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New Patagonian baurusuchids (Crocodylomorpha; Notosuchia) from the Bajo de la Carpa Formation (Upper Cretaceous; Neuquén, Argentina): New evidences of the early sebecosuchian diversification in Gondwana

Nouveaux baurusuchidés de Patagonie (Crocodylomorpha, Notosuchia) de la formation de Bajo de la Carpa (Crétacé supérieur ; Neuquén, Argentine) : nouvelles preuves de la diversification sébécosuchienne précoce au Gondwana

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ABSTRACT

The Bajo de la Carpa Formation (Santonian) of the Neuquén basin (southwestern Argentina) has one of the most complete crocodyliform records of South America, together with the Adamantina and Marília formations of Brazil. In this contribution we report two fragmentary individuals from two different localities of the Bajo de la Carpa Formation: a middle-sized individual (MLP 26-IV-30-2), represented by postcranial remains from the Boca del Sapo locality and a large-bodied individual (MACN Pv-RN 1150), consisting only of snout elements from Paso Córdoba locality. Despite the remains of both specimens are fragmentary, they display anatomical characters of a specialized notosuchian carnivore clade: Baurusuchidae. Our phylogenetic analysis recovers these new individuals as non-baurusuchine baurusuchids, although they take multiple phylogenetic positions on the different most parsimonious trees. These new remains highlight the relevance of the Bajo de la Carpa Formation for understanding the rise of notosuchians during the Late Cretaceous.

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RÉSUMÉ

La formation de Bajo de la Carpa (Santonien) sur le bassin de Neuquén (Sud-Ouest de l'Argentine) possède l'un des enregistrements crocodyliformes les plus complets du continent, ainsi que la formation de Marília au Brésil. Dans cette contribution, nous rapportons

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deux individus fragmentaires de deux localités différentes de la formation de Bajo de la Carpa: un individu de taille moyenne (MLP 26-IV-30-2), représenté par des restes postcrâniens de la localité de Boca del Sapo et un individu de grande taille (MACN Pv-RN 1150), constitué uniquement d'éléments de museau de la localité de Paso Córdoba. Bien que les restes des deux spécimens soient rares, ils présentent tous deux des caractères anatomiques d'un clade carnivore notosuchien spécialisé : Baurusuchidae. Notre analyse phylogénétique conduit à considérer ces nouveaux individus comme des baurusuchiens non baurusuchinés, bien qu'ils prennent de multiples positions phylogénétiques sur les différents arbres les plus parcimonieux. Ces nouveaux vestiges soulignent la pertinence de la formation Bajo de la Carpa pour comprendre la montée de notosuchiens au cours du Crétacé et leur diversification postérieure.

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1. Introduction

The continental deposits of the Upper Cretaceous of the Neuquén Basin, grouped mostly in the Neuquén Group, form a remarkable and an almost continuous succession from the lower Cenomanian to the mid to late Campanian (Garrido, 2010). The outcrops of the Neuquén Group are noteworthy for their vertebrate fossils, which lead the recognition of several tetrapod assemblages by Leanza et al. (2004). One of the major components of these tetrapod assemblages is crocodyliforms, which are very abundant and diverse in many of the units of the Neuquén Group. This diversity is exclusively concentrated in a single clade: Notosuchia (Pol and Gasparini, 2007). Up to the date, thirteen different taxa are known from the Neuquén basin, being the Bajo de la Carpa Formation the unit with the highest diversity and abundance of notosuchians (eight taxa; Leardi et al., 2015a; Pol and Leardi, 2015). However, the Bajo de la Carpa Formation is not the only Upper Cretaceous lithostratigraphic unit in Gondwana with notosuchian hyperdiversity. The Adamantina Formation of the Bauru Group in Brazil bears an outstanding diversity of notosuchians totaling up to now 21 notosuchian species (e.g., Marinho and Carvalho, 2009; Montefeltro et al., 2011; Nobre and Carvalho, 2006; Pol et al., 2014). The diversity of the Adamantina Formation surpasses by far any other lithostratigraphical unit in Gondwana (Pol and Leardi, 2015). The crocodyliform assemblage of the Adamantina Formation is formed by a high diversity of sphagesaurids and close relatives (i.e. *Mariliasuchus*, *Morrinosuchus*, *Caipirasuchus steneognathus*; Iori and Carvalho, 2009; Pol et al., 2014; Zaher et al., 2006) and an equally remarkable record of baurusuchids (Carvalho et al., 2005; Godoy et al., 2014; Marinho et al., 2013; Montefeltro et al., 2011; Pol and Leardi, 2015).

Although there is a considerable difference in the amount of species known in each unit, both the Bajo de la Carpa Formation and the Adamantina Formation represent the two units with the highest amount of notosuchian taxa known for the whole Gondwana, constituting true “hotspots” of the group. The main difference in the crocodyliform assemblages of both units is given by the complete lack of sphagesaurids and the low abundance and diversity of baurusuchids in the Bajo de la Carpa Formation (Leardi et al., 2015a; Pol and Leardi, 2015). These differences in the faunal assemblages cannot be

paleoclimatically explained, as in general both units have been regarded as deposited under a warm semiarid climatic regime (Fernandes and Ribeiro, 2015; Garrido, 2010). Thus, other factors need to be considered to account for the differences in the assemblages such as biogeographical differences in the distribution of the notosuchian clades or specific differences between these two formations, including temporal differences, distinct specific environmental conditions and different taphonomical biases affecting the fossils of these two formations.

Baurusuchids are a highly derived group of large-bodied notosuchians with inferred predatory habits, due to the presence of several convergences with theropod dinosaurs (Riff and Kellner, 2011). Typical features of the members of the family include high and laterally compressed skull, high mandibular symphyses and blade-like compressed teeth (Gasparini, 1981). The dentition of the baurusuchids is reduced in number and restricted to the anterior half of both jaws and bear hypertrophied posterior premaxillary and anterior maxillary and mandibular teeth (Riff and Kellner, 2011). The baurusuchid record is very diverse in Brazil, where seven different taxa have been recognized (Campos et al., 2001; Carvalho et al., 2005; Carvalho et al., 2011; Marinho et al., 2013; Montefeltro et al., 2011; Nascimento and Zaher, 2011; Price, 1945). On the other hand, up to the date, two taxa have been assigned to Baurusuchidae from the Bajo de la Carpa of the Neuquén basin: *Cynodontosuchus rothi* Woodward, 1896 and *Wargosuchus australis* Martinelli and Pais, 2008.

In the present contribution we describe two new crocodyliform remains from the Bajo de La Carpa Formation with baurusuchid affinities. The first of them, MLP 26-IV-30-2, is a small sized crocodyliform represented exclusively by postcranial remains of the pectoral girdle and forelimb. The second specimen, MACN Pv-RN 1150, is a medium to large individual known solely by a partial snout. These new findings increase the already large crocodyliform specimens known from the Neuquén Basin and have anatomical traits that are relevant for understanding the baurusuchid diversification in southern Gondwana.

2. Materials and methods

MLP 26-IV-30-2 was collected in the early 20th century by Walter Schiller and Santiago Roth on the early

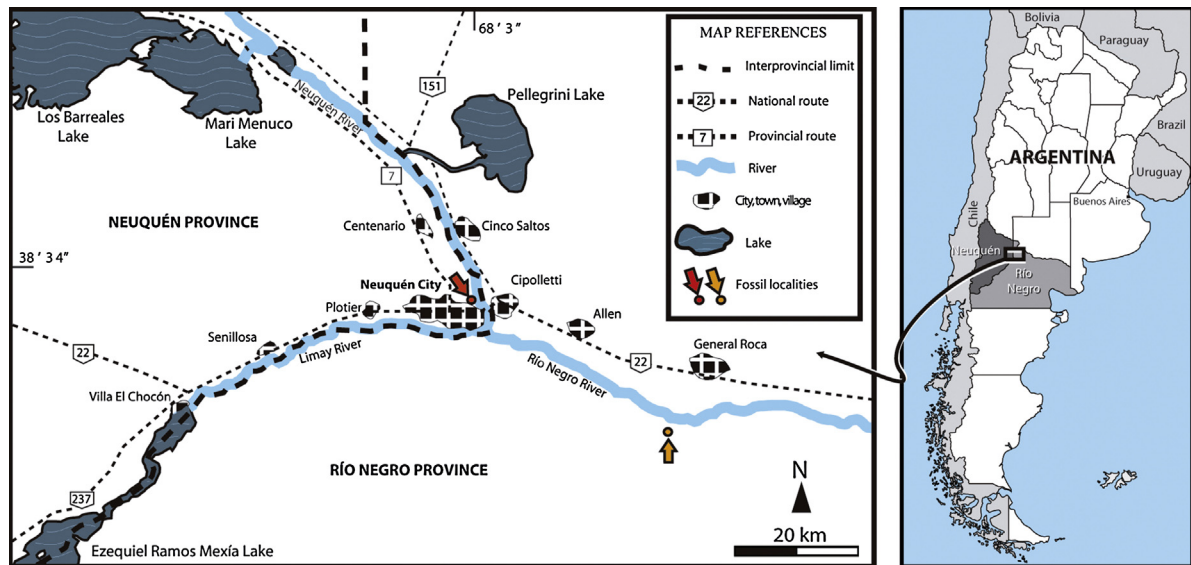


Fig. 1. Geographical map of the areas where the both crocodyliforms studied in this contribution were recovered. Red: MLP 26-IV-30-2; Orange: MACN Pv-RN 1150.

Fig. 1. Carte géographique des zones où les deux crocodyliformes étudiés dans cet article ont été collectés. Rouge : MLP 26-IV-30-2 ; orange : MACN Pv-RN 1150.

expeditions to the area north of Neuquén city (Neuquén Province), a locality known as “Boca del Sapo” (Leardi et al., 2015a; Pol and Gasparini, 2007) (Fig. 1). The jacket containing this specimen was found at the collections of the Museo de La Plata by one of the authors (ZG). On the other hand, MACN Pv-RN 1150 was found by an expedition organized by Jose F. Bonaparte (Museo Argentino de Ciencias Naturales) in the mid 1990s to the fossil locality known as Paso Córdoba, on the northern part of the Río Negro Province, south to the General Roca city. Both specimens are very fragmentary, but are treated separately and may represent different taxa, as MLP 26-IV-30-2 is a medium sebecosuchian while MACN Pv-RN 1150 represents a large-sized specimen. MACN Pv-RN 1150 was associated with remains of another crocodyliform that was found in the surroundings, which includes the posterior part of a maxilla and a left coracoid. However, careful examination of the specimen allowed us to identify traits that are present in “advanced notosuchians” (*sensu* Pol et al., 2014), such as oblique posterior teeth on the maxilla that are not placed in discrete alveoli. Thus, these remains were separated from MACN Pv-RN 1150 and likely represent a specimen of *Notosuchus terrestris* (MACN Pv-RN 1150B; (Supplementary Information)).

In the Description and Phylogenetic Analysis (see below) both specimens, MLP 26-IV-30-2 and MACN Pv-RN 1150, will be considered as two separate operational taxonomical units (OTUs). This course of action is a conservative one, as both specimens come from different localities and do not have any superposition between them. However, this claim is partially supported based on the different sizes of both specimens, MLP 26-IV-30-2 represents a medium-sized sebecosuchian, while MACN Pv-RN 1150 represents a large one (see Discussion for further details on this).

