

A new peirosaurid from the Bajo de la Carpa Formation (Upper Cretaceous, Santonian) of Cerro Overo, Neuquén, Argentina



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ABSTRACT

In this article we present a new peirosaurid crocodyliform: *Kinesuchus overoi* gen. et sp. nov. The specimen was recovered from the Bajo de la Carpa Formation (Santonian, Upper Cretaceous) and is composed of an incomplete mandible consisting of dentaries, splenials, and portion of the left surangular. The specimen shares some features with the peirosaurids *Hamadasuchus*, *Pepesuchus* and *Itasuchus*, including a narrow symphyseal region in lateromedial and dorsoventral views with a planar dorsal surface and an anterior projection of the splenial. This new material increases the diversity of peirosaurids in the Neuquén Group, and the faunal richness of the Bajo de la Carpa Formation.

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1. Introduction

The peirosaurids are a prolific group of medium-sized, continental mesoeucrocodylian crocodyliforms currently known from the Cretaceous with an exclusively Gondwanan distribution (Pol and Gasparini, 2007; Sertich and O'Connor, 2014). Most abundant records come from the Cretaceous of South America, specifically from Brazil and Argentina (e.g., Candeiro and Martinelli, 2006). In Brazil, known taxa include: *Peirosaurus tormini* Price, 1955 (Maastrichtian, Marília Formation); *Itasuchus jesuinoi* Price, 1955 (Late Maastrichtian, Marília Formation); *Montealtosuchus arrudacamposi* Carvalho et al., 2007 (Turonian-Santonian, Adamantina Formation), *Uberabasuchus terrificus* Carvalho et al., 2004 (upper Maastrichtian, Marília Formation), and *Pepesuchus deiseae* Campos et al., 2011 (Campanian-Maastrichtian, Presidente Prudente Formation). To this point, the Argentinian record includes: *Barcosuchus gradilis* Leardi and Pol, 2009 (Aptian-Albian, Cerro Barco Formation), *Lomasuchus palpebrosus* Gasparini, et al., 1991 (Turonian-Coniacian, Portezuelo Formation), *Gasparinisuchus peirosauroides* Martinelli et al., 2012 (Santonian-lower Campanian, Bajo de Carpa and Anacleto formations), *Patagosuchus anielensis* Lío et al., 2016 (Turonian-Coniacian, Portezuelo Formation), and *Bayomesasuchus hernandezi*

Barrios et al., 2015 (Turonian, Cerro Lisandro Formation). The record of the group in Africa is also extensive, and controversial in some cases: *Hamadasuchus rebouli* Buffetaut, 1994 (Larsson and Sues, 2007; Albian-Cenomanian, Kem Kem beds), *Rukwasuchus yajabaliyekundu* Sertich and O'Connor, 2014 (Aptian-Cenomanian, Galula Formation), *Stolokrosuchus lapparenti* Larsson and Gado, 2000 (Aptian-Albian, Elhraz Formation), and *Trematochampsia taqueti* Buffetaut, 1974 (Turonian, Beceten Formation). Until now, these taxa represent three different rostral morphotypes: one oreinorostral (dorsoventrally tall, mediolaterally narrow; i.e. *Montealtosuchus*), one broad-snouted (i.e. *Gasparinisuchus*) and other narrow-snouted (i.e. *Pepesuchus*) (sensu Lío et al., 2016).

The Bajo de la Carpa Formation (Santonian, Neuquén Group) of northern Patagonia is a notably fossiliferous continental unit (Garrido, 2010). Remains of fishes, testudines, ophidians, sauro-pods, avian and non-avian theropod dinosaurs, and many crocodyliforms have been recovered from this unit at several different localities in Neuquén Province and Rio Negro Province (e.g. Bonaparte, 1991; Leanza et al., 2004; Salgado et al., 2009; Garrido, 2010). Previously, several mesoeucrocodylian specimens were described from the Bajo de la Carpa Formation in the Neuquén Province, five from the Neuquén City area: *Notosuchus terrestris* Woodward, 1896, *Microsuchus schilleri* Dolgopol de Saez, 1928, *Comahuesuchus brachybuccalis* Bonaparte, 1991, *Wargosuchus australis* Martinelli and Pais, 2008, and Peirosauridae indet (Bonaparte, 1991; Pol and Gasparini, 2007; Fiorelli, 2010; Leardi et al., 2015).

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Another specimen was reported from the Loma de la Lata locality, the peirosaurid *Gasparinisuchus peirosauroides* (Martinelli et al., 2012). A third peirosaurid specimen represented by the skull and postcranial skeleton was recovered from the Sierra Barrosa area, near Plaza Huincul (Ortega et al., 2012), is currently under study.

In the Cerro Overo locality, southwest of Rincón de los Sauces, Neuquén Province (Fig. 1), the Bajo de la Carpa Formation only produced fragmentary vertebrate remains, so far (Cruzado-Caballero et al., 2016a, b), in addition to one relatively complete and articulated sauropod dinosaur (*Overosaurus paradasorum* Coria et al., 2013). Here we present a new specimen of Peirosauridae that adds to the taxonomic diversity of the group, providing a new record for this unit and the first published record of Crocodyliformes for the Cerro Overo locality.

2. Materials and methods

2.1. Abreviaturas institucionales

AMNH, American Museum of Natural History, New York, U.S.A.; **CPPLIP**, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price – Peirópolis, Uberaba, Minas Gerais, Brazil; **DGM**, Departamento Nacional de Produção Mineral, Rio de Janeiro, Rio de Janeiro, Brazil; **MACN-RN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; **MAL**, Malawi Department of Antiquities, Lilongwe, Malawi; **MAÑE-PV**, Museo Municipal de Añelo, Añelo, Neuquén, Argentina; **MAU-Pv-CO**, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Neuquén, Argentina; **MCF PVPH**, Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina; **MN**, Museo Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil; **MNN**, Musée National de Niger, Niamey, Niger; **MPCA-PV**, Museo Paleontológico Carlos Ameghino, Cipolletti, Río Negro, Argentina; **MPMA**, Museu de Paleontologia de Monte Alto, Monte Alto, Brazil; **MOZ-Pv**, Museo de Ciencias Naturales Prof. Juan Olsacher, Zapala, Neuquén, Argentina; **MUC-PV**, Museo de la Universidad Nacional del Comahue, Comahue, Neuquén, Argentina; **ROM**, Royal Ontario Museum, Ontario, Canada; **UA**, Université d'Antananarivo, Antananarivo, Madagascar.

3. Systematic paleontology

Crocodylomorpha Hay, 1930 (sensu Walker, 1970)
 Crocodyliformes Hay, 1930 (sensu Clark, in Benton and Clark, 1986)
 Mesoeucrocodylia Whetstone and Whybrow, 1983
 Notosuchia Gasparini, 1971 (sensu Sereno et al., 2001)
 Peirosauridae Gasparini, 1982 (sensu Turner and Sertich, 2010)

Kinesuchus overoi gen. et sp. nov.

Derivation of the name. From the Mapuche language: *kiñe*; one and the Greek *souchus*, in reference to the Egyptian, crocodile-headed deity. The specific, *overoi*, refers to the first record of this group from the Cerro Overo locality.

Holotype. MAU-Pv-CO-583. (Figs. 2, 3) Incomplete mandible consisting of right and left dentaries and surangulans and a portion of the left surangular.

