógeno de Argentina*, pp. 191–238. Serie de Correlación geológica del Instituto Superior de Correlación Geológica, San Miguel de Tucumán.
- Colbert, E.H. 1946. *Sebecus*, representative of a peculiar suborder of fossil Crocodylia from Patagonia. *Bulletin of the American Museum of Natural History* 87 (4): 217–270.
- Del Río, D.C., S. Martínez, J. McArthur, T. Matthew, & L.M. Pérez. 2018. Dating late Miocene marine incursions with Sr-Isotope stratigraphy (Argentina and Uruguay): a reappraisal of the paleogeography of the “Paranense” sea. *Journal of South American Earth Sciences* 85: 312–33
- Freguelli, J. 1920. Contribución al conocimiento de la geología de Entre Ríos. *Boletín de la Academia Nacional de Ciencias de Córdoba* 24: 55–256.
- Gasparini, Z. 1968. Nuevos restos de *Rhamphostomopsis neogaeus* (Burm.) Rusconi 1933, (Reptilia, Crocodylia) de “Mesopotamiense” (Plioceno Medio-Superior) de Argentina. *Ameghiniana* 5 (8): 299–308.
- Gasparini, Z. 1981. Los Crocodylia fósiles de la Argentina. *Ameghiniana* 18: 177–205.
- Gasparini, Z. 1985. Un Nuevo cocodrilo (Eusuchia) Cenozoico de América del Sur. *Ministerio das Minas e Energia, Departamento Nacional da Produção Mineral, serie Geología Paleontología: / Estratigrafía* 2: 51–53.
- Gasparini, Z., L.M. Chiappe & M. Fernández. 1991. A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodylians. *Journal of Vertebrate Paleontology* 11(3): 316–333.
- Gasparini, Z., D. Pol & L.A. Spalletti. 2006. An unusual marine crocodyliiform from the Jurassic-Cretaceous boundary of Patagonia. *Science* 311(5757): 70–73.
- Gmelin, J. 1789. *Linnei systema naturae*. GE Beer, Leipzig, 1057.
- Gray, J.E. 1862. A synopsis of the species of alligators. *Annals and Magazine of Natural History* 10(35): 327–331.
- Greb, S.F., W.A. DiMichele & R.A. Gastaldo. 2006. Evolution and importance of wetlands in earth history. In: S.F. Greb & W.A. DiMichele (eds.), *Wetlands through time*, pp. 1–40. Geological Society of America, Washington.
- Gürich, G.J.E. 1912. *Gryposuchus jessei*: ein neues schmalschnauziges Krokodil aus den jüngeren Ablagerungen des oberen Amazonas-Gebietes. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* 26: 59–71.
- Hastings, A.K., J.I. Bloch, C.A. Jaramillo, A.F. Rincón & B.J. MacFadden. 2013. Systematics and biogeography of crocodylians from the Miocene of Panama. *Journal of Vertebrate Paleontology* 33: 239–263.
- Hay, O.P. 1930. *Second bibliography and catalogue of fossil Vertebrata of North America*. Carnegie Institution of Washington Publication, Wasinton, 1077pp.
- Hoorn, C., F.P. Wesselingh, J. Hovikoski & J. Guerrero. 2010. The development of the Amazonian megawetland (Miocene; Brazil, Colombia, Peru, Bolivia). In: C. Hoorn & F.P. Wesselingh (eds.), *Amazonia, Landscape and Species Evolution: A Look into the Past*, pp. 123–142. Wiley-Blackwell Publishing, Oxford.
- Hoorn, C., T. Kukla, G. Bogotá-Angel, E. van Soelen, C. González-Arango, F.P. Wesselingh, H. Vonhof, P. Val, G. Morcote-Ríos, M. Roddaz, E.L. Dantas, R. Ventura Santo, J.S. Sinninghe, J.H. Damsté Kim & R.J. Morley. 2022. Cyclic sediment deposition by orbital forcing in the Miocene wetland of western Amazonia? New insights from a multidisciplinary approach. *Global and Planetary Change* 210: 103717.
- International Commission on Stratigraphic. 2022. International chronostratigraphic chart. www.stratigraphy.org
- Kellner, A.W., A.E. Pinheiro & D.A. Campos. 2014. A new sebecid from the Paleogene of Brazil and the crocodyliiform radiation after the K–Pg boundary. *PLoS One* 9: e81386.
- Kuhn, O. 1938. Die Crocodilier aus dem mittleren Eozän des Geiseltales bei Halle. *Nova Acta Leopoldina* 39: 313–28.
- Langston, W. 1965. *Fossil Crocodylians from Colombia and the Cenozoic history of the Crocodylia in South America*. University of California Press, Berkeley, 167 pp.
- Langston, W. 1966. *Mourasuchus* Price, *Nettosuchus* Langston, and the family Nettosuchidae (Reptilia: Crocodylia). *Copeia* 4: 882–885. doi:10.2307/1441424.