2.1. Postcranial osteological and muscular terminology

The appendicular postcranial remains of MLP 26-IV-30-2 and MACN Pv-RN 1150 were described following the osteological nomenclature proposed by Mook (1921) and Romer (1956). Although, in contrast to the semi-erect postures of extant crocodylians, basal crocodyliforms have been inferred to possess erect postures (Parrish, 1986, 1987; Pol, 2005). Furthermore, in recent contributions (Godoy et al., 2016; Riff and Kellner, 2011) a permanent parasagittal posture has been inferred, based on their postcranial anatomy, for two baurusuchids (*Stratiotosuchus* and *Pissarrachampsia*). In order to reflect that posture, we follow the limb bone orientation of Pol (2005), where they are oriented as if they were held in vertical position. The inference of forelimb appendicular myology was inferred following Meers (2003) and Jasinowski et al. (2006).

In order to contrast adequately the range of morphologies of the taxa studied in this contribution these are compared with a wide array of notosuchians. The source of information for each individual taxon is supplied separately in Table 1.

3. Description

3.1. Systematic paleontology

CROCODYLIFORMES Clark, 1986
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NOTOSUCHIA Gasparini, 1971 (*sensu* Sereno et al., 2001)
SEBECOSUCHIA Simpson, 1937 (*sensu* Gasparini, 1972)
BAURUSUCHIDAE Price, 1945 (*sensu* Montefeltro et al., 2011)
MLP 26-IV-30-2

Table 1

List of taxa used for comparisons in the text.

Tableau 1

Liste des taxons utilisés pour les comparaisons dans le texte.

Taxon	Source
<i>Aplestosuchus sordidus</i>	Godoy et al., 2014
<i>Araripesuchus gomesii</i>	AMNH 24450
<i>Araripesuchus tsangatsangana</i>	Turner, 2006
<i>Ayllusuchus fernandesi</i>	MLP 72-X-4-2; Gasparini, 1984
<i>Barinasuchus arveloi</i>	Palillo and Linares, 2007
<i>Baurusuchus albertoi</i>	MZSP-PV 140; Nascimento and Zaher, 2010; Nascimento and Zaher, 2011
<i>Baurusuchus pachecoi</i>	DGM 299-R
<i>Baurusuchus salgadoensis</i>	MPMA 62-0001-02; Carvalho et al., 2005
<i>Bergisuchus dietrichbergi</i>	HLMD-Me-7003; Kuhn, 1968; Rossmann et al., 2000
<i>Bretesuchus bonapartei</i>	PVL 4735; Gasparini et al., 1993
<i>Caiman latirostris</i>	MPEF-AC 205; MACN 30.522
<i>Caipirasuchus stenognathus</i>	MZSP-PV 139; Pol et al., 2014
<i>Campinasuchus dinizi</i>	CPP1234-1237; Carvalho et al., 2011; Cotts et al., 2017
<i>Chimaerasuchus paradoxus</i>	IVPP V 8274
<i>Comahuesuchus brachybuchalis</i>	MACN PV- RN 30, 31; Martinelli, 2003
<i>Cynodontosuchus rothi</i>	MLP 64-IV-16-25; Gasparini, 1972; Pol and Gasparini, 2007
<i>Gondwanasuchus scabrosus</i>	Marinho et al., 2013
<i>Iberosuchus macrodon</i>	Ortega, 2004
<i>Lorosuchus nodosus</i>	PVL 6219; Pol and Powell, 2011
<i>Lumbrera form</i>	PVL 6385
<i>Mahajanasuchus insignis</i>	UA 8654, 9737; FMNH PR 2448-2450; MAD 5347
<i>Marillasuchus amarali</i>	MZSP-PV 50; Zaher et al., 2006; Nobre and Carvalho, 2013
<i>Montealtosuchus</i>	Carvalho et al., 2007
<i>Notosuchus terrestris</i>	MACN PV-RN 1037; MACN PV-RN 1042; MACN PV-RN 1122; MACN PV-RN S/N; MUCPV 900; Pol, 2005; Fiorelli and Calvo, 2008
<i>Orthosuchus stormbergi</i>	SAM-PK 409
<i>Pissarrachampsia sera</i>	LRP-USP L0018, L0019; Montefeltro et al., 2011; Godoy et al., 2016
<i>Sebecus icaeorhinus</i>	AMNH 3159; MPEF-PV 1776; MPEF-PV 3971; MPEF-PV 3972; Pol et al., 2012
<i>Sebecus querejazus</i>	Buffetaut and Marshall, 1991
<i>Simosuchus clarki</i>	UA 8679; FMNH PR 2596; FMNH PR 2597; FMNH PR 2598; Georgi and Krause, 2010; Sertich and Groenke, 2010
<i>Stratiotosuchus maxhechti</i>	Riff, 2007; Riff and Kellner, 2011
<i>Uruguaysuchus aznarezi</i>	Soto et al., 2011
<i>Wargosuchus australis</i>	Martinelli and Pais, 2008

Referred specimen. MLP 26-IV-30-2, fragmentary postcranial materials belonging to the left pectoral girdle (proximal scapula and coracoid) (Fig. 2) and forelimb (proximal humerus, distal radius and ulna, complete radiale, ulnare and pisiform and partial manus).

Geographic occurrence. Outcrops located to the north of Neuquén city from the locality known as “Boca del Sapo”, now the campus (and surrounding areas) of the National University of Comahue, Neuquén Province, Argentina.

Stratigraphic occurrence. Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (middle to upper Santonian; Lanza et al., 2004).

Remarks: Although no new taxon is erected we highlight some of the more diagnostic traits present in MLP 26-IV-30-2 (autapomorphies marked as an asterisk, *): a teardrop-shaped pit dorsal to the glenoid facet of the scapula; coracoid without a pendant glenoid, which lacks a crest for insertion of the scapulocoracoidal ligament; medially exposed internal tuberosity of the humerus; a low deltopectoral crest; posterior oblique process of the ulna greatly projected laterally, forming a distinct posterior heel*; articular surface for the ulnare on the radiale not separated by a crest from the one for the ulna*; highly convex proximal ends of the metacarpals*.

Despite the relatively few materials recovered for this specimen, these elements have proved to be diagnostic of several notosuchian lineages (Leardi et al., 2015b; Pol et al., 2012), which allow inferring the phylogenetic affinities of this specimen (see below).

3.1.1. Pectoral girdle

Only the proximal parts of the scapula and the coracoid were recovered. Although these elements are very fragmentary and are heavily damaged, both elements were found articulated.

Scapula. The scapula only preserves partial remains of its proximal end, lacking any traces of the scapular blade and the acromion. The articular surface for the coracoid on the scapula is only preserved in its posteriormost part. This region bears a bulge, which has also been reported previously for most notosuchians (Leardi et al., 2015b). The proximal end is markedly concave in lateral view, a rare condition among notosuchians as in most taxa this region is almost flat (e.g., *Yacarerani*, *Notosuchus*, *Mahajanasuchus*, *Araripesuchus gomesii*). The glenoid facet on the scapula projected posterolaterally, unlike the condition of most notosuchians where it forms a dorsal “roof” of the glenoid facet of the coracoid (Leardi et al., 2015b). Dorsally to the glenoid a teardrop-shaped pit can be observed, limited both laterally and medially by two low crests. These can be interpreted as the scapular attachment of the Mm. triceps brachii (M. triceps longus lateralis; sensu Meers, 2003). The development of a crest dorsal to the glenoid is absent in most ziphosuchians (e.g., *Notosuchus*, *Yacarerani*, *Marillasuchus*) with the exception of *Simosuchus* and the baurusuchids *Baurusuchus albertoi* and *Campinasuchus* (Cotts et al., 2017, as no crest is mentioned in this region on the description). The proximal end of the scapula and the dorsal border of the glenoid are only

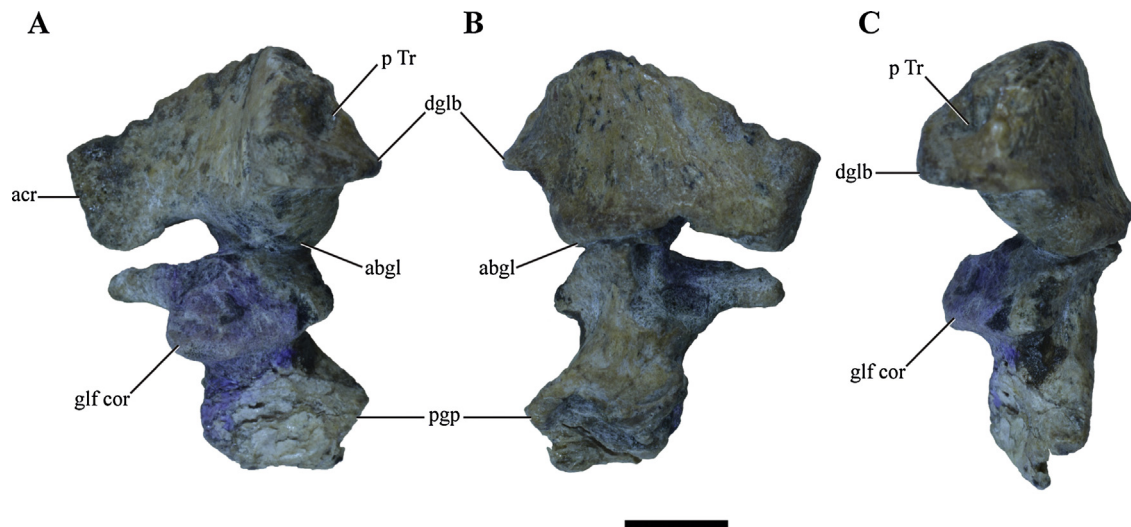


Fig. 2. Left pectoral girdle of MLP 26-IV-30-2 in: A. Lateral. B. Medial. C. Posterior views. abgl: anterior bulge of the glenoid; acr: acromial region; dglb: dorsal glenoid buttress; glf cor: glenoid facet of the coracoid; pgp: postglenoid process; p Tr: pit for the scapular attachment of the Mm. triceps brachii. The scale bar equals 1 cm.

Fig. 2. Gaine pectorale gauche de MLP 26-IV-30-2 en vues : A. Latérale. B. Médiale. C. Postérieure. abgl : renflement antérieur de la glène ; acr : région acromiale ; dglb : contrefort glénoïdien dorsal ; glf cor : facette glénoïde de la coracoïde ; pgp : processus postglénoïde ; p Tr : fosse pour la fixation scapulaire du Mm. triceps brachii. La barre d'échelle représente 1 cm.

known in *B. albertoi* and partially in *Campinasuchus* among baurusuchids, thus, if this reversion represents a synapomorphy of these ziphosuchians remains as a question to be addressed when more complete scapulae are reported for taxa of the group.

Coracoid. Only the posterior third of the proximal end and the proximal part of the postglenoid process of the coracoid are preserved. The most prominent feature is its glenoid facet, which is anteroposteriorly elongated as in the “advanced notosuchians” (*Notosuchus*, *Yacararani*, *Mariliassuchus*) and baurusuchids (*B. albertoi*, *Stratiotosuchus*) while this trait is absent in *Sebecus icaeorhinus* among derived ziphosuchians. The glenoid process of the coracoid is almost continuous with the postglenoid process, unlike the condition seen in baurusuchids (*B. albertoi*, *Stratiotosuchus*), *Simosuchus*, *A. tsangatsangana* and *A. gomesii* in which this process is projected ventrally forming a marked ventral recess to the glenoid. MLP 26-IV-30-2 lacks the presence of a ventral crest for the attachment of the scapulocoracoidal ligament ventral to the glenoid. This crest is variably present among baurusuchids (present in *B. albertoi* but absent in *Stratiotosuchus*), while is present in *Araripesuchus* (*A. gomesii* and *A. tsangatsangana*), *Simosuchus*, and *Yacararani*. Finally, only the proximal part of the postglenoid process is preserved in MLP 26-IV-30-2. This process is directed posteroventrally as in all crocodyliforms and is anteroposteriorly elongated.