Diagnosis. Crocodyliform with the following unique combination of characters: mandible with alveolar row slightly festooned; splenial participation in the symphysis and ziphodont teeth, as in all known peirosaurids; symphyseal region slender, elongate, spatulate shaped, and compressed dorsoventrally (shared with *Itasuchus* Price 1955); mandible with eighteen alveoli (shared with *Gasparinisuchus*, *Montealtosuchus*, *Itasuchus* and *Pepesuchus*) distributed in two waves of enlargement centered over the fourth alveolus and 12th–13th alveoli; small diastema between the fourth and fifth alveoli (shared with *Bayomesasuchus*); anterior alveoli circular and discrete while alveoli posterior to position ten are mesiodistally oval and confluent. Potential autapomorphies are: (1) elongated mandibular symphyseal region (including dentary + splenial) posteriorly extending to 12th alveolus, (2) medial margin of the foramen intermandibularis oralis located on symphyseal suture, and (3) dentary with marked lateral constriction at level the eighth and ninth alveoli.

Type locality. Cerro Overo (Fig. 1), 50 km southwest of the City of Rincón de los Sauces, Neuquén, Argentina (S37°36'35.0"-W69°18'59.0").

Stratigraphic horizon. Bajo de la Carpa Formation, (Santonian, Upper Cretaceous), Río Colorado Subgroup, Neuquén Group, Neuquén Basin (Garrido, 2010).

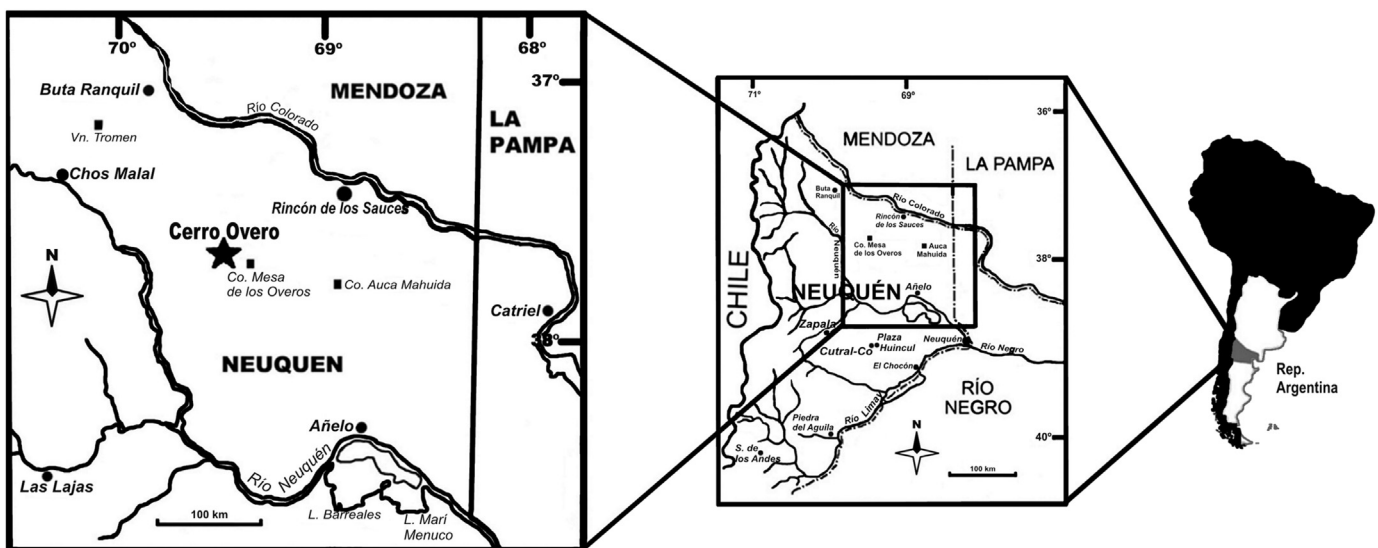


Fig. 1. Map showing the location of the Cerro Overo site in Neuquén Province, Argentina.

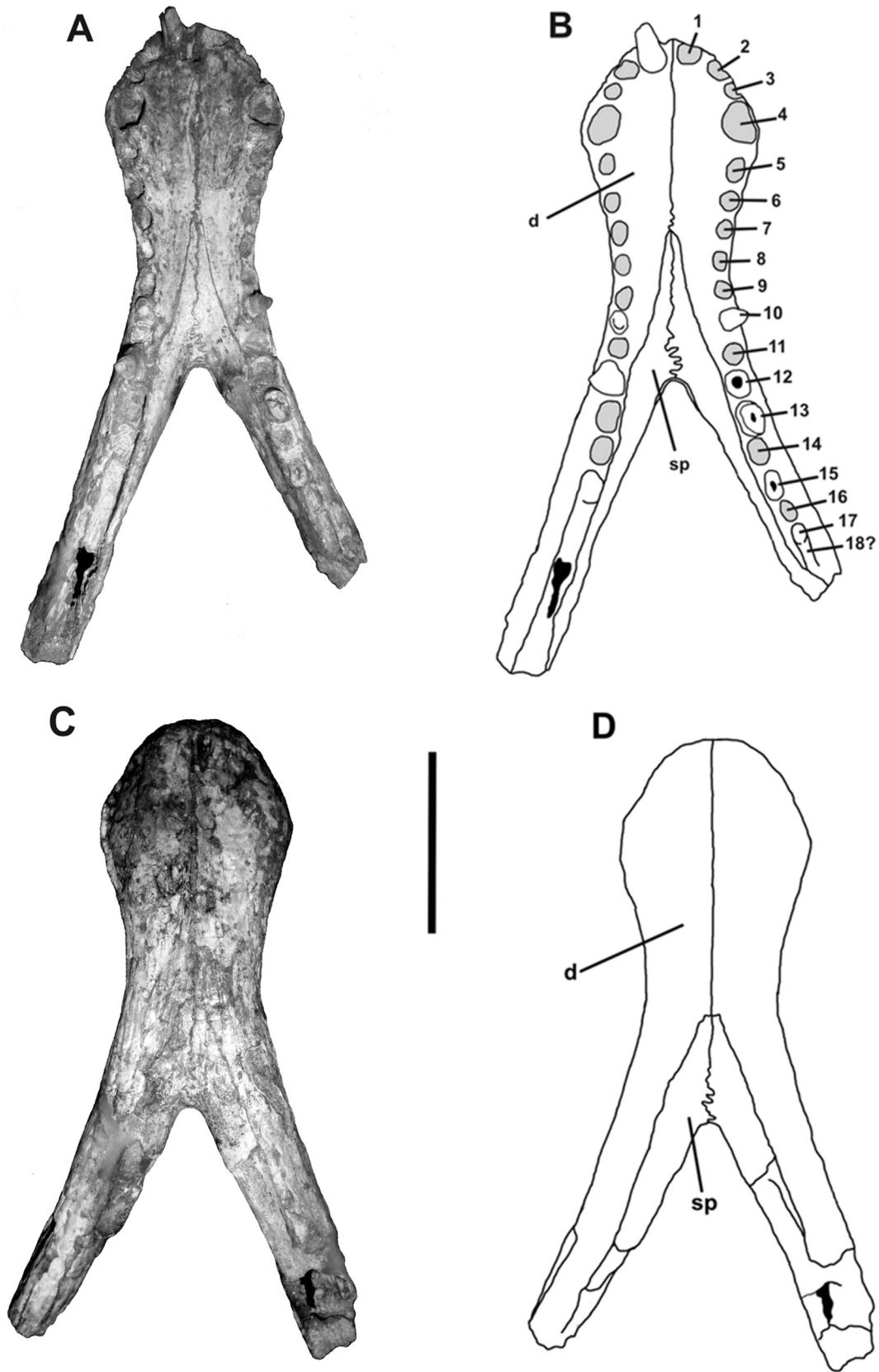


Fig. 2. Photograph and associated line drawing of the mandible of *Kinesuchus overoi* gen. et sp. nov. (MAU-Pv-CO-583), in dorsal (A, B) and ventral (C, D) views. Anatomical abbreviations: **d**, dentary; **sp**, splenial. Numbers from 1 to 18 correspond to alveoli or teeth. Scale bar: 5 cm.