- Leardi, J.M. & D. Pol. 2009. The first crocodyliiform from the Chubut Group (Chubut Province, Argentina) and its phylogenetic position within basal Mesoeucrocodylia. *Cretaceous Research* 30(6): 1376–1386.
- Li, J.L. 1976. Fossils of *Sebecosuchia* discovered from Nanxiong, Guangdong. *Vertebrata Palasiatica* 14: 169–173.
- Molnar, R.E. 1981. Pleistocene ziphodont crocodyl-

- ians of Queensland. *Records of the Australian Museum* 33(19): 803–834. doi:10.3853/j.0067-1975.33.1981.198.
- Mook, C.C. 1941. A new fossil crocodylian from Colombia. *Proceedings of the National Museum, Smithsonian Institution* 91(3122): 55–58.
- Orfeo, O. & J.J. Neiff. 2008. Esteros del Iberá. Un enorme laboratorio a cielo abierto. *Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino*: 415–425.
- Paolillo, A. & O.J. Linares. 2007. Nuevos cocodrilos Sebecosuchia del Cenozoico Suramericano (Mesosuchia: Crocodylia). *Paleobiología Neotropical* 3: 1–25.
- Pérez, L.M. 2013a. Nuevo aporte al conocimiento de la edad de la Formación Paraná, Mioceno de la provincia de Entre Ríos, Argentina. In: D. Brandoni & J. I. Noriega (eds.), *El Neógeno de la Mesopotamia argentina*, pp 13–27, Asociación Paleontológica Argentina, Publicación Especial.
- Pérez, L.M. 2013b. Sistemática, Tafonomía y Paleoecología de los Invertebrados de la Formación Paraná (Mioceno), provincia de Entre Ríos, Argentina. Tesis Doctoral Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 403 pp.
- Prasad, G.V.R. & F.L. De Broin. 2002. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Annales de Paléontologie* 88: 19–71.
- Price. L.I. 1945. A new reptil from the Cretaceous of Brazil. *Ministério da Agricultura, Divisão de Geología e Mineralogia* 25: 1–8.
- Price, L.I. 1964. Sobre o crânio de um grande crocodylideo extinto do alto Rio Juruá, Estado do Acre. *Anais da Academia Brasileira de Ciências* 36(1): 59–66.
- Pujos, F. & R. Salas-Gismondi. 2020. Predation of the giant Miocene caiman *Purussaurus* on a mylodontid ground sloth in the wetlands of proto-Amazonia. *Biological Letters* 16: 20200239, <http://dx.doi.org/10.1098/rsbl.2020.0239>
- Quiroz, L.I. & C.A. Jaramillo. 2010. Stratigraphy and sedimentary environment of Miocene shallow to marginal marine deposits in the Urumaco trough, Falcon Basin, Western Venezuela. In: M. Sánchez-Villagra, O.A. Aguilera & A.A. Carlini (eds.), *Urumaco & Venezuelan Paleontology*, pp. 153–172. Indiana University Press Bloomington, ciudad. doi: 10.1007/s13358-015-0071-4.
- Riff, D. & O.A. Aguilera. 2008. The world's largest gharials *Gryposuchus*: description of *G. croizati* n. sp. (Crocodylia, Gavialidae) from the Upper Miocene Urumaco Formation, Venezuela. *Paläontologische Zeitschrift* 82(2): 178–195. doi:10.1007/bf02988408
- Riff, D., P.S.R. Romano, G.R. Oliveira & O.A. Aguilera. 2010. Neogene crocodile and turtle fauna in Northern South America. In: C. Hoorn & F.P. Wesselingh (eds.), *Amazonia, Landscape and Species Evolution*, pp. 259–280. Wiley-Blackwell, Oxford.
- Riff, D. & A.W.A. Kellner. 2011. Baurusuchid crocodyliforms as theropod mimics: clues from the skull and appendicular morphology of *Stratiotosuchus maxhechti* (Upper Cretaceous of Brazil). *Zoological Journal of the Linnean Society* 163(S1): 37–56.
- Rovereto, C. 1912. Los cocodrilos fósiles en las capas del Paraná. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 22: 339–368.
- Rusconi, C. 1933. Observaciones críticas sobre reptiles Terciarios de Paraná (Familia Alligatoridae). *Revista de la Universidad Nacional de Córdoba* 20: 1–52.
- Salas-Gismondi, R., J.J. Flynn, P. Baby, J.V. Tejada-Lara, F.P. Wesselingh & P.O. Antoine. 2015. A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proceeding of the Royal Society B* 282: 20142490. <http://dx.doi.org/10.1098/rspb.2014.2490>.
- Salas-Gismondi, R., J.J. Flynn, P. Baby, J.V. Tejada-Lara, J. Claude & P.O. Antoine. 2016. A new 13-million-year-old gavialoid crocodylian from Proto-Amazonian Mega-Wetlands reveals parallel evolutionary trends in skull shape linked to longirostry. *PLoS One* 11(4): e0152453. doi:10.1371/journal.pone.0152453.