3.1.2. Forelimb

As it was mentioned above, the elements of the forelimb were found partially articulated with the pectoral girdle. Although there are elements missing (e.g., large parts of the humerus and zeugopodium) there are no evidences to support that this does not belong to the same individual. In fact, the bones from the forelimb are in the same scale that

the ones of the pectoral girdle, have similar preservational features and are all from the left side of the animal.

Humerus. Only the proximal part of the humerus is preserved. The proximal end of the humerus is markedly expanded, having a much larger area when it is compared with the proximal part of the diaphysis. This proximal expansion is mostly due to the peculiar medial projection of the medial tuberosity that gives an asymmetrical shape to the proximal end of the humerus in anterior view. A similar condition is also observed in the “advanced notosuchians” (*Notosuchus*, *Mariliassuchus*, *Yacararani*), *Stratiotosuchus*, *Campinasuchus* (CPPLIP 1437; Cotts et al., 2016) and extant crocodylians (*Caiman latirostris*), but not in *Iberosuchus*, *S. icaeorhinus* or other more basal notosuchians (e.g. *Simosuchus*, *Mahajangasuchus*, *A. tsangatsangana*). The condition in other baurusuchids besides *Stratiotosuchus* and *Campinasuchus* is unknown, as the well-preserved humeri have been reported only in *B. albertoi* but the proximomedial region of those elements is damaged. The humeral head is elongated lateromedially as in most archosauriforms and bears a central boss that overhangs the posterior surface of the proximal end of the humerus. The humeral head is crescent shaped in proximal view, unlike most crocodyliforms where the main axis of the head is almost straight. Medially, the internal tuberosity is markedly projected and has the surface for the insertion of the M. subscapularis oriented medially as in sebecosuchian crocodyliforms (*S. icaeorhinus*, *B. albertoi*, *Stratiotosuchus*; Pol et al., 2012).

The anterior surface of the proximal end of the humerus is concave. Just ventrally to the articular surface of the humeral head it bears a shallow semicircular depression, which corresponds topographically with the insertion of the M. coracobrachialis brevis ventralis (Meers, 2003). The lateral third of the anterior surface of the proximal end of the humerus is divided by

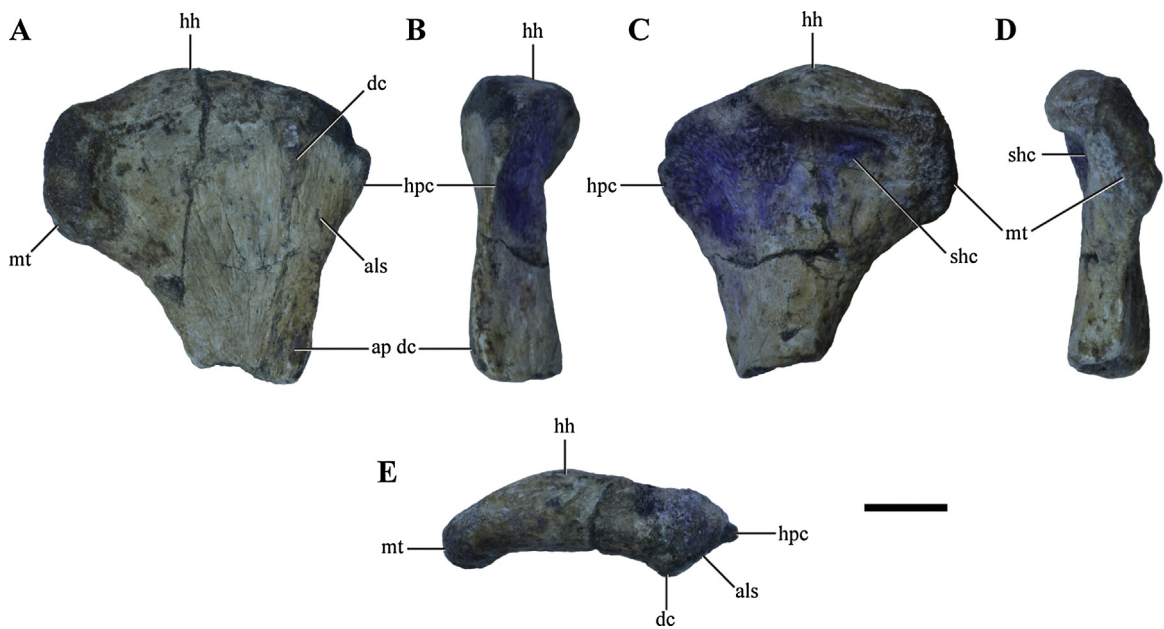


Fig. 3. Proximal end of the left humerus of MLP 26-IV-30-2 in: A. Anterior. B. Lateral. C. Posterior. D. Medial. E. Proximal views. als: anterolateral facing surface of the humerus; dc: deltopectoral crest; hh: humeral head; hpc: proximolateral crest of the humerus; mt: medial tuberosity; shc: depression for the M. scapulohumeralis caudalis. The scale bar equals 1 cm.

Fig. 3. Extrémité proximale de l'humérus gauche de MLP 26-IV-30-2 en vues : A. Antérieure. B. Latérale. C. Postérieure. D. Médiale. E. Proximale. als : face antéro-latérale de l'humérus ; dc : crête deltopectorale ; hh : tête humérale ; hpc : crête proximo-latérale de l'humérus ; mt : tubérosité médiale ; shc : dépression pour M. scapulohumeralis caudalis. La barre d'échelle représente 1 cm.

the deltopectoral crest. The deltopectoral crest originates proximally contacting the humeral head and slightly medially, leaving an anterolaterally-exposed surface between the crest and the lateral surface of the humerus. This anterolaterally-exposed surface has been reported in derived ziphosuchians such as advanced notosuchians (e.g., *Notosuchus*, *Mariliasuchus*) and sebecosuchians (*S. icaeorhinus*, *B. albertoi*, *Stratiosuchus*). Lateral to this surface, a sharp crest is present which is present in all taxa, which also have medially displaced deltopectoral crest. However, such a lateral crest is particularly sharp in MLP 26-IV-30-2. The deltopectoral crest has a straight path along the preserved part of the humerus. As in baurusuchids (*Stratiosuchus* and *B. albertoi*), *Simosuchus* and most advanced notosuchians (with the exception of *Yacarerani*), the deltopectoral crest is markedly low and does not form a distinct apex. Ventrally to the level of the ventral border of the medial tuberosity, the deltopectoral crest widens and forms a rugose anteriorly exposed platform (Fig. 3A). This arrangement resembles the wide deltopectoral crest of the baurusuchids *B. albertoi* and *Stratiosuchus* and is interpreted that way. However, unlike those taxa the deltopectoral crest has a very low anteroposterior development (Fig. 3A, B and E).

The posterior surface of the humerus of MLP 26-IV-30-2 bears very deep subcircular depression, just ventrally to the central bulge of the humeral head. This depression was recognized a notosuchian synapomorphy and is probably related with the insertion of the M. scapulohumeralis caudalis (Meers, 2003; Pol et al., 2012). Laterally to this depression a low and proximodistally oriented crest

divides the posterior surface of the humerus. The lateral part of the posterior surface of the humerus does not bear any particular pit for muscular insertion, such as the one for the common insertion for the Mm. teres major and latissimus dorsi. However, this should be handled with care as the preservation of MLP 26-IV-30-2 is far from optimal.

Ulna. The left ulna is preserved in two isolated fragments: one comprising the posterior part of the proximal end and the other preserving the distal third of the element Fig. 4A–C. The remains of the proximal end are very fragmentary as only the posterior third of this region is preserved. The posteromedial surface of the ulna is separated from the medial one by a very sharp crest that delimits a concave surface for the ulnar origin of the M. pronator quadratus (Meers, 2003) (Fig. 4A). Such a sharp posteromedial crest is also present in *Stratiosuchus* and *B. albertoi*, two taxa that have a pointed posterior process of the ulna. In contrast, most notosuchians lack a sharp posteromedial crest on the proximal end and have a rounded posterior process of the ulna (e.g., *Notosuchus*, *S. icaeorhinus*, *Yacarerani*, *Simosuchus*) (Fig. 4).

The preserved part of the diaphysis is subcylindrical in transverse section. Although the distal end of the ulna is not completely preserved, its general shape can be defined. MLP 26-IV-30-2 bears a well-developed anterior bulge and an anterior oblique process as in most notosuchians, with the exception of *Yacarerani*. The anterior oblique process is located relatively posteriorly on the medial surface, determining an articular surface for the radius that forms an angle of approximately 30°. This condition resembles the one present in *Notosuchus* and *S. icaeorhinus*, unlike the

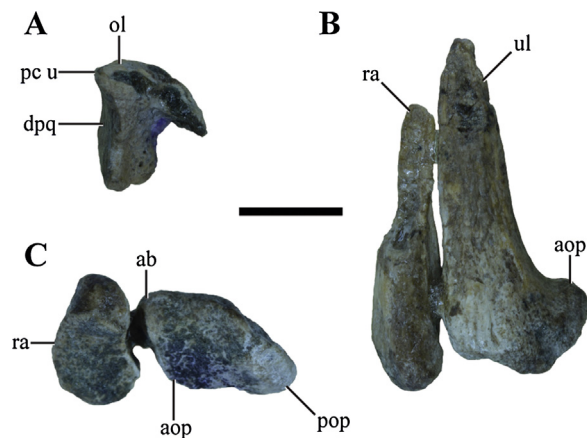


Fig. 4. MLP 26-IV-30-2 zeugopodium. A. Proximal end of the ulna in proximal view. Distal parts of the ulna and radius in: B. Anterior. C. Distal views. ab: anterior bulge; aop: anterior oblique process; dpq, depression for the origin of the M. pronator quadratus; ol: olecranon; pop: posterior oblique process; ra: radius; ul: ulna. The scale bar equals 1 cm.

Fig. 4. MLP 26-IV-30-2 zeugopodium. A. Extrémité proximale de l'ulna en vue proximale. Parties distales du cubitus et du radius en vues : B. Antérieure. C. Distale. ab : renflement antérieur ; aop : processus oblique antérieur ; dpq : dépression pour l'origine du M. pronator quadratus ; ol : olécrane ; pop : processus oblique postérieur ; ra : radius ; ul : ulna. La barre d'échelle représente 1 cm.

lesser degree of lateral exposition of the radial articular surface present in *Mahajangasuchus*, *Simosuchus*, *Yacarerani* and *Caiman*. The posterior oblique process is markedly projected posteriorly in MLP 23-IV-30-2 forming a distinct posterior heel in the distal end of the ulna which has an anteroposterior development of more than half of the distal end in lateral view. This condition is unique of MLP 26-IV-30-2, as in other crocodyliforms (e.g., *Pissarrachamps*, *Stratiotosuchus*, *B. albertoi*) the posterior oblique process is anteroposteriorly shorter and it is not curved posteriorly, thus, not forming a platform dorsally to the articular surface (Fig. 4B).

Radius. Only the distal end of the radius is preserved. The distal end of the radius is convex in anterior view and concave in posterior view, thus giving the distal end a crescent shape (Fig. 4B–C).