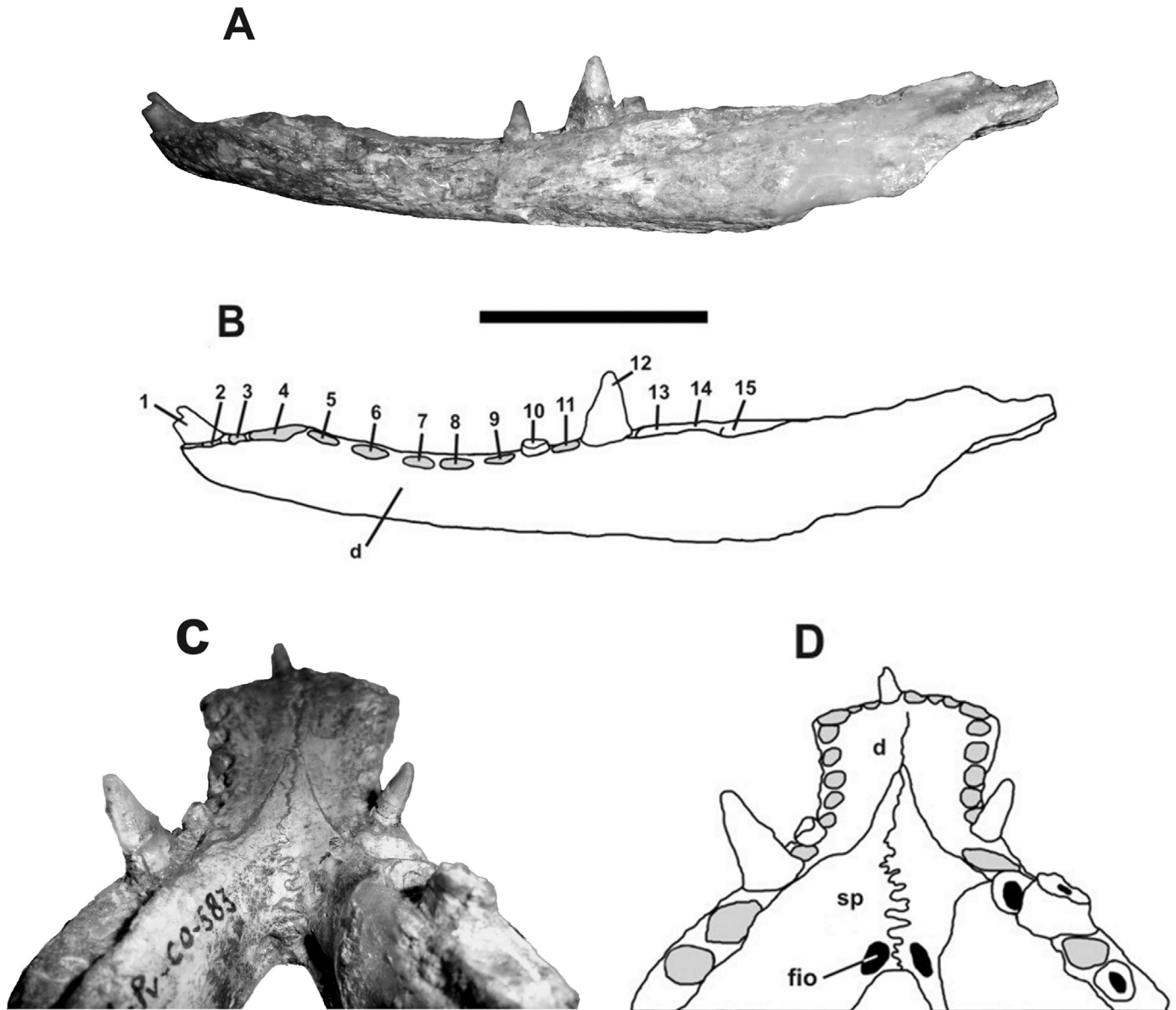


Fig. 3. Photograph and associated line drawing of the mandible of *Kinesuchus overoi* gen. et sp. nov. (MAU-Pv-CO-583), in lateral (A, B) and postdorsal (C, D) views. Anatomical abbreviations: **d**, dentary; **fio**, foramen intermandibularis oralis; **sp**, splenial. Numbers from 1 to 15 correspond to alveolus or teeth. Scale bar: 5 cm.

4. Description and comparison

Cretaceous South American crocodyliforms with splenial symphysis, ziphodont teeth, and relatively long snout are presently constrained to Peirosauridae and Baurusuchidae (e.g., Gasparini, 1996; Candeiro and Martinelli, 2006; Pol and Gasparini, 2007). Considering that baurusuchids possess a robust mandible with reduced dentition and extensive ornamentation consisting of ridges and furrows (e.g., Montefeltro et al., 2011), the primary comparisons were made with peirosaurids that preserved comparable elements [*Stolokrosuchus lapparenti* (MNN GDF 602, Larsson and Gado, 2000); *Hamadasuchus rebouli* (ROM 49282, Larsson and Sues, 2007, fig. 6), *Montealtosuchus arrudacamposi* (MPMA-16-0007-04, Carvalho, et al., 2007), *Uberabasuchus terrificus* (CPPLIP 630, Carvalho et al., 2004), *Pepesuchus deiseae* (MN 7005 – V, Campos et al., 2011), *Itasuchus jesuinoi* (DGM 434-R, Price, 1955), *Patagosuchus anielensis* (MANE-PV 1, Lío et al., 2016),

Bayomesasuchus hernandezii (MCF PVPH-822, Barrios et al., 2015), and *Gasparinisuchus peirosauroides* (MOZ-Pv 1750, Martinelli et al., 2012)] (Fig. 4). *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández (1991) does not possess a preserved symphyseal region, and *Barcinosuchus gradilis* Leardi and Pol (2009) is too fragmentary for comparisons.