- Salas-Gismondi, R., J.W. Moreno-Bernal, T.M. Scheyer, M.R. Sánchez-Villagra & C. Jaramillo. 2018. New Miocene Caribbean gavialoids and patterns of longirostry in crocodylians. *Journal of Systematic Palaeontology* 1–27. doi: 10.1080/14772019.2018.1495275.
- Scheyer, T.M., O.A. Aguilera, M. Delfino, D.C. Fortier, A.A. Carlini, R. Sánchez, J. Carrillo-Briceño & L. Quiroz. 2013. Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nature Communications* 4: 1907, doi:10.1038/ncomms2940
- Schmidt, G.I., J.M. Diederle, E.R. Vallone, F. Góis, J. Tarquini, M.A. Fernández Osuna, M.G. Gottardi & D. Brandoni. 2020. New vertebrates from the Late Miocene of Entre Ríos Province, Argentina: diversity, age, and paleoenvironment. *Journal of South American Earth Sciences* 101: 102618. <https://doi.org/10.1016/j.jsames.2020.102618>
- Sill, W.D. 1970. Nota preliminar sobre un nuevo gavial del Plioceno de Venezuela y una discusión de los gaviales sudamericanos. *Ameghiniana* 7:151–159.
- Simpson, G.G. 1937. An ancient eusuchian crocodile from Patagonia *American Museum Novitates* 965: 19–20.
- Smith, J.B. & P. Dodson. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23(1):1–12.
- Souza, R.G., G.M. Cidade, D.D.A. Campos & D. Riff. 2016. New crocodylian remains from the Solimões Formation (Lower Eocene–Pliocene), state of Acre, Southwestern Brazilian Amazonia. *Revista brasileira de paleontologia* 19(2): 217–232.
- Souza, R.G., K.L. Bandeira, R.V. Pêgas, A.S. Brum, R. Machado, E. Guilherme & J.P. Souza-Filho. 2021. The history, importance and anatomy of the

- specimen that validated the giant *Purussaurus brasiliensis* Barbosa-Rodrigues 1892 (Crocodylia: Caimaninae). *Anais da Academia Brasileira de Ciências* 93: 1–20.
- Souza-Filho, J.P., R.G. Souza, A.S. Hsiou, D. Riff, E. Guilherme, F.R. Negri & G.M. Cidade. 2018. A new caimanine (Crocodylia, Alligatoroidea) species from the Solimões Formation of Brazil and the phylogeny of Caimaninae. *Journal of Vertebrate Paleontology* 38(5): e1528450, doi:10.1080/02724634.2018.1528450. ISSN 0272-4634. S2CID 91964360.
- Spix, J.B. 1825. *Animalia nova sive Species novae lacertarum quas initinere per Brasiliam annis. MDCCCXVII–MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae Regis suscepto collegit et descripsit Dr. J.B. de Spix. T.O. Weigel, Lipsiae*, 26 pp.
- Tineo, D.E. 2020. Facies model of a sedimentary record for a Pantanal-like inland wetland. *Sedimentology* 67: 3683–3717.
- Tineo, D.E., P. Bona, L.M. Pérez, G.D. Vergani, G. González, D.G. Poiré, Z.N. Gasparini & P. Legarreta. 2015. Palaeoenvironmental implications of the giant crocodylian *Mourasuchus* (Alligatoridae, Caimaninae) in the Yecua Formation (late Miocene) of Bolivia. *Alcheringa* 39: 224–235.
- Tineo, D.E., M.A. Comerio, L.H. Vigiani, G.S. Kurten Moreno & D.G. Poiré. 2021. Tectonic and paleoclimatic controls on the composition of inland wetland deposits, Chaco foreland basin, Central Andes. *Journal of Sedimentary Research* 92 (2): 112–133. <https://doi.org/10.2110/jsr.2021.033>
- Tineo, D.E., D. Moyano-Paz, A.N. Varela & D.G. Poiré. 2022. Onset of the Miocene Chaco foreland basin: depositional conditions, provenance and paleogeographic implications of the Tranquitas Formation (Argentina). *International Journal of Earth Sciences* 111: 1739–1771. <https://doi.org/10.1007/s00531-022-02203-3>
- Uba, C.E., C.A. Hasler, L.A. Buatois, A.K. Schmitt & B. Plessen. 2009. Isotopic, paleontologic, and ichnologic evidence for late Miocene pulses of marine incursions in the Central Andes. *Geology* 37: 827–830.
- Venczel, M. & V.A. Codrea. 2019. A new *Theriosuchus*-like crocodyliform from the Maastrichtian of Romania. *Cretaceous Research* 100: 24–38.
- Wesselingh, F.P., M.E. Räsänen, G. Irion, H.B. Vonhof, R. Kaandorp, W. Renema & M. Gingras 2001. Lake Pebas: a palaeoecological reconstruction of a Miocene, longlived lake complex in western Amazonia. *Cainozoic Research* 1(1/2): 35–68.
- Willis, P.M.A., R.E. Molnar & J.D. Scanlon. 1993. An early Eocene crocodylian from Murgon, southeastern Queensland. *Kaupia* 3: 27–33.

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