Radiale. The left radiale is complete and as in all crocodylomorphs, represents the largest of the proximal carpals (Fig. 5A–D). The radiale is asymmetrical in anterior view, as the proximal end is lateromedially wider than the distal end (Fig. 5A). In proximal view, the proximal end of the radiale is L-shaped due to the presence of a proximolateral process (Fig. 5C), which bears the articular surfaces for the ulna and the ulnare. The proximal articular surface is bow-shaped with its medial border tapering to an acute point. This surface is separated from ulnar articular facet by a proximally projected process. This proximal process is present in all notosuchians with the exception of *S. icaeorhinus*, but in MLP 26-IV-30-2 this process attains a notable height. The proximolateral surface has a large proximodistal development, as it occupies almost half of the posterior surface of the radiale. The articular surfaces for the ulna and ulnare on this process are markedly different and as in all crocodylomorphs, the articular surface is smaller than

the one for the ulna. The surface for the ulnare is located on the proximolateral process of the radiale, as in all notosuchians, but it is not separated from the one for the ulna by a marked crest (Fig. 5B). This is a very rare condition among notosuchians and either preservational or preparation causes cannot be ruled out completely. Medially to the proximolateral process a triangular depression is present, which corresponds topographically with origin of the M. flexor digiti quinti pars superficialis and profundus.

The anterior surface of the radiale bears a longitudinal crest, which attenuates rapidly at the proximal third of the radiale (Fig. 5A). Such crest is present in most ziphosuchians and variably present in *Mahajangasuchus* (Leardi et al., 2015b). The shaft of the radiale is mediolaterally narrow. The distal articular surface of the radiale is markedly concave.

Ulnare. The ulnare is preserved almost complete, only with the proximal and distal ends separated due to breakage along the shaft of the ulnare (Fig. 5E–F). Despite that there is not an exact match between both pieces there is not a considerable part of shaft missing. As in all crocodylomorph archosaurs, the ulnare is proximodistally shorter than the radiale and its distal end is wider than the proximal one. The proximal surface is triangular in proximal view. The posteromedial apex of the proximal surface is more projected than the rest of the proximal surface and it bears the articular surface for the radiale. The anterior surface of the radiale bears a triangular platform on the proximal end (Fig. 5E). This platform corresponds topologically with the origin of the pars ulnare of the M. extensor digiti IV pars superficialis (Meers, 2003) and has not been reported in other crocodylomorph to the date, thus, representing an autapomorphy of MLP 26-IV-30-2.

The distal end of the radiale is anteroposteriorly compressed, being much wider than long. The distal end is teardrop-shaped in distal view and bears a distomedial process that articulates with the radiale distally, as in most crocodylomorphs. This distomedial process is at the same level of the rest of the distal end, as most notosuchians (Fig. 5F), with the exception of *B. albertoi*, *Stratiotosuchus* and *Notosuchus* where it is distinctly more projected.

Pisiform. The left pisiform is complete (Fig. 5G–H). As in most crocodyliforms and unlike the condition present in *Simosuchus*, the pisiform is a small proximal carpal being approximately one third of the length of the radiale. The proximal surface is rounded and has the articular facet for the ulnare. The medial surface of the pisiform is flat and the lateral surface is convex. The distal end is expanded and has a longitudinal depression representing the insertion of the M. flexor carpi ulnaris (Meers, 2003).

Distal carpal. A single distal carpal is preserved in MLP 26-IV-30-2 (Fig. 6A, B and D). The distal carpal is compressed dorsoventrally and elongated lateromedially, giving it an ovoid shape in proximal or distal view. The proximal surface bears a deep pit and a flat surface, which is interpreted as the articular surface for the distal end of the ulnare (Fig. 6D). On the other hand, the distal surface is concave. The elongated shape of this carpal is consistent with its identification as the distal carpal 4 + 5. Among notosuchians, two ossified distal carpals have been reported in *Notosuchus*, *Chimaerasuchus*, *Stratiotosuchus*; while a single

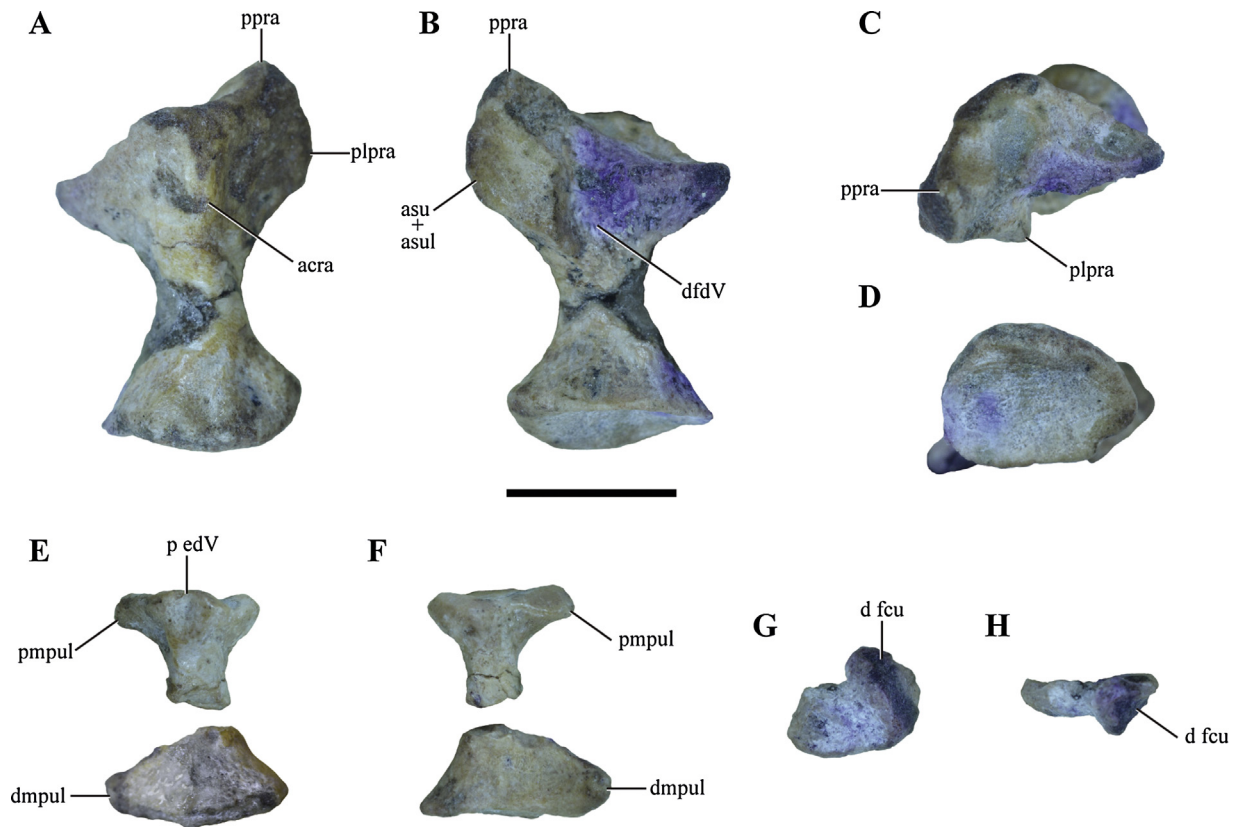


Fig. 5. MLP 26-IV-30-2 carpus. Left radiale in A. Anterior. B. Posterior. C. Proximal. D. distal views. Left ulnare in: E. Anterior; F. Posterior views. Left pisiform in G. Lateral. H. Dorsal views. acra: anterior crest of the radiale; asu + asul: articular surfaces of the ulna and ulnare; d fcu: depression for the insertion of the M. flexor carpi ulnaris; dmpul: distomedial process of the ulnare; p ed V: plate for the insertion of the extensor digitii V; pmpul: proximomedial process of the ulnare; ppra: proximal process of the radiale; plpra: proximolateral process of the radiale. The scale bar equals 1 cm.

Fig. 5. Carpe MLP 26-IV-30-2. Radiale gauche en vues : A. Antérieure. B. Postérieure. C. Proximale. D. Distale. Ulnare gauche en vues, E. Antérieure. F. Postérieure. Pisiforme gauche en vues. G. Latérale. H. Dorsale. acra : crête antérieure du radiale ; asu + asul : surfaces articulaires du cubitus et de l'unlaire ; d fcu : dépression pour l'insertion du M. flexor carpi ulnaris ; dmpul : processus distomédial de l'unlaire ; p ed V : plaque pour l'insertion de l'extenseur du doigt V ; pmpul : processus proximomédial de l'unlaire ; ppra : processus proximal de la radiale ; plpra : processus proximolateral de la radiale. La barre d'échelle représente 1 cm.

one has been reported in *Simosuchus*, *B. albertoi* and *Yacar-erani*. However, the when only a single distal carpal has been reported is not always the same element, as *Yacar-erani* has the distal carpal 2 + 3, while *B. albertoi* and *Simosuchus* have a distal carpal 4 + 5.

Manus. A partial left articulated manus was recovered in association with the proximal and distal carpals (Fig. 6A–D). This partial manus includes at least remains of the three inner digits (I–III), although the metacarpals (MCs) and some of the phalanges are broken through the shaft in several places. MC I is only represented by its proximal end, while MCs II and III are complete, but very badly preserved. MCs II and III were found in natural articulation, with their proximal ends abutted as in all crocodyliforms (Fig. 6A–B). As in *Orthosuchus* and more derived crocodyliforms, MC I is the stoutest and the rest become progressively more gracile laterally (Pol et al., 2012). The proximal ends of the MCs are very convex in proximal view and they taper to a rounded point in their palmar side. The lateral side of the MCs is flat. As in most archosaurs, MC III is the longest, with MC II being slightly shorter. The shafts are dorsoventrally flattened and the

distal ends of the metacarpals are moderately expanded, being narrower than the proximal ends of their respective MC. Digit II preserves the complete phalangeal count (3), including partial remains of the ungual phalanx and can be clearly identified as they are aligned with MC II (Fig. 6A). The phalanges of digit II are better preserved than the others (see below) and they lack deep collateral pits, but have well-developed flexor processes (Fig. 6C). The distal articular surfaces are quadrangular in distal view. The ungual phalanx is rounded and relatively wide in ventral view, unlike the highly lateromedially compressed unguals of *Yacar-erani*. Digit III preserves very fragmentary remains of the proximal two phalanges, while a large non-ungual phalanx is identified as the one of digit I.

3.2. Systematic paleontology

CROCODYLIFORMES Clark, 1986
MEOEUCROCODYLIA Whetstone and Whybrow, 1983
NOTOSUCHIA Gasparini, 1971 (sensu Sereno et al., 2001)
SEBECOSUCHIA Simpson, 1937 (sensu Gasparini, 1972)

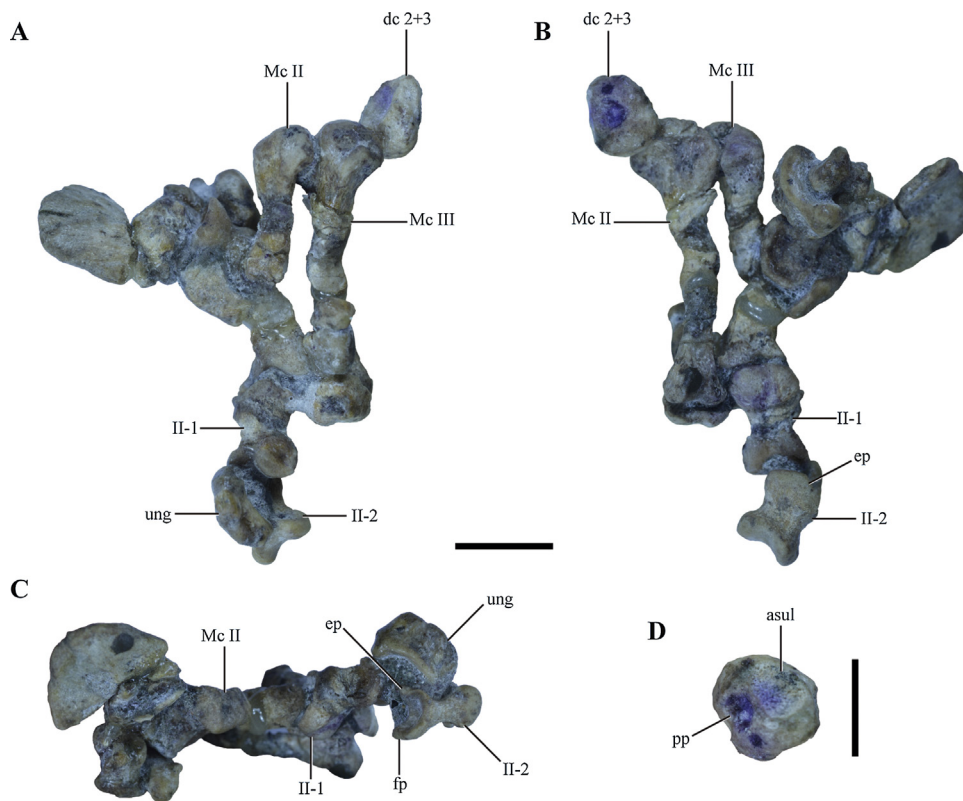


Fig. 6. Anterior autopodium of MLP 26-IV-30-2 in: A. Dorsal. B. Ventral. C. Medial views. D. Distal carpal 2 + 3 in proximal view. asul: articular surface for the ulnare; col: collateral ligament depressions; dc 2 + 3: distal carpal 2 + 3; ep: extensor process; fp: flexor process; Mc roman number: metacarpal roman number; pp: proximal pit of the distal carpal 4 + 5; ung: ungual phalanx; roman number-arabic number: digit-phalanx. The scale bar equals 1 cm.