4.1. Mandible

The holotype specimen (MAU-Pv-CO-583) of *Kinesuchus overoi* gen. et sp. nov., includes a partial mandible with the two rami firmly articulated (Figs. 2, 3). The lateral and ventral surfaces of the dentaries are ornamented with sets of pits of different sizes distributed regularly and separated by ridges, as in all known peirosaurids. Dentaries and splenials are articulated in the anterior end and incomplete in the posterior end. The mandibular symphysis of *Kinesuchus* gen. nov. is elongated, extending posteriorly to reach

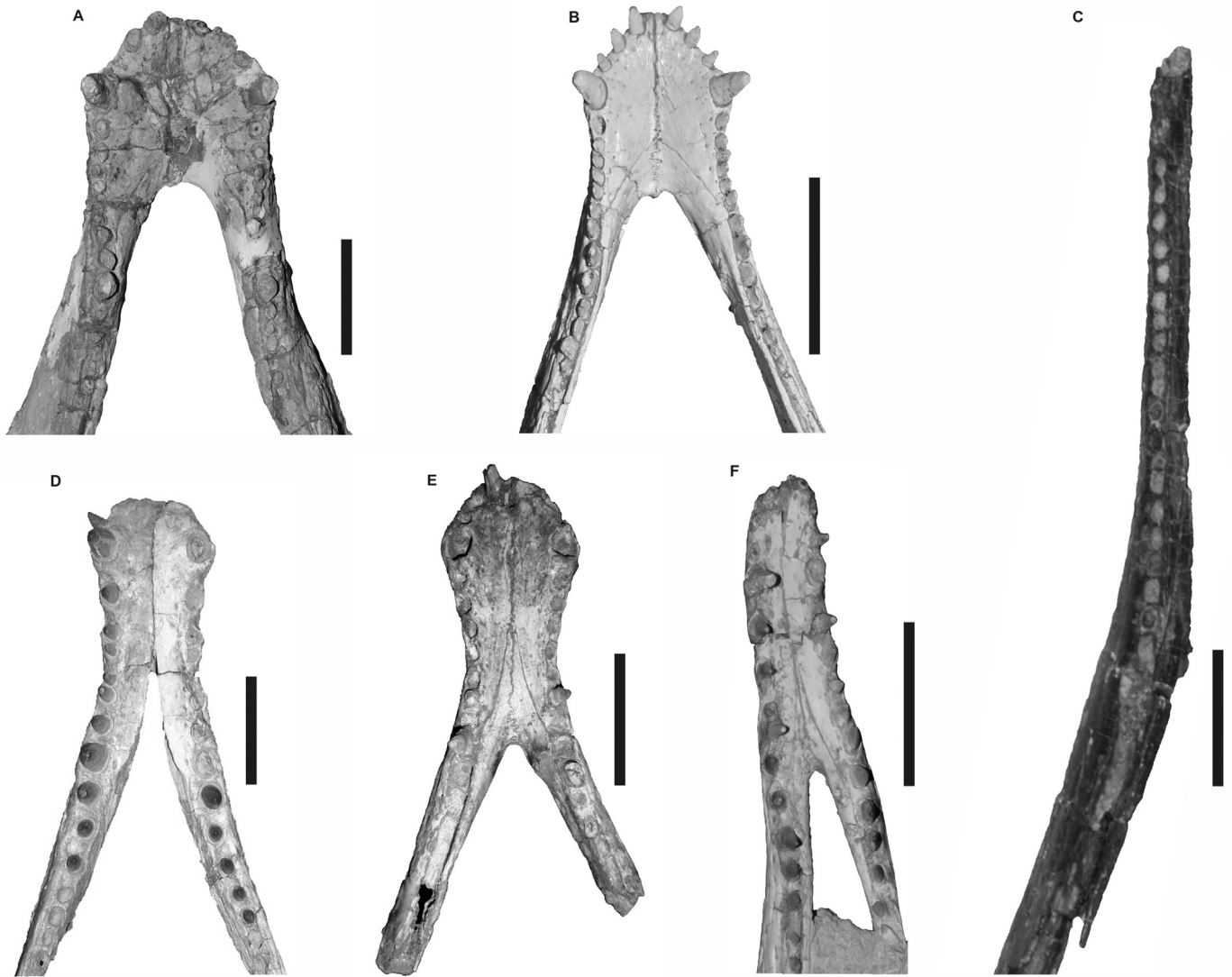


Fig. 4. Comparison of the anterior region of the mandibles of (A) *Gasparinisuchus peirosauroides*, MOZ-Pv 1750, (B) *Montealtosuchus arrudacamposi*, MPMA-16-0007-04, (C) *Stelokrosuchus lapparenti*, MNN GDF 602, (D) *Itasuchus jesunoi*, DGM 434-R, (E) *Kinesuchus overoi* gen. et. sp. nov., MAU-Pv-CO-583, and (F) *Pepesuchus deiseae*, MN 7005 – V. Scale bar: 5 cm.

the twelfth alveolus (Fig. 2B, 3B), unlike others peirosaurids (see Section 5). The dorsal surface of the symphyseal region in *Kinesuchus* gen. nov. is almost flat along its entire length with a slight posterior convexity to the fourth alveolus. A dorsally flat symphyseal region is present in *Hamadasuchus*, *Stelokrosuchus* and *Itasuchus* (e.g., Larsson and Sues, 2007). In dorsal view the lateral edges of the mandible of *Kinesuchus* gen. nov. are markedly concave, in others peirosaurids this lateral edges are slightly concave (absent in *Pepesuchus* and *Stelokrosuchus*). The long and spatulate mandibular morphology of *Kinesuchus* gen. nov., is similar to *Itasuchus* (Fig. 4). The isolated surangular of *Kinesuchus* gen. nov. is too fragmentary for thorough description.

4.1.1. Dentary

In lateral view (Fig. 3A, B), the dentary is dorsoventrally low along the entire preserved length, and contacts the splenial posteromedially. In dorsal view, the symphyseal region is anteroposteriorly long and expanded laterally in the anterior portion, giving it a spatulate shape, its maximum width located at the level of the fourth alveolus where an enlarged tooth was presumably

housed. On the dorsal surface, the dentary symphysis extends posteriorly to the seventh alveolus as in *Itasuchus*, but unlike *Pepesuchus* where it extends to space between the fifth and sixth alveoli. On the ventral surface, the dentary symphysis of *Kinesuchus* gen. nov. extends to the ninth alveolus. In dorsal view, the dentary of *Kinesuchus* gen. nov. gradually narrows and presents a constriction at the level of the eighth and ninth alveoli and diverge caudally.

There are eighteen alveoli distributed in two waves of enlargement as in *Gasparinisuchus*, *Montealtosuchus*, *Itasuchus*, and *Pepesuchus* (Price, 1955; Carvalho et al., 2007; Campos et al., 2011; Martinelli et al., 2012); *Stelokrosuchus* has a dentary with a very long symphyseal region, up to twenty-six alveoli, and lacks waves. In *Kinesuchus* gen. nov., the fourth alveolus is largest, presumably containing a caniniform anterior tooth, followed in size by the 12th and 13th alveoli as in *Hamadasuchus*, *Montealtosuchus*, and *Gasparinisuchus* (Carvalho et al., 2007; Larsson and Sues, 2007; Martinelli et al., 2012); in *Stelokrosuchus* the first alveolus is largest. In *Itasuchus* the 11th and 12th, and in *Pepesuchus* the 10th and 11th, are the largest postcaniniform alveoli (Price, 1955;

Campos et al., 2011). Between the fourth and fifth alveoli, *Kinesuchus* gen. nov. presents a small diastema as in *Bayomesasuchus*, but unlike in *Hamadasuchus*, *Stolokrosuchus*, *Gasparinisuchus*, *Patagosuchus* and *Montealtosuchus* that all lack diastema (Carvalho et al., 2007; Larsson and Sues, 2007; Martinelli et al., 2012; Barrios et al., 2015; Lío et al., 2016). *Pepesuchus* and *Itasuchus* possess two wide diastema between the fourth and sixth alveoli (Campos et al., 2011). In addition, *Itasuchus* possesses diastema between the seventh and eighth and ninth and tenth alveoli, while in *Pepesuchus* diastema are present between the fifth and sixth, and sixth and seventh alveoli.

Confluent alveoli in *Kinesuchus overoi* gen. et sp. nov. are located posterior to the tenth alveolus. In *Itasuchus*, confluent alveoli begin posterior to the eighth and ninth (fourth and fifth, sixth and seventh in original description), in *Bayomesasuchus* confluent alveoli are posterior to the fifth and sixth, in *Pepesuchus* confluent alveoli are posterior to the eighth and ninth and posterior to the 12th, in *Gasparinisuchus* and *Hamadasuchus* confluent alveoli are posterior to the sixth, in *Montealtosuchus* confluent alveoli are posterior to 11th, and in *Stolokrosuchus* confluent alveoli are 12th – 13th and 14th – 17th (Price, 1955; Campos et al., 2011; Larsson and Sues, 2007, figure 6D; Martinelli et al., 2012; Barrios et al., 2015); *Patagosuchus* lacks confluent alveoli (Lío et al., 2016; pers. obs.). On the other hand, in *Kinesuchus* gen. nov. the size of the fifth alveolus is less than half of the diameter of the fourth alveolus, in *Pepesuchus* the fourth and fifth alveoli are subequal in size, while in *Itasuchus* the fourth alveolus is twice the size of the fifth, in *Stolokrosuchus* the posterior alveoli to the first are subequal (pers. obs.). In *Kinesuchus* gen. nov., alveoli from the fifth to the 11th are subequal in size, oval and larger than the anterior alveoli (except the fourth alveolus). Posterior to the 11th the alveoli are oval in cross section, gradually reduced in size distally, and are confluent in an alveolar groove located between the dentary and splenial.

The alveolar edge of the dentary is slightly festooned in lateral view. The ventral surface of the dentary (Fig. 2C, D) is flat, with the anterior end slightly elevated along a gradual curve at an angle of approximated 20° (Fig. 3A, B). Medial and lateral to the alveolar edge, a row of small neurovascular foramina are present. Anteriorly, the articulated dentaries have a spatulate morphology as in *Itasuchus*; but unlike in *Pepesuchus* and *Stolokrosuchus* where the anterior dentary is elongated, lateromedially narrow with parallel lateral margins, and terminates at a blunt end. In lateral view, the mandible of *Kinesuchus overoi* gen. et sp. nov. is dorsoventrally compressed, the fourth alveolus and the first alveolus at the same dorsoventral level as in *Pepesuchus* and *Stolokrosuchus*, but differing from the condition in *Hamadasuchus*, *Gasparinisuchus*, and *Patagosuchus* where the fourth alveolus is dorsally elevated from the rest of the alveolar row.

4.1.2. Splenial

The splenial articulates with the ipsilateral splenial at its anterior end, forming part of the mandibular symphysis. In articulation, the splenials contact the dentaries anterolaterally along a V-shaped suture (Fig. 2). Dorsally, this suture is pointed with a thin end, is slightly concave laterally, and extends anteriorly to the level of the seventh alveolus. Ventrally, the dentary-splenial suture can also be described as V-shaped, but with a more blunt anterior end, straight sides along its entire anteroposterior length (as in *Hamadasuchus*, Larsson and Sues, 2007, figures 6C and D), and extends anteriorly to the level of the ninth alveolus. In dorsal view, the strongly pointed anterior end and slightly concave lateral margins of the splenial-dentary suture is shared with other long-snouted peirosaurids (e.g., *Hamadasuchus*, *Stolokrosuchus*, *Pepesuchus*, *Itasuchus*) but is unlike *Bayomesasuchus*, *Patagosuchus*, *Gasparinisuchus*, and

Montealtosuchus where the splenial-dentary suture do not terminate in a strong point and possess slightly convex lateral margins (Fig. 4).

Immediately posterior to the mandibular symphysis, both splenials present a conspicuous foramen intermandibularis oralis with an overall oval shape (Fig. 3C, D), a feature shared with others peirosaurids (*Hamadasuchus*, *Bayomesasuchus*, *Patagosuchus*, *Montealtosuchus*, and *Gasparinisuchus*), uruguaysuchids (*Araripesuchus*, *Uruguaysuchus*, *Anatosuchus*), *Simosuchus*, and baurusuchids (e.g., Pol and Apesteguía, 2005; Larsson and Sues, 2007; Sereno and Larsson, 2009; Kley et al., 2010; Montefeltro et al., 2011; Soto et al., 2011; Pol et al., 2014; Barrios et al., 2015) (see Section 5). This foramen intermandibularis oralis is presumably an exit for the mandibular branch of the trigeminal nerve (V₃) as in extant crocodylians (Iordansky, 1973). The splenial of *Kinesuchus overoi* gen. et sp. nov. extends caudolaterally and widens dorsoventrally reaching the 12th alveolus. From this level, the splenial forms the medial wall of the alveolar groove for last seven alveoli of mandible. Posterior to the symphyseal region, the splenial laminae have a slightly convex medial surface.

4.2. Dentition

Because the distal portion of the mandible is incomplete (Fig. 2A, B), we estimate that the dentary should have housed at least eighteen teeth, including incisiviforms, caniniforms and postcaniniforms. All preserved teeth are conical in overall shape. Only one partially preserved incisiviforms crown and two complete postcaniniforms are present. The first left incisiviform is medium-sized (6 mm of labiomesial diameter), recurved anterodorsally, without carinae. The alveoli for the second and third incisiviforms are circular and subequal in size, remarkably smaller than the first alveolus. The fourth alveolus is the largest of the alveolar row (approximately 11 mm of diameter) and circular in shape. The interalveolar space between first and fourth alveoli is regular and narrow. Posterior to the fourth alveolus, the interalveolar space is greater and equidistant.

The tenth position of right dentary preserves the complete crown. This tooth is subtriangular with a concave lingual surface and a convex labial surface. The tooth projects laterally and curves slightly labiolingually. The 12th and 13th alveoli are the largest of the postcaniniform series, the former slightly smaller than the latter (7.92 mm versus 10.0 mm of diameter). The only other complete crown is located at the 12th position of the left dentary. This tooth is twice the size, more triangular, and less curved than the tenth tooth. These teeth have the same inclination angle (75°) with respect to the alveolar row. The preserved crowns have denticulated carinae but their preservation does not reveal the particular denticles to permit an accurate count of their density.