Fig. 6. Autopodium antérieur de MLP 26-IV-30-2 en vues : A. Dorsale. B. Ventrale. C. Médiale. D. Carpe distal 2 + 3 en vue proximale. asul : surface articulaire pour l'ulnaire ; col : dépressions ligamentaires collatérales ; dc 2 + 3 : carpe distal 2 + 3 ; ep : processus d'extenseur ; fp : processus fléchisseur ; Mc : nombre romain : nombre romain métacarpien ; pp : fosse proximale du carpe distal 4 + 5 ; ung : phalange unguéale ; nombre romain-arabe : doigt-phalange. La barre d'échelle représente 1 cm.

BAURUSUCHIDAE Price, 1945 (sensu Montefeltro et al., 2011)

MACN Pv-RN 1150

Referred specimen. MACN Pv-RN 1150, fragmentary cranial remains, belonging to part of the snout (partial left premaxilla; facial laminae of both maxillae; partial lacrimal; partial frontal and palpebral?; fragmentary nasals) and anterior end of the mandibles (symphysis).

Geographic occurrence. Paso Córdoba locality, near the General Roca city area, Río Negro Province (Argentina).

Stratigraphic occurrence. Deposits of the Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (middle to upper Santonian; Leanza et al., 2004).

Remarks: Hypertrophied posterior premaxillary tooth; at least five (5) maxillary teeth; the second maxillary tooth is the largest of the maxilla; large foramina on the palatal lamina of the maxilla, near its suture with the premaxilla; shallow mandibular symphysis (unlike other baurusuchids which have a deep and narrow mandibular symphysis) (Fig. 6).

3.2.1. Skull

The skull remains of MACN Pv-RN 1150 are restricted to elements of its snout. Most of the elements are highly

damaged, with the maxillae being the better-preserved ones.

Premaxilla. Partial remains of both premaxillae are preserved however, despite being in articulation, the preservation is really bad and few anatomical details can be identified (Fig. 7A–C). The left premaxilla is better preserved, including parts of the facial and palatal laminae, while the right one is only represented only by the later. The left premaxilla preserves a single tooth, which lacks large part of the crown and has subcircular to oval root in section (Fig. 7B–C). The size of this tooth is larger than the first maxillary tooth and about the same size than the third, while it is smaller than the second maxillary tooth (see below). A hypertrophied posterior premaxillary tooth is widely present among ziphosuchians (e.g., *Notosuchus*, *Pakasuchus*, *Chimaerasuchus*, *Stratiotosuchus*) with the exception of sebecids (e.g., *S. icaeorhinus*, *Lorosuchus*, *Cynodontosuchus* (see Discussion) and *Simosuchus*). Among baurusuchids an enlarged premaxillary tooth with these similar proportions (i.e. larger than the first maxillary tooth) is present in *Pissarrachamps*, *Campinasuchus*, *Gondwanasuchus*, *B. salgadoensis*, *B. pachecoi*, *Apletosuchus* and *Stratiotosuchus*. In these taxa, the hypertrophied premaxillary tooth is present in the third position, thus we interpret

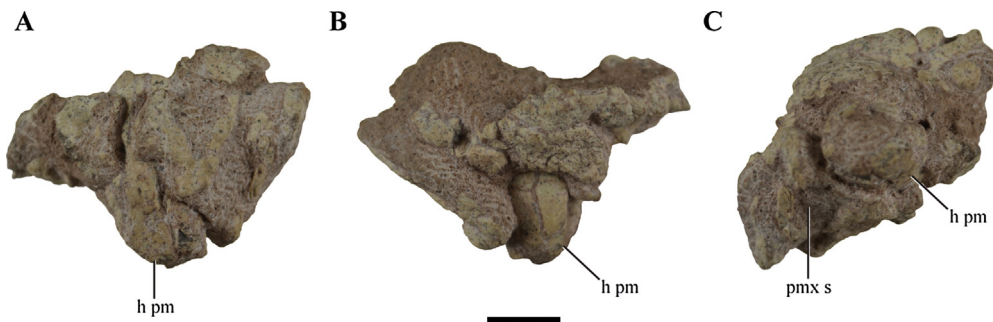


Fig. 7. Left premaxilla of MACN Pv-RN 1150 in: A. Lateral. B. Medial. C. Ventral views. h pm: hypertrophied premaxillary tooth; pmx s: premaxillary-premaxillary suture. Scale bar equals 1 cm.

Fig. 7. Prémaxillaire gauche de MACN Pv-RN 1150 en vue : A. Latérale. B. Médiale. C. Ventrale. h pm : dent prémaxillaire hypertrophiée ; pmx s : suture prémaxillaire-prémaxillaire. La barre d'échelle représente 1 cm.

it as the third premaxillary tooth. Medially, only a small part of the palatal laminae of both premaxillae is preserved, where a wide contact between them can be seen as in all crocodylomorphs.

Maxilla. Both maxillae are represented in MACN Pv-RN 1150, and despite being incomplete, these bones are the best preserved and the most informative of this specimen (Fig. 8A–F). Associated with the left maxilla, partial remains of a large tooth are present, although this tooth does not belong to the maxilla and is identified as the hypertrophied (see below), fourth mandibular tooth present in many sebecosuchians (e.g., *Pissarrachampsa*, *Campinasuchus*, *Gondwanasuchus*, *S. icaeorhinus*) which is housed in a notch between the premaxilla and maxilla (Fig. 8B). The facial lamina of the maxilla has a high dorsoventral development and is almost vertical, being perpendicular to the palatal lamina (Fig. 8A, C and D), as in most oreinitorostral crocodylomorphs (e.g., *Araripesuchus gomesii*, *Caipirasuchus stenognathus*, *Notosuchus terrestris*, *B. salgadoensis*). Nutrient foramina are present on the ventral edge of the facial lamina of the maxilla, just dorsolaterally to the tooth row and they are particularly large on the anterior part of the maxilla where they are near larger teeth (Fig. 8A and D). Large nutrient foramina are also present in the palatal lamina of the left maxilla, with the size of the foramina being larger towards the anterior end of the maxilla (Fig. 8B–C).

Posterior to the notch for the enlarged mandibular tooth, and combining what can be observed in both maxillae, at least five maxillary teeth (m) could be identified: the first four in the right one (m1–4, Fig. 8A–C) and posterior four teeth in the left one (m2–m5, Fig. 8D–F). However, given the incomplete preservation of MACN Pv-RN 1150 it is not possible to discern if the posterior most tooth is the last one of the maxillary series or there are some elements missing. A reduced number of maxillary teeth is widespread among baurusuchids, as these crocodyliforms have a highly reduced in number maxillary dentition bearing only five (*Cynodontosuchus*, *Stratiotosuchus*, *Aplestosuchus*, *Gondwanasuchus*, *B. salgadoensis* and *B. pachecoi*) or four (*Pissarrachampsa*) teeth in this bone. Maxillary dentition is reduced in a similar fashion in ziphosuchians more closely related to sebecosuchians (*Comahuesuchus* and *Chimaerasuchus*), contrasting with the

unreduced number of maxillary teeth of most sebecids (*S. icaeorhinus*, *S. querejazus*, *Lorosuchus*, *Bergisuchus*, *Barnasuchus*, and *Bretesuchus*) and *Cynodontosuchus*. These maxillary teeth are housed in individual alveoli. The m1 is the smallest of the anterior five teeth, while the m2 is the largest of the maxillary teeth, and as the m3 and m4, is strongly labiolingually compressed. An enlarged m2 is present in all non-baurusuchine baurusuchids (*Pabwehshi*, *Cynodontosuchus*, *Pissarrachampsa*, *Gondwanasuchus*, unknown in *Wargosuchus*) and *Stratiotosuchus*; while in *Campinasuchus*, *B. salgadoensis*, *B. pachecoi*, *Aplestosuchus*, and the sebecids *Lorosuchus*, *S. icaeorhinus* and *Ayllusuchus*, *Bretesuchus* the largest maxillary teeth is the m3. The only exception among sebecids in the relative size of their maxillary teeth is *Lumbrera* form, in which its largest tooth is the m2. The maxillary teeth of MACN Pv-RN 1150 gradually reduce their size up to the m5. The maxillary teeth bear posterior denticulated carinae, as in *Comahuesuchus* and all sebecosuchians with the exception of the *Pehuenchesuchus* and the sebecid *Lorosuchus*. However, the preservation of many teeth of MACN Pv-RN 1150 precludes the observation of the posterior carina in most teeth, with the exception of the m3 and m4 of the right maxilla.

Other cranial remains. Two additional cranial fragments were also recovered (Fig. 9A–C). These include fragmentary remains of the skull roof, specifically of the circumorbital region, such as: the left half of the frontal, the anterodorsal part of the postorbital and fragmentary remains of the palpebrals. These remains are preserved in two isolated fragments, which do not preserve many anatomical details. Both fragments (right and left) preserve partially the frontal, which displays ornamentation as irregular furrows and depressions and has well developed crista cranii on its ventral surface (Fig. 9A–B). The postorbitals are only preserved on their dorsal portion and the dorsal most part of the postorbital bar, which is lateromedially elongated. The right fragment of the skull roof preserves part of a palpebral in articulation with the postorbital and the frontal (Fig. 9C).