5. Discussion

The general morphology of the mandible of *Kinesuchus overoi* gen. et sp. nov. corresponds to mesoeucrocodylians with a relatively long snout. Among long-snouted forms, a splenial symphysis is present in neosuchians (e.g., *Thalattosuchia*, *Pholidosauridae*, *Dyrosauridae*, crocodylians *Gavialoidea* and *Crocodyloidea*) (e.g., Brochu, 2003; Jouve et al., 2006; Young et al., 2010; Martin et al., 2013; Walmsley et al., 2013). Within *Notosuchia* (sensu Sereno et al., 2001), a splenial symphysis is present in both long and short-snouted taxa (e.g., sphagesaurids and relatives, uruguaysuchids, baurusuchids, peirosaurids, and sebecids (e.g., Price, 1945, 1955, 1959; Gasparini, 1971; Larsson and Gado, 2000; Carvalho et al., 2005, 2007, 2011; Zaher et al., 2006; Larsson and Sues,

2007; Pol and Powell, 2011; Iori et al., 2013; Pol et al., 2014; Barrios et al., 2015; Lío et al., 2016).

Among peirosaurids known to date, morphological similarities are present between *Kinesuchus overoi* gen. et sp. nov. and *Hamadasuchus rebouli*, *Pepesuchus deiseae*, and primarily with *Itasuchus jesuinoi*. Some of the similarities noted are the slender and elongate symphyseal region in lateral and dorsal view, the flat dorsal surface of the mandible, foramen intermandibularis oralis adjacent to the mandibular symphysis, and the dorsal anterior projection of the splenial. In *Stolokrosuchus lapparenti* a similar morphology of the symphyseal region is observed but with anteroposteriorly very elongated anterior portion and straight lateral margins (Fig. 4D). *Kinesuchus* gen. nov. differs from the peirosaurids *Gasparinisuchus peirosauroides*, *Patagosuchus anielensis*, *Bayomesasuchus hernandezi*, *Montealtosuchus arrudacamposi*, and *Uberabasuchus terrificus*, which present robust mandibular symphyseal regions with concave dorsal surfaces and slightly laterally convex dentary-splenial sutures (Fig. 4). The dentary of *Kinesuchus overoi* gen. et sp. nov. is remarkably more spatulated than in any other known peirosaurid, with a marked lateral expansion at the level of the fourth alveolus and a marked lateral constriction at the level of the eighth and ninth alveoli. The only synapomorphy of Peirosauridae recognized in the new species is the presence of ziphodont and pseudoheterodont dentition (character 120.0, Barrios et al., 2015). The possible autapomorphies of *Kinesuchus overoi* gen. et sp. nov. are discussed below.

5.1. Mandibular symphysis extension

The mandibular symphyseal region of *Kinesuchus overoi* gen. et sp. nov. is anteroposteriorly elongated and spatulate shaped as in *Itasuchus*. In *Kinesuchus* this region extends posteriorly to the level of the 12th alveolus, in *Itasuchus* it is not possible to determine the posterior extension of the mandibular symphysis because the splenial is not preserved and the first alveoli are missing (Price, 1955). In others peirosaurids (Fig. 4), the symphyseal extension is variable: to the 11th alveolus in *Hamadasuchus*, to the 10th alveolus in *Montealtosuchus* and *Bayomesasuchus*, to the 9th–10th alveolus level in *Pepesuchus* and *Patagosuchus*, while in *Gasparinisuchus* it does not extend beyond the 8th alveolus (Carvalho et al., 2007; Larsson and Sues, 2007; Campos et al., 2011; Martinelli et al., 2012; Barrios et al., 2015; Lío et al., 2016). Considering this variation within Peirosauridae, we propose the posterior extent of the symphysis to the 12th alveolus as an autapomorphy for *Kinesuchus* gen. nov.

5.2. Foramen intermandibularis oralis

The foramen intermandibularis oralis in extant crocodylians is an opening for the anterior exit of the mandibular branch of the trigeminal nerve (V_3) (Iordansky, 1973). In these mesoeucrocodylians, as well as in derived notosuchians, the foramen is centrally positioned in the splenial lamina (e.g., Pol et al., 2014). Basal notosuchians (e.g., *Simosuchus*, uruguaysuchids, peirosaurids, baurusuchids) have an anteriorly positioned foramen intermandibularis oralis adjacent to the mandibular symphysis (e.g., Pol and Apesteguía, 2005; Larsson and Sues, 2007; Sereno and Larsson, 2009; Kley et al., 2010; Montefeltro et al., 2011; Soto et al., 2011; Pol et al., 2014; Barrios et al., 2015). *Kinesuchus* gen. nov. presents a foramen intermandibularis oralis very close to the mandibular symphysis, with the medial margin of the opening located on the splenial-splenial contact, a feature not observed in any another peirosaurid (e.g., *Hamadasuchus*, *Montealtosuchus*, *Patagosuchus*, *Bayomesasuchus*).

5.3. Mandibular lateral constriction

In dorsal view (Fig. 4), the long-snouted peirosaurids *Stolokrosuchus* and *Pepesuchus* lack mandibular lateral constriction while than broad-snouted and oreinirostral peirosaurids (e.g., *Gasparinisuchus*, *Montealtosuchus*, *Hamadasuchus*) present a slight lateral constriction posterior to the caniniforme tooth (4th). The mandible of the long-snouted peirosaurid *Itasuchus* has a slightly marked lateral constriction at level the eighth tooth. A marked lateral constriction at level the eighth and ninth alveoli is present in the mandible of *Kinesuchus* gen. nov. This condition determines a spatulated morphology of the anterior region of the mandible in the new species.

6. Biostratigraphic implications

The vertebrate fossil record of the Bajo de la Carpa Formation in the Neuquen Basin of Argentina is very diverse, and crocodyliforms are particularly abundant (Woodward, 1896; Dolgopod de Saez, 1928; Bonaparte, 1991; Pol and Gasparini, 2007; Fiorelli, 2010; Garrido, 2010; Martinelli et al., 2012). This abundance is concentrated north of Neuquén city, Argentina (e.g., Bonaparte, 1991; Garrido, 2010). In contrast, the northern region of the basin, near the Rincon de los Sauces city, contains a scarce record of crocodyliforms (Turner and Calvo, 2005; Arcucci et al., 2011; Filippi et al., 2013; Filippi et al., 2015). From record, only isolated teeth recovered from levels of the Bajo de la Carpa Formation were attributed to Peirosauridae indet (Filippi et al., 2015). The sebecosuchian *Pehuechesuchus enderi* Turner and Calvo, 2005, originally assigned to the Río Neuquén Group (Late Turonian - Coniacian), has since been revised to occurring in the Anacleto Formation (Lower to Middle Campanian, Garrido, 2010).

In this context, the record of the peirosaurid *Kinesuchus overoi* gen. et sp. nov., as the first crocodyliform from the Cerro Overo locality, near of the Rincon de los Sauces city, confirms the presence of Peirosauridae from significant remains. The exceptional preservation of the sauropod titanosaurid *Overosaurus paradasorum* (Coria et al., 2013) in this locality indicates the possibility of finding more complete specimens of other vertebrates, as well as additional material of crocodyliforms. The systematic fieldwork currently being carried out in this area and in the neighboring locality of La Invernada, are beginning to provide specimens corresponding to different groups of vertebrates (Cruzado-Caballero et al., 2016a, b) which will likely enable a better understanding of the paleoecology of the Santonian of the region.

7. Conclusions

Kinesuchus overoi is a new peirosaurid from the Upper Cretaceous of Patagonia and represents the first crocodyliform recorded from the Cerro Overo locality, Neuquén Province. This record increases the crocodyliform richness of the Bajo de la Carpa Formation (Santonian), a particularly diverse assemblage among known Gondwanan localities. The new taxon shares characteristics with other long-snouted peirosaurids including *Hamadasuchus*, *Pepesuchus*, and *Itasuchus*, including a dorsoventrally low and elongated symphyseal region and an anteriorly pointed dentary-splenial suture with slight lateral concavity. A spatulate shaped anterior mandibular region is shared between *Kinesuchus* and *Itasuchus*. However, three potential autapomorphies of *Kinesuchus overoi*, the mandibular symphysis extending posteriorly to the 12th alveolus, mandible with marked lateral constriction at level the eighth and ninth alveoli, and the presence of the medial margin of the foramen intermandibularis oralis on the symphysis, distinguish the new species from other peirosaurids. Additional, more complete

specimens will permit more thorough testing of the phylogenetic relationships of *Kinesuchus overoi*.

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References

- Arcucci, A.B., Filippi, L.S., Calvo, J.O., 2011. Un Nuevo Mesoeucrocodylia cretácico del Norte de la Cuenca Neuquina, Argentina. *Revista Brasileira de Paleontologia* 14, 51–60. <https://doi.org/10.4072/rbp.2011.1.05>.
- Barrios, F., Paulina Carabajal, A., Bona, P., 2015. A new peirosaurid (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Patagonia, Argentina. *Ameghiniana* 53, 14–25.
- Bonaparte, J.F., 1991. Los vertebrados fósiles de la Formación Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico superior, Argentina. Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Revista (Sección Paleontología) 4, 15–123.
- Brochu, C.A., 2003. Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Sciences* 31, 357–397.
- Buffetaut, E., 1974. Trematochampsa taqueti, un crocodylien nouveau du Sónonian inférieur du Niger. *Comptes Rendus de l'Académie des Sciences (Paris)* 279 (D), 1749–1752.
- Buffetaut, E., 1994. A new crocodylian from the Cretaceous of southern Morocco. *Comptes Rendus de l'Académie des Sciences* 319, 1563–1568.
- Campos, D.A., Oliveira, G.R., Figueiredo, R.G., Riff, D., Azevedo, S.A.K., Carvalho, L.B., Kellner, A.W.A., 2011. On a new peirosaurid crocodyliform from the Upper Cretaceous, Bauru Group, southeastern Brazil. *Anais da Academia Brasileira de Ciências* 83, 317–327.
- Candeiro, C.R., y Martinelli, A.G., 2006. Paleogeographical and chronostratigraphical distribution of mesoeucrocodylian species from the Upper Cretaceous beds from Bauru (Brazil) and Neuquén (Argentina) groups, southern South America. *Journal of South America Earth Sciences* 22, 116–129.
- Carvalho, I.S., Ribeiro, L.C., Ávila, L., 2004. *Uberabasuchus terrificus* sp. nov. a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous) Brazil. *Gondwana Research* 7, 975–1002.
- Carvalho, I.S., Campos, A.C.A., Nobre, P.H., 2005. Baurusuchus salgadoensis, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research* 8, 11–30.
- Carvalho, I.S., Vasconcellos, F.M., Tavares, S.A.S., 2007. *Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. *Zootaxa* 1607, 35–46.
- Carvalho, I.S., Teixeira, V.P.A., Ferraz, M.L.F., Ribeiro, L.C.B., Martinelli, A.G., Neto, F.M., Sertich, J.J.W., Cunha, G.C., Cunha, I.C., Ferraz, P.F., 2011. *Campinasuchus dinizi* gen. et sp. nov., a new Late Cretaceous baurusuchid (Crocodyliformes) from the Bauru Basin, Brazil. *Zootaxa* 2871, 19–42.
- Coria, R.A., Filippi, L.S., Chiappe, L.M., García, R., Arcucci, A.B., 2013. *Overosaurus paradasorum* gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Zootaxa* 3683 (4), 357–376.
- Cruzado-Caballero, P., Filippi, L.S., Méndez, A.H., Díaz-Martínez, I., 2016a. Primeros restos de Ornitópodos en la Formación Bajo de la Carpa en Rincón de los Sauces (Cretácico Superior). Buenos Aires. *Ameghiniana* 53 (6). Suplemento Resúmenes, pp. 13.
- Cruzado-Caballero, P., Méndez, A.H., Filippi, L.S., Juárez Valieri, R.D., Garrido, A.C., 2016b. Paleobiodiversity of the Bajo de la Carpa Formation (Santonian, Upper Cretaceous) in the Cerro Overo-La Invernada area, northern Patagonia, Argentina. VII Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno. Sala de los Infantes, Burgos, España, pp. 53.
- De Saz, M.D., 1928. Un nuevo goniofolido Argentino. *Anales de la Sociedad Científica Argentina*, Buenos Aires 105, 287–290.
- Filippi, L.S., Cerda, I., y Garrido, A.C., 2013. Morfología e histología de osteodermos de un peirosauridae de la Cuenca Neuquina. *Ameghiniana* 50 (1), 3–13.
- Filippi, L.S., Martinelli, A.G., Garrido, A.C., 2015. Una nueva asociación de dientes de vertebrados para la Formación Bajo de la Carpa (Santonense, Cretácico Superior) en Rincón de los Sauces, Neuquén, Argentina. *Spanish Journal of Palaeontology* 30, 223–238.
- Fiorelli, L.E., 2010. Predation bite-marks on a peirosaurid crocodyliform from the Upper Cretaceous of Neuquén Province, Argentina. *Ameghiniana*. 47 (3), 387–400.
- Garrido, A.C., 2010. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): nueva propuesta de ordenamiento litoestratigráfico. *Revista del Museo Argentino de Ciencias Naturales* 12, 121–177.
- Gasparini, Z.B., 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo Infraorden de los Mesosuchia (Crocodylia). *Ameghiniana* 8, 83–103.
- Gasparini, Z.B., 1982. Una nueva familia de cocodrilos zifodontes cretácicos de América del Sur. Vth Congreso Latinoamericano de Geología (Buenos Aires), Actas 4, pp. 317–329.
- Gasparini, Z., 1996. Biogeographic evolution of the South American crocodylians. In: Arratia, G. (Ed.), *Contributions of Southern South America to Vertebrate Paleontology*. München Geowissenschaftliche Abhandlungen A 30, pp. 159–184.
- Gasparini, Z.B., Chiappe, L., Fernández, M., 1991. A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodylians. *Journal of Vertebrate Paleontology* 11, 316–333.
- Hay, O.P., 1930. Second Bibliography and Catalogue of the Fossil Vertebrata of North America, vol. 2. Carnegie Institution of Washington, Washington DC 2, 1094 p.
- Iordansky, N.N., 1973. The skull of the Crocodylia. In: Gans, C., Parsons, T.S. (Eds.), *Biology of the Reptilia*, Volume 4: Morphology D. Academic Press, London, pp. 201–262.
- Iori, F.V., Marinho, T.S., Carvalho, I.S., Arruda Campos, A.C., 2013. Taxonomic reappraisal of the sphagesaurid crocodyliform *Sphagesaurus montealtensis* from the Late Cretaceous Adamantina Formation of Sao Paulo State, Brazil. *Zootaxa* 3686, 183–200.
- Jouve, S., Iarochène, M., Bouya, B., Amaghaz, M., 2006. A new species of *Dyrosaurus* (Crocodylomorpha, Dyrosauridae) from the early Eocene of Morocco: phylogenetic implications. *Zoological Journal of the Linnean Society* 148, 603–656.
- Kley, N.J., Sertich, J.J.W., Turner, A.H., Krause, D.W., O'Connor, P.M., Georgi, J.A., 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* Memoir 10, 13–98.
- Larsson, H.C.E., Gado, B., 2000. A new Early Cretaceous crocodyliform from Niger. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 217, 131–141.
- Larsson, H.C.E., Sues, H.D., 2007. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society* 149, 533–567.
- Leanza, H.A., Apesteguía, S., Novas, F.E., de la Fuente, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research* 25, 61–87.
- Leardi, J.M., Pol, D., 2009. The first crocodyliform from the Chubut Group (Chubut Province, Argentina) and its phylogenetic position within basal Mesoeucrocodylia. *Cretaceous Research* 30, 1376–1386.
- Leardi, J.M., Fiorelli, L.E., Gasparini, Z., 2015. Redescription and reevaluation of the taxonomical status of *Microsuchus schilleri* (Crocodyliformes: Mesoeucrocodylia) from the Upper Cretaceous of Neuquén, Argentina. *Cretaceous Research* 52, 153–166.
- Lío, G., Juárez Valieri, R., Filippi, L.S., Agnolín, F.L., Rosales, D., 2016. Peirosaurid (Crocodyliformes) remains from the Portezuelo Formation (Turonian-Coniacian) at Anelo locality, Neuquén. *Historical Biology* 28 (6), 835–841.
- Martin, J.E., Lauprasert, K., Buffetaut, E., Liard, R., Suteethorn, V., 2013. A large pholidosaurid in the Phu Krading Formation of North-Eastern Thailand. *Palaeontology* 1–13. <https://doi.org/10.1111/pala.12086>.
- Martinelli, A.G., Pais, D.F., 2008. A new baurusuchid crocodyliform (Archosauria) from the Late Cretaceous of Patagonia (Argentina). *Comptes Rendus Palevol* 7, 371–381.
- Martinelli, A., Sertich, J., Garrido, A.C., Praderio, A.M., 2012. A new peirosaurid from the Upper Cretaceous of Argentina: Implications for specimens referred to *Peirosaurus torminni* Price (Crocodyliformes: Peirosauridae). *Cretaceous Research* 37, 191–200.
- Montefeltro, F.C., Larsson, H.C.E., Langer, M.C., 2011. A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the Late Cretaceous of Brazil and the phylogeny of Baurusuchidae. *PLoS One* 6, 1–26.
- Ortega, F.J., Arcucci, A.B., Coria, R.A., Currie, P., 2012. A new and completed specimen of peirosaurid (Archosauria, Mesoeucrocodylia) from the Neuquén Basin, Argentina. *Ameghiniana* 49, R33.
- Pol, D., Apesteguía, S., 2005. New *Araripesuchus* remains from the Early Late Cretaceous (Cenomanian-Turonian) of Patagonia. *American Museum Novitates* 3490, 1–38.
- Pol, D., y Gasparini, Z.B., 2007. Crocodyliformes. In: Gasparini, Z.B., Salgado, L., Coria, y R.A. (Eds.), *Patagonian Mesozoic Reptiles*. Indiana University Press, Bloomington, pp. 116–142.
- Pol, D., Powell, J.E., 2011. A new sebecid mesoeucrocodylian from the Rio Loro Formation (Palaeocene) of north-western Argentina. *Zoological Journal of the Linnean Society* 163, S7–S36.
- Pol, D., Nascimento, P.M., Carvalho, A.B., Riccomini, C., Pires-Domingues, R.A., Zaher, H., 2014. A new Notosuchian from the Late Cretaceous of Brazil and the Phylogeny of Advanced Notosuchians. *PLoS One* 9 (4), e93105. <https://doi.org/10.1371/journal.pone.0093105>.
- Price, L.L., 1945. A new reptile from the Cretaceous of Brazil. *Notas Preliminares e Estudos, Serviço Geologia Mineralogia do Brasil* 25, 1–8.
- Price, L.L., 1955. Novos crocodylídeos dos Arenitos da Serie Bauru, Cretáceo do Estado de Minas Gerais. *Anais Academia Brasileira de Ciências* 27, 487–498.
- Price, L.L., 1959. Sobre um crocodylídeo notossuquio do Cretáceo Brasileiro. *Boletim Divisão de Geologia e Mineralogia Rio de Janeiro* 118 1–55.
- Salgado, L., Canudo, J.L., Garrido, A.C., Ruiz-Omeñaca, J.L., García, R.A., de la Fuente, M., Barco, J.L., Bollati, R., 2009. Upper Cretaceous vertebrates from El