3.2.2. Mandible

Dentary. The anterior end of the mandibular symphysis was preserved, including only the anterior part of both

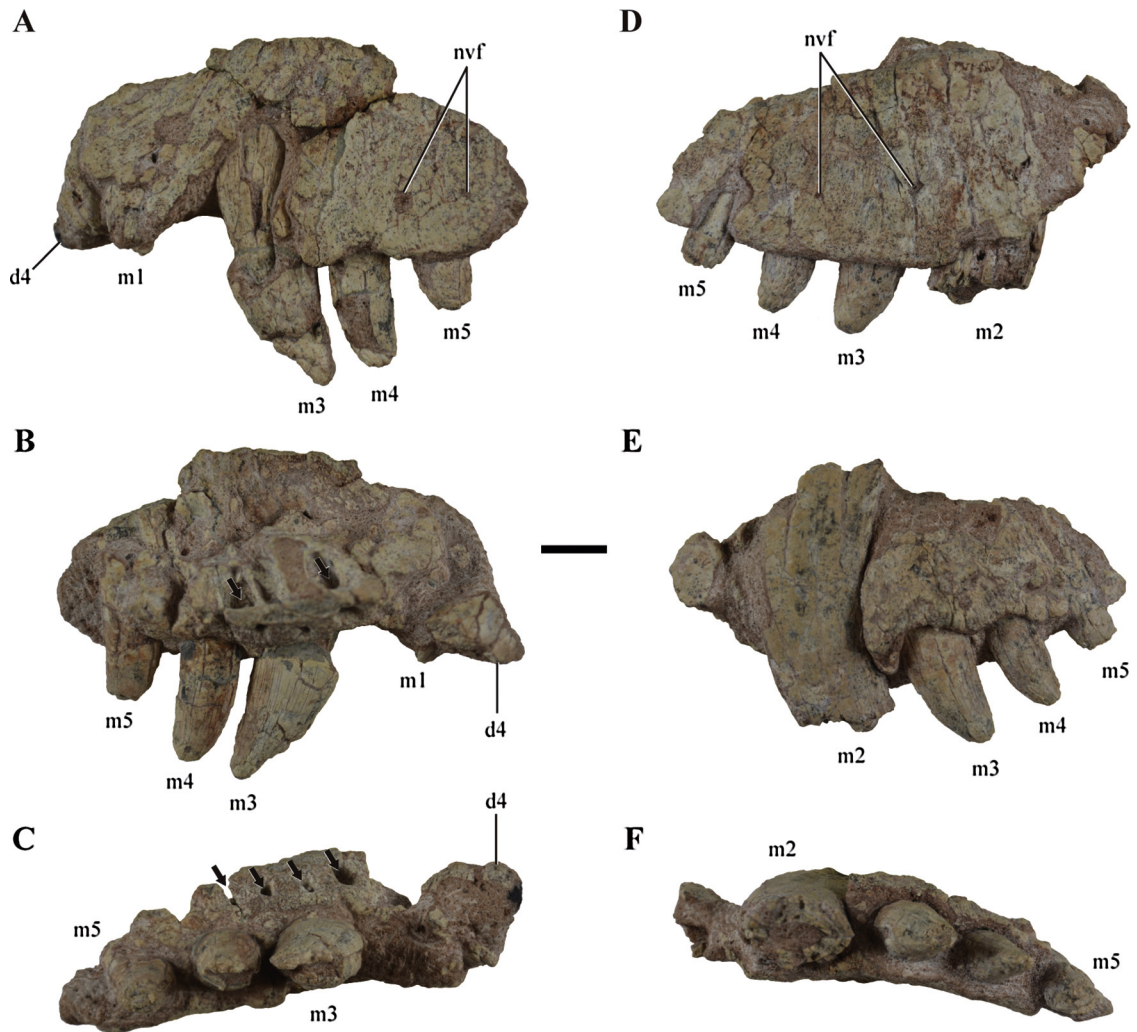


Fig. 8. Left and right maxillae of MACN Pv-RN 1150 in: A, D. Lateral. B, E. Medial. C, F. Ventral views. d4: fourth dentary tooth; m1–5: maxillary teeth 1–5; nvf, neurovascular foramina. Black arrows indicate large nutrient foramina. The scale bar equals 1 cm.

Fig. 8. Maxillaires gauche et droit de MACN Pv-RN 1150 en vues : A, D. Latérales. B, E. Médiales. C, F. Ventrales. d4 : quatrième dent du dentaire ; m1–5 : dents maxillaires 1–5 ; nvf : foramina neurovasculaires. Les flèches noires indiquent de grands foramens nutritifs. La barre d'échelle est égale à 1 cm.

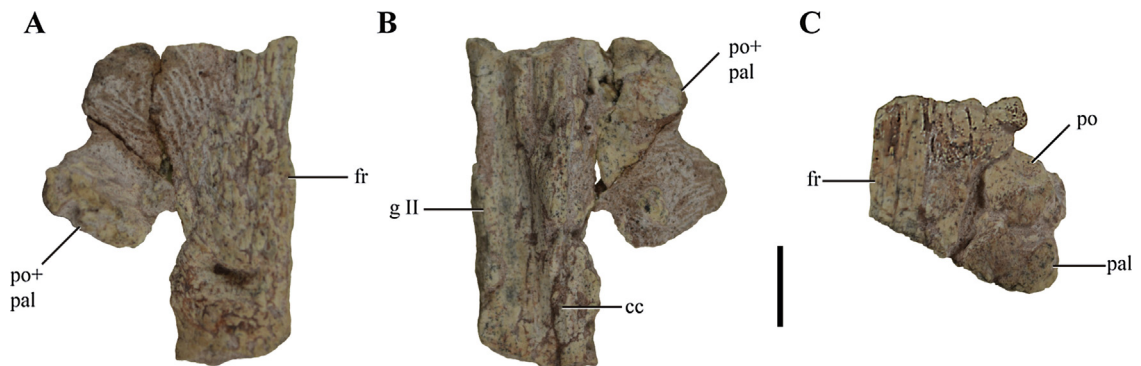


Fig. 9. Left half of the dorsal part of the snout of MACN Pv-RN 1150 in: A. Dorsal. B. Ventral views. Fragment of the posterior right half of the snout in C. Dorsal view. cc: crani crest; fr: frontal; pal: palpebral; po: postorbital. The scale bar equals 1 cm.

Fig. 9. La moitié gauche de la partie dorsale du museau de MACN Pv-RN 1150 en vues : A. Dorsale. B. Ventrale. Fragment de la moitié postérieure droite du museau en C. Vue dorsale. cc : crête crânienne ; fr : frontal ; pal : palpébral ; po : postorbitale. La barre d'échelle est égale à 1 cm.

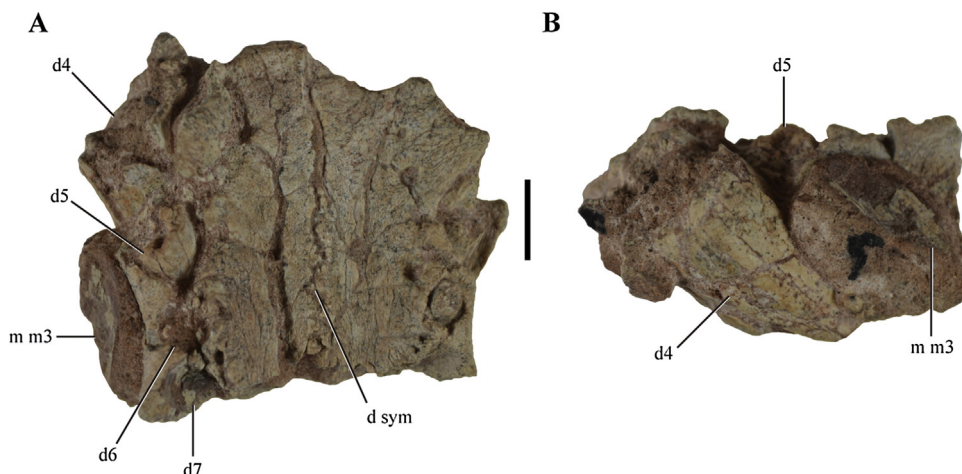


Fig. 10. Mandibular symphysis of MACN Pv-RN 1150 in: A. Dorsal. B. Lateral views. d4–d7: dentary tooth 4–7; d sym: dentary symphysis; m m3: mark of the third maxillary tooth. The scale bar equals 1 cm.

Fig. 10. Symphyse mandibulaire de MACN Pv-RN 1150 en vues : A. Dorsale. B. Latérale. d4–d7 : dent du dentaire 4–7 ; d sym : symphyse dentaire ; m m3 : marque de la troisième dent maxillaire. La barre d'échelle est égale à 1 cm.

dentaries, lacking the tip of the mandible (Fig. 10A–B). The dentaries are tightly sutured between them, having an interdigitated suture. Given the state of preservation of the mandibles, not much can be added to the general anatomy of this region of MACN Pv-RN 1150 besides the shape, size and number of teeth observed. Both sides of the mandibles preserve evidence of up to four teeth, given either by the preserved tooth or solely by the alveoli (Fig. 10A). The anterior most tooth is much larger than the others, exceeding in more than twice the size in section when compared to the second preserved tooth, which is the second in size. This hypertrophied tooth has a circular root and towards the origin of the crown it displays a labiolingual compression. The root of the large mandibular tooth is obliquely placed within the mandible, which has a more dorsoventral orientation once it leaves the boundaries of the mandible through its alveolous (Fig. 10B). Partial remains of this tooth were found in the right maxilla (see above), allowing us to infer that this tooth is housed within a notch between the premaxilla and maxilla, typical of many sebecosuchians (e.g., *B. salgadoensis*; *Pissarrachampsa*; *Campinasuchus*; *S. icaeorhinus*). All these traits described above are consistent with the identification of this tooth as the fourth dentary tooth. Posteriorly, the fifth mandibular tooth is the second in size and part of its crown is preserved on the right side. This tooth is almost in direct contact with the hypertrophied mandibular tooth, as the anterior alveolar wall is very thin (Fig. 10A). This condition is also present in *B. salgadoensis*, but not in sebecids (e.g., *S. icaeorhinus*; Lumbreira form; *Bretesuchus*). It is worthy to note that evaluating this condition among baurusuchids is complex, as many taxa preserve their mandibles in articulation, thus not allowing observing this condition. The sixth mandibular tooth is the smallest of the ones preserved, while the seventh has a slightly larger section, based on what it is preserved of its alveolus. Finally, based on our identification of the relative order of the mandibular alveoli we can conclude that the dentary symphysis involved at least up to the seventh mandibular tooth. Such rather elongated

mandibular symphysis is observed in uruguaysuchids and peirosaurids (in *Montealtosuchus* it reaches up to the sixth mandibular tooth; while *Uruguaysuchus* and *Araripesuchus* it reaches up to the level of the tenth mandibular tooth), *B. salgadoensis* and some sebecids (in *S. icaeorhinus* up to the sixth mandibular tooth). The dorsal surface of mandibular symphysis of MACN Pv-RN 1150 is flat as in *Pabwehshi*, *Lorosuchus* and *Pehuenchesuchus* (Fig. 10A–B). This condition is rare among sebecosuchians, which typically have strongly concave and though shaped symphyses in dorsal view (e.g., *B. pachecoi*, *B. salgadoensis*, Lumbreira Form, *Bretesuchus*).

4. Phylogenetic analysis

In order to evaluate the phylogenetic affinities of MLP 23-IV-30-2 and MACN Pv-RN 1150 we included them in the dataset of Martínez et al. (in press). This dataset is a modification of previous datasets (Fiorelli et al., 2016; Leardi et al., 2015a and b; Pol et al., 2014), where a new protosuchid taxon and a new character were included (Martínez et al., in press). The dataset used in our analysis includes several modifications: the inclusion of an additional baurusuchid taxon (*Wargosuchus australis* [Martinelli and Pais, 2008]) and the inclusion of two characters. One of the characters describes the dorsal surface of the posterior part of the nasals (Montefeltro et al., 2011; char. 4) and the other character is new and describes the distance between the fourth and fifth mandibular teeth (char. 442; see Supplementary Information). Additionally, character 184, which evaluates the position of the first enlarged mandibular tooth (Ortega et al., 2000), was modified. We recognize three states, depending on the alveoli in which this hypertrophied mandibular tooth is positioned: in the second, in the third, or in more posterior alveoli (see Supplementary Information). The dataset used also includes new scorings for *Pissarrachampsa* based on its recently described postcranium (Godoy et al., 2016). Finally, one character entry was modified, as after careful evaluation we consider that the

area of insertion of the M. subscapularis in *Chimaerasuchus* is exposed proximomedially (char. 309, changed from 1 to 0). Thus, the modified dataset resulted in 442 characters and 116 taxa.

The resulting dataset was analyzed using TNT version 1.5 (Goloboff and Catalano, 2016; Goloboff et al., 2008a, 2008b) under equally weighted parsimony. The analysis consisted in using a combination of heuristic algorithms known in TNT as the New Technology Searches. These were sequentially employed in independent replicates until 100 hits to the minimum length were achieved ($xmult = hits$ 100) and this was followed by a round of TBR branch-swapping on the most parsimonious trees (MPTs) found with the $xmult$ search. After the second round of TBR the tree buffer was full (800,000 MPTs; $L = 1715$; $CI = 0.308$; $RI = 0.743$). An iterPCR analysis (Pol et al., 2012) of the MPTs indicates the large amount of MPTs is caused by five unstable terminals within “advanced notosuchians” (sensu Pol et al., 2014) and Sebecosuchia: *Coringasuchus*, *Caryonosuchus*, *Pehuenchesuchus*, MLP 26-IV-30-2, and MACN Pv-RN 1150. When their different placements are ignored from the strict consensus the topology is fairly well resolved (Fig. 11A), with the exception of a large polytomy present in Baurusuchidae. Both MLP 26-IV-30-2 and MACN Pv-RN 1150 take multiple positions within baurusuchids, either in the base of the clade or as the basal most members of Baurusuchinae or Pissarrachampsinae (sensu Montefeltro et al., 2011), thus causing a collapse of this node on the strict consensus (Fig. 11B). When the different phylogenetic positions of the new fragmentary specimens added in this contribution are ignored, a fairly well-resolved topology is recovered with only a basal polytomy at the base of Baurusuchidae (Fig. 11B).

Unlike previous analyses (Leardi et al., 2015a, 2015b; Martínez et al., in press; Pol et al., 2014) we recovered a stable phylogenetic position for one fragmentary taxa: *Pabweshi pakistanensis* (Wilson et al., 2001), which was recovered as a basal baurusuchid either as the basal most member of the clade or as more derived than *Cynodontosuchus* in the different MPTs (which also takes a basal position in our analysis; Fig. 11B). The placement of *Pehuenchesuchus enderi* (Turner and Calvo, 2005) is worth discussing, as it is depicted either as the sister group of Sebecosuchia or forming a clade with *Lorosuchus*. These two alternative positions for *Pehuenchesuchus* cause a large polytomy within the base of Sebecosuchia (see Supplementary Information). The non-sebecosuchian placement is supported by two characters: the lack of an unsculpted region below the dentary tooth row (char. 155-0; Pol, 1999) and a vertically oriented lateral region of the dentaries below the mid-posterior tooth row (char. 193-0; Pol and Apesteguía, 2005). On the other hand, the group formed by *Lorosuchus* and *Pehuenchesuchus* is supported by a single synapomorphy: the lack of denticulated carinae in both taxa (char. 120-1; Ortega et al., 1996). However, *Pehuenchesuchus* lacks the only sebecosuchian unambiguous synapomorphy in our analysis: a hypertrophied tooth, which is at least twice the length of other dentary teeth, opposite to the premaxilla-maxilla contact (char. 80-1; Clark, 1994). It is important to mention, that the only sebecosuchian unambiguous synapomorphy

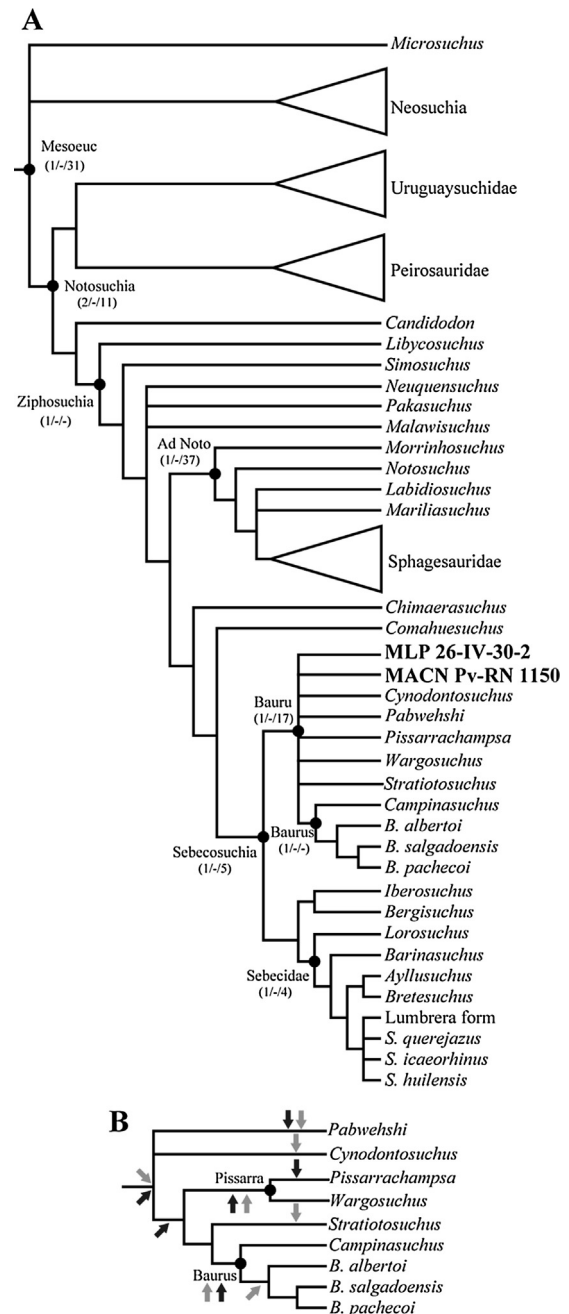


Fig. 11. A. Reduced strict consensus of 800,000 MPTs ignoring the different phylogenetical positions of *Pehuenchesuchus*, *Coringasuchus*, and *Caryonosuchus*. B. Detail of the baurusuchid phylogenetical relationships when the positions of both the taxa studied in this contribution (MLP 26-IV-30-2 and MACN Pv-RN 1150) are ignored. Ad Noto: “advanced notosuchians” sensu Pol et al. (2014); Bauru: Baurusuchidae; Baurus: Baurusuchinae; Mesoeucroc: Mesoeucrocodylia; Pissarra: Pissarrachampsinae. Support measures are placed next to relevant nodes (Bremer support/Bootstrap support/Jackknife support). The arrows indicate the different positions in the MPTs for: grey, MLP 26-IV-30-2; black, MACN Pv-RN 1150.

retrieved in our analysis contrasts with the several ones reported in previous studies (e.g., Nascimento and Zaher, 2011; Pol et al., 2012). This difference is merely caused by the placement as basal baurusuchids of *Cynodontosuchus* and *Pawewshi*, which are very incompletely known; the abundant missing entries in these taxa introduce ambiguous optimizations for many characters.

No unambiguous synapomorphies of Baurusuchidae were found common to all the MPTs, given the various taxa that take a basal position within the clade in these trees (e.g., *Cynodontosuchus*, *Pabwehshi*, MLP 26-IV-30-2, MACN Pv-RN 1150). Among the characters that can be recognized as synapomorphies in the various MPTs, there are some that are relevant for the present contribution given that they are relevant for the inclusion of MACN Pv-RN 1150 and MLP 26-IV-30-2 within Baurusuchidae. The presence of an enlarged maxillary tooth opposite to the enlarged dentary teeth (char. 81-0; Clark, 1994) and an enlarged second maxillary tooth (char. 184-1; Ortega et al., 2000, but modified on this contribution) support the placement of MACN Pv-RN 1150 within Baurusuchidae. Also, the latter (char. 184-1) is informative to recover *Pabwehshi* as a baurusuchid. The phylogenetic position of MLP 26-IV-30-2 is supported by the presence of several characters, most of which have been previously identified as synapomorphies of Notosuchia or less inclusive clades (Leardi et al., 2015b; Pol et al., 2012). The notosuchian affinities of MLP 26-IV-30-2 are supported by the presence of a circular depression on the posterior surface of the proximal end of the humerus (char. 314.1; Pol et al., 2012), and the presence of a bulge anteriorly to the scapular glenoid facet (char. 415.1; Leardi et al., 2015b). A medially displaced deltopectoral crest leaving an anterolaterally-exposed surface (char. 311.1; Pol et al., 2012) is also present in MLP 26-IV-30-2, a feature interpreted as a synapomorphy of “advanced notosuchians”, sebecosuchians, and allied taxa. Finally, MLP 26-IV-30-2 preserves a single baurusuchid synapomorphy, a low and wide distal part of the deltopectoral crest (char. 313-1; Pol et al., 2012). This character is optimized as an ambiguous baurusuchid postcranial synapomorphy in our analysis, as it is present in *Stratiotosuchus*, *B. albertoi*, and MLP 26-IV-30-2 while being unknown in the rest of the baurusuchids included in our analysis. Only one of the characters included in this dataset is recovered as an autapomorphy of MLP 26-IV-30-2 because unlike most notosuchians the articular surfaces for the ulna and ulnare in the radiale are continuous in this specimen (char. 321.1; Pol et al., 2012; Fig. 5B).

Most of the important nodes in our MPTs have low support values (Bremer=1 and Bootstrap values below

50). In order to test the position of MLP 26-IV-30-2 and MACN Pv-RN 1150 we forced their phylogenetic position outside Baurusuchidae. Under that constrain one extra step ($L=1716$) is needed to place MLP 26-IV-30-2 outside Baurusuchidae, and it takes different positions among taxa closely related to Sebecosuchia (as the sister group or as closely related to *Chimaerasuchus*) or as closely related to *Morrinosuchus*, an advanced notosuchian (sensu Pol et al., 2014). In a similar way, MACN Pv-RN 1150 is positioned outside Baurusuchidae also with an additional step ($L=1716$), and is depicted as the sister group of Sebecosuchia under this constrain. Furthermore, when both specimens (MLP 26-IV-30-2 and MACN Pv-RN 1150) are forced outside Sebecosuchia two additional steps are needed ($L=1717$). Despite both specimens are very fragmentary, the preserved morphology indicates their affinities with sebecosuchians.

5. Discussion

Previously known baurusuchids from Cretaceous levels of the Neuquén Basin of Argentina include two basal baurusuchid taxa: *Cynodontosuchus rothi* and *Wargosuchus australis*. Additionally, according to our analysis and supporting previous interpretations (Turner and Calvo, 2005), a form closely related to Sebecosuchia is also recorded in this region (*Pehuenchesuchus enderi*). Despite their incompleteness, it is important to note the affinities previously postulated for these Patagonian baurusuchids. Montefeltro et al. (2011) recovered *Cynodontosuchus* as the basalmost baurusuchid and *Wargosuchus* forming a clade with *Pissarrachampsia* (Pissarrachampsinae). These positions are corroborated here and together with the phylogenetic position of the two specimens described here (taking variable positions among non-baurusuchinae baurusuchids), show the potential of the Neuquén Basin for providing information on the early diversification of the baurusuchids. The far more diverse baurusuchid record of the Adamantina Formation in Brazil, instead, includes a broader sample of taxa, including the diverse and derived clade Baurusuchinae (sensu Montefeltro et al., 2011).