- Anfiteatro área, Río Negro, Patagonia, Argentina. *Cretaceous Research* 30, 767–784. <https://doi.org/10.1016/j.cretres.2009.01.001>.
- Sereno, P.C., Larsson, H.C.E., 2009. Cretaceous crocodyliforms from the Sahara. *Zookeys* 28, 1–143.
- Sertich, J.J.W., O'Connor, P.M., 2014. A new crocodyliform from the middle Cretaceous Galula Formation, southwestern Tanzania. *Journal of Vertebrate Paleontology* 34, 576–596.
- Sereno, P.C., Larsson, H.C.E., Sidor, C.A., Gado, B., 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science* 294, 1516–1519.
- Soto, M., Pol, D., Perea, D., 2011. A new specimen of *Uruguaysuchus aznarezi* (Crocodyliformes: Notosuchia) from the middle Cretaceous of Uruguay and its phylogenetic relationships. *Zoological Journal of the Linnean Society* 163, S173–S198.
- Turner, A.H., Calvo, J.O., 2005. A new sebecosuchian crocodyliform from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 25, 887–898.
- Walker, A.D., 1970. A revision of the Jurassic *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. *Philosophical Transactions of the Royal Society of London, B* 257, 323–372.
- Walmsley, C.W., Smits, P.D., Quayle, M.R., McCurry, M.R., Richards, H.S., Oldfield, C.C., Wroe, S., Clausen, P., McHenry, C.R., 2013. Why the long face? The mechanics of mandibular symphysis proportions in crocodiles. *PLoS One* 8, e53873. <https://doi.org/10.1371/journal.pone.0053873>.
- Whetstone, K.N., Whybrow, P.J., 1983. A “cursorial” crocodylian from the Triassic of Lesotho (Basutoland), southern Africa. *Occasional Papers of the Museum of Natural History, University of Kansas* 106, pp. 1–37.
- Woodward, A.S., 1896. On two Mesozoic crocodylians *Notosuchus* nov. gen. and *Cynodontosuchus* nov. gen. from the red sandstones of the Territory of Neuquén (Argentina). *Anales del Museo de la Plata, Paleontología* 4, 1–20.
- Young, M.T., Brusatte, S.L., Ruta, M., Andrade, M.B., 2010. The evolution of Metriorhynchoidea (Mesoeucrocodylia, Thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. *Zoological Journal of the Linnean Society* 158, 801–859.
- Zaher, H., Pol, D., Carvalho, A.B., Riccomini, C., Campos, D., Nava, W., 2006. Redescription of the cranial morphology of *Marilyasuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). *American Museum Novitates* 3512, 1–40.