Patagonian baurusuchids have always caught the attention of the researchers (e.g., Martinelli and Pais, 2008) due to their small size when compared with the ones from the Adamantina Formation in Brazil. In fact, the type specimens of *Cynodontosuchus* and *Wargosuchus* have been tentatively interpreted as juvenile and adult specimens of the same taxon (Montefeltro et al., 2011). The only known specimen of *Cynodontosuchus* is an isolated rostrum and establishing its ontogenetic stage is difficult. Montefeltro et al. (2011) noted that Gasparini (1972, 1981) suggested this specimen could be a juvenile but in fact Gasparini only stated that might be a different genus or species (Gasparini, 1972: 30). Montefeltro et al. (2011: 23) argue that the specimen could be a juvenile based on the presence of three traits: small size, lack of a palatal median rugosity and associated foramina, and the lack of hypertrophied premaxillary teeth (Montefeltro et al., 2011). The lack of hypertrophied premaxillary teeth has been previously noted in juvenile of other notosuchian taxa (e.g., *Notosuchus terrestris*; Lecuona and Pol, 2008) and a similar pattern can also be observed

Fig. 11 (continued). A. Consensus strict réduit de 800 000 MTP ignorant les différentes positions phylogénétiques de *Pehuenchesuchus*, *Coringasuchus* et *Caryonosuchus*. B. Détail des relations phylogénétiques baurusuchidiées lorsque les positions des deux taxons étudiés dans cette contribution (MLP 26-IV-30-2 et MACN Pv-RN 1150) sont ignorées. Ad Noto : « notosuchiens avancés » sensu Pol et al. (2014) ; Bauru : Baurusuchidae ; Baurus : Baurusuchinae ; Mesoeucroc : Mesoeucrocodylia ; Pissarra : Pissarrachampsinae. Les mesures de support sont placées à côté des nœuds concernés (support Bremer/support Bootstrap/support Jackknife). Les flèches indiquent les différentes positions dans les MPT pour : gris, MLP 26-IV-30-2 ; noir, MACN Pv-RN 1150.

in the baurusuchid *Campinasuchus dinizi* (Carvalho et al., 2011) that is known by several individuals (including several skull remains). Cotts et al. (2017) inferred a juvenile ontogenetic stage for one of the specimens (CPPLIP 1237) based on its postcranial and cranial features (i.e. open neurocentral sutures in dorsal and cervical vertebrae; poorly developed condyles on the stylopodium; “less marked” muscle scars; longer rostrum with more teeth). CPPLIP 1237 lacks the development of a hypertrophied posterior premaxillary tooth (Carvalho et al., 2011: figs. 7–8), while larger specimens (CPPLIP 1234 and 1236; Carvalho et al., 2011: figs 3–6) have an enlarged tooth on the third premaxillary position. Thus, size variation in the posterior premaxillary teeth is present outside and within Baurusuchidae and supports the interpretation of Montefeltro et al. (2011) that the type of *Cynodontosuchus* is a juvenile. The lack of the palatal rugosities is another trait that can support the claim of *Cynodontosuchus* being a juvenile specimen. This feature is present in all baurusuchids where the palatines are well preserved, and recently it has been identified in *Comahuesuchus* (Montefeltro et al., 2013), which most recent phylogenetic hypothesis found it closely related to Sebecosuchia (Pol et al., 2012, 2014; Turner et al., 2011). *Cynodontosuchus* also bears seven maxillary teeth, a plesiomorphic tooth count that is reduced in all other baurusuchids. This variation exceeds the range reported for the ontogenetic series of the baurusuchid *Campinasuchus* (Cotts et al., 2012). Considering the anatomical traits discussed above, especially the number of dentary teeth, *Cynodontosuchus rothi* is for the moment still treated as an independent taxonomical unit in the phylogenetic analysis in concordance with most recent analyses dealing with the baurusuchid phylogeny (Godoy et al., 2014; Montefeltro et al., 2011).

In contrast with the small size inferred for *Cynodontosuchus*, one of the individuals studied in this contribution clearly represents a larger specimen (Table 2). Given the scarce remains of MLP 26-IV-30-2 and MACN RN-PV 1150 reliable size estimations of these specimens are difficult, as they are usually based on femoral measures (e.g., Farlow et al., 2005; but see Pol et al., 2012). Fortunately, in recent years several sebecosuchian with well-preserved and represented postcrania have been reported (e.g., Nascimento and Zaher, 2011; Pol et al., 2012; Riff and Kellner, 2011), allowing us to compare the remains of MLP 26-IV-30-2 and MACN RN-PV 1150 with better known taxa that have an approximate size estimation. However, it is important to mention that size estimations for crocodylomorphs are usually made using Farlow et al. (2005) equation based on their study of *Alligator mississippiensis*. It has been previously noted in other contributions (Pol et al., 2012) that non-eusuchian crocodylomorphs usually have more slender and elongated femora than their extant relatives. Thus, the body mass estimations based on femoral lengths might not be a good predictor for these animals. Godoy et al. (2016) found great disparities on their results when estimating the body mass of *Pissarrachampsia* (with differences of almost 100 kg), and estimated a much lower body mass using Campione and Evans (2012) equations. In the following lines we will use body mass estimations for other

sebecosuchians, which were obtained using Farlow et al. (2005) estimations. Thus, it should be considered that these values are used just as a comparing tool between different sebecosuchians and as rough estimator of the body size (by comparison) of the specimens studied in this contribution. When we compare the new specimens described above with other sebecosuchians it can be noted that MLP 26-IV-30-2 (proximal width of the humerus equals 38 mm) represents one of the smallest known sebecosuchians, even smaller than *Sebecus icaeorhinus* (proximal width of the humerus equals 47 mm) which has an estimated body mass of 85 kg (see Table 2). Estimated body masses of baurusuchine baurusuchids are well above 200 kg (e.g., *B. albertoi*, *B. salgadoensis*, *Stratiotosuchus*). MACN RN-PV has a maxilla, which has an alveolar length comparable (even larger) than the one of the baurusuchine *Aplestosuchus* (see Table 2). Based on the data presented by Farlow et al. (2005; Table 2) the body mass of *Aplestosuchus* can be estimated to be slightly above 200 kg (see Supplementary Information). Thus, a large body mass can be inferred for MACN RN-PV 1150 based on these comparisons.

Although sebecosuchian taxa of the Neuquén basin are known from fragmentary remains, they potentially represent important taxa for understanding baurusuchid origins. However, the sebecosuchian diversity of the Upper Cretaceous of the Neuquén basin and the Bajo de la Carpa Formation in particular, must be handled with care. Many of the specimens reported from the formation are very incomplete, being represented by isolated snout (*Cynodontosuchus*, 87.56% missing data; *Wargosuchus*, 92.77% missing data; and MACN Pv-RN 1150, 92.31% missing data), mandibular (*Pehuenchesuchus*, from the Anacleto Formation, 94.8% missing data) or postcranial remains (MLP 26-IV-30-2; 95.21% missing data). Furthermore, the definition of formal taxa (i.e. new genus or species) based on this kind of incomplete materials add a complex element to the study of the baurusuchid diversity in the Cretaceous of Patagonia. Taxa like *Wargosuchus* are very poorly represented and make very difficult the posterior comparison with new materials (e.g., the ones described in this contribution). *Wargosuchus* and MACN RN-PV 1150 both represent large bodied baurusuchids, but there are not any diagnostic traits present on either specimen that justify co-generic assignment. Therefore, to avoid similar taxonomic problems and despite some unique and diagnostic traits can be recognized in the specimens studied in this contribution (such as the ones mentioned in MLP 26-IV-30-2), we prefer to leave them as open taxonomical units until new more complete sebecosuchians are recovered from the Bajo de la Carpa Formation. Given the age of the Bajo de la Carpa Formation (Santonian; Garrido, 2010), further collecting efforts in this unit can provide key information for determining changes in the notosuchian lineage that led to the rise of the large baurusuchid hypercarnivores that thrived in the Late Cretaceous of Brazil and were among the apex predators in their communities (Candeiro and Martinelli, 2006; Godoy et al., 2014; Riff and Kellner, 2011). As noted before, this is the time in which the highest rise in diversity is recorded for notosuchians (Pol and Leardi, 2015; Pol et al., 2014).

Table 2

Measures and size estimations of sebecosuchian taxa.

Tableau 2

Mesures et estimations de taille des taxons sébécosuchiens.

Taxon	Hp	Mx Al L	SL	FL	BM
Sebecidae					
<i>Sebecus icaeorhinus</i> (MPEF-PV 1776)	46.96	–	–	198.53	85.46
Baurusuchidae					
MLP 26-IV-30-2	38	–	–	–	–
MACN RN-Pv 1150	–	49.19	–	–	–
<i>Cynodontosuchus</i>	–	37.55	–	–	–
<i>Gondwanasuchus</i>	–	26.02	128.88	–	–
<i>Pissarrachampsia</i> (LPRP/USP 0019)	–	54.06	300.85*	241	162.97
<i>Aplestosuchus</i>	–	40.21	310.53	–	–
<i>Stratiosuchus</i> (DGM 1477-R)	87	86.73	459.09	353	580.88
<i>Campinasuchus</i> (CPP 1237)	19.28	36.85	126.88	143	28.66
<i>Baurusuchus albertoi</i>	58	–	–	262	215.25
<i>Baurusuchus salgadoensis</i> (UFRJ-DG 417-R)	75.16	–	–	300	337.92
<i>Baurusuchus salgadoensis</i> (MPMA 62-0001-02)	–	78.74	439.68	–	–
<i>Baurusuchus pachei</i>	–	61.33	364.46	–	–

BM: estimated body mass (in kg); FL: femoral length; Hp, humeral proximal width; Mx Al L: maximum maxillar alveolar length; SL: Skull length. The asterisk (*) for the SL of *Pissarrachampsia* denotes that the skull is incomplete, with the anterior part of the snout missing. All distances are measured in mm. Body masses were estimated using the equations of Farlow et al. (2005).

6. Conclusion

Two new incomplete specimens from the Bajo de la Carpa Formation are described. The smallest specimen (MLP 23-IV-30-2) is represented by isolated forelimb remains whereas the second and larger specimen (MACN Pv-RN 1150) has only partial remains of the snout preserved. Despite their incompleteness, our phylogenetic analysis depicts both new specimens within Baurusuchidae, a highly specialized group of notosuchian hypercarnivores that thrived during the Late Cretaceous of Gondwana. These findings add new information to the knowledge of the baurusuchids from the Bajo de la Carpa Formation.

Both specimens studied in this contribution were left as open taxonomical units, although one (MLP 26-IV-30-2) of them has some unique characters preserved (e.g., dorsal pit to the glenoid; posterior heel on the ulna; convex proximal ends of the metacarpals), as we wish to avoid future taxonomical problems. We hope that additional material might reveal the identity and will help to clarify the taxonomical status of the baurusuchids from the Bajo de la Carpa Formation. However, despite this taxonomical conflict there is no denying in the fact that this Patagonian Formation bears an unexpectedly high amount of crocodyliform taxa. As previously highlighted by the authors of this contribution (Pol and Leardi, 2015; Leardi et al., 2015a) the Bajo de la Carpa Formation represents a unique case to study the notosuchian diversity, as both the diversity and abundance of reptiles from this clade are very high. Thus, the Bajo de la Carpa Formation might be one of the key units to understand the sudden rise and dominance of the notosuchians among the rest of the crocodyliforms in the Upper Cretaceous of Gondwana, an event known as the “Turonian-Santonian Radiation” (Pol et al., 2014).

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MLP 26-IV-30-2 was found during the process of writing a previous manuscript by ZG, and later skillfully mechanically prepared by L. Acosta, with final details by J. Kaluza. We thank A. Kramarz for access and loan of the specimen MACN Pv-RN 1150 and we thank P. Puerta for the preparation of this specimen. TNT is a free program made available by the Willi Hennig Society. Research for this contribution was partially covered by the grant PICT 2013–2725 (to JML) and 2013–0132 (to DP). This manuscript was greatly improved by the comments of A. Martinelli and an anonymous reviewer. This is JML’s R-239 contribution to the Instituto de Estudios Andinos Don Pablo Groeber.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2018.02.002>.

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