Available online at www.sciencedirect.com
ScienceDirect
C. R. Palevol 7 (2008) 371–381
COMPTES RENDUS PALEVOL
http://france.elsevier.com/direct/PALEVO/

Systematic Palaeontology

A new baurusuchid crocodyliform (Archosauria) from the Late Cretaceous of Patagonia (Argentina)

Agustín G. Martinelli [a,*], Diego F. Pais [b]

[a] *Sección Paleontología, Museo de Historia Natural de San Rafael. Parque Mariano Moreno s/n, CP. 5600, San Rafael, Mendoza, Argentina*
[b] *Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470 (1405), Buenos Aires, Argentina*

Received 19 July 2007; accepted after revision 6 May 2008
Available online 24 June 2008

Presented by Philippe Taquet

Abstract

A new baurusuchid, *Wargosuchus australis* gen. et sp. nov., coming from the Bajo de La Carpa Formation, Neuquén Province (Argentina), is described. This new taxon is based on a fragment of snout and a portion of the cranial roof. *Wargosuchus* differs from other crocodyliforms by possessing a deep median groove on the frontals, a contact between nasals and frontals extremely reduced, a large depression for the olfactory bulbs, three large foramina surrounding the large, smooth perinarial depression, and a hypertrophied, conical last premaxillary tooth followed by a large paracanine fossa. The finding of *Wargosuchus* in Patagonia (Argentina), a taxon with a strong resemblance to Brazilian baurusuchids, reinforces the hypothesis of a similar biota between both regions by the Late Cretaceous. *Wargosuchus* and *Cynodontosuchus* represent the only Argentinian mesoeucrocodylians to be included within Baurusuchidae. This finding extends the number of crocodyliforms from the Bajo de la Carpa Formation, which, in turn, corresponds to the most taxonomically diverse one in Argentina. ***To cite this article: A.G. Martinelli, D.F. Pais, C. R. Palevol 7 (2008).***

Résumé

Un nouveau crocodyliforme baurusuchidé (Archosauria) du Crétacé supérieur de Patagonie (Argentine). Un nouveau baurusuchidé *Wargosuchus australis* gen. et sp. nov. de la formation Bajo de la Carpa, dans la province de Neuquén (Argentine), est décrit ici. Le nouveau taxon est établi à partir d'un fragment de museau et d'une portion de voûte crânienne. *Wargosuchus* diffère des autres crocodyliformes en ce sens qu'il possède un profond sillon médian sur les frontaux, un contact extrêmement réduit entre les nasaux et les frontaux, une larde dépression pour les bulbes olfactifs, trois foramens larges entourant la dépression périnariale, large et lisse, et une dernière dent prémaxillaire conique, hypertrophiée, suivie par une large fosse paracanine. La découverte, en Patagonie (Argentine), de *Wargosuchus*, un taxon présentant une grande ressemblance avec les baurusuchidés du Brésil, renforce l'hypothèse d'un biotype similaire entre les deux pays, à la fin du Crétacé. *Wargosuchus* et *Cynodontosuchus* représentent les deux seuls mésoeucrocodyliens à être inclus dans les Baurusuchidae. Cette découverte augmente le nombre de crocodyliformes de la

* Corresponding author.
E-mail address: agustin_martinelli@yahoo.com.ar (A.G. Martinelli).

1631-0683/$ – see front matter
doi:10.1016/j.crpv.2008.05.002

formation Bajo de la Carpa, qui, à son tour, présente la plus grande diversité taxonomique d'Argentine. ***Pour citer cet article : A.G. Martinelli, D.F. Pais, C. R. Palevol 7 (2008).***

Keywords: Late Cretaceous; Mesoeucrocodylia; Baurusuchids; Argentina

Mots clés : Crétacé supérieur ; Mésoeucrocodylia ; Baurusuchidé ; Argentine

1. Introduction

Non-neosuchian mesoeucrocodylian remains are relatively frequent in continental Late Cretaceous assemblages of Gondwana such as those of Argentina, Brazil, Uruguay, Madagascar, and a few countries of continental Africa [6,7,16,18,21,23,28,30,31,36–39,44,48,50]. The continental Late Cretaceous record of these regions contains a diverse and peculiar assemblage of taxa that includes the taxonomically diverse notosuchians (including typical Cretaceous basal notosuchians and sebecosuchians), several species of *Araripesuchus*, peirosaurids, and the enigmatic trematochampsids, among few others.

Among notosuchians, the Sebecosuchia comprises an extensive clade still far from being adequately understood. Its monophyly, nonetheless, is widely accepted [22,34,37,47,49,50; contra 29]. Since the recognition of this group [14], several controversial taxa were discovered from Late Cretaceous to Middle Tertiary age, which were placed and removed unconditionally over the years. The taxonomic swaying of this group may have its answer in the poorly preserved nature of most of the known specimens and in the a priori assumption of the lack of convergences among crocodylians [18]. For example, the presence of ziphodont teeth (i.e. theropodomorph-like with laterally compressed crown and serrated edges) was used arbitrarily to nest species within sebecosuchians [4,24,27]. Nowadays, this trait is considered to be independently evolved in several lineages.

Traditionally, sebecosuchians include sebecids, bretesuchids, baurusuchids, and a few problematic taxa [9,14,17,19,22]. Sebecids appear to be a paraphyletic group of sebecosuchians basal to baurusuchids [34,49]. They are worldwide distributed in Late Cretaceous to Middle Tertiary strata [9,19,33,35]. Bretesuchids appear to be, at the moment, monotypic, endemic of the Early Tertiary of South America [22]. Baurusuchids comprise highly specialized sebecosuchians. They were recognized in Brazil, Argentina, and Pakistan [52]. In South America, they were prolific in Brazil [2,11,13,38], where not only the diversity is high, but also the amount of available specimens. The baurusuchid taxa hitherto recovered in Brazil include *Baurusuchus pachecoi* [5,30,38,42], *B. salgadoensis* [13,50], and *Stratiotosuchus maxhechti* [11] from the Turonian–Santonian Adamantina Formation. Conversely, only one likely representative of this group is known in Argentina, *Cynodontosuchus rothi*, based on a solely poorly preserved skull [17,55]. Historically, *Cynodontosuchus* was the first known baurusuchid but, at that time, it was related with *Notosuchus* [55]. Later, Price [38,40] included it within Baurusuchidae. Gasparini [17,18] discussed the relationships of *Cynodontosuchus*, remarking that new material will elucidate the validity of this genus. Subsequently, *Cynodontosuchus* was interpreted as possibly co-generic with *Baurusuchus* [10,13,20,22], but no new data compelling this problem was provided.

In this contribution, a new baurusuchid, *Wargosuchus australis* gen. et sp. nov., is described. The specimen was found in the northern region of the Neuquén city (Neuquén Province, Argentina) in outcrops of the Bajo de La Carpa Formation, in the same levels as *Notosuchus terrestris*. The material was discovered by Sr. Garate Zubillaga of the Museo 'Profesor-Dr. Juan A. Olsacher' (Neuquén Province) during the 1980s and offered to Dr. J.F. Bonaparte. The new taxon supports the occurrence of baurusuchids in Argentina by the Late Cretaceous and enlarges the number of crocodyliforms from the Bajo de la Carpa Formation, which hitherto represents the most taxonomically diverse one in Argentina.

2. Terminology

We use Notosuchia [16] as a stem group composed of all crocodyliforms more closely related to *Notosuchus terrestris* than to *Crocodylus niloticus* [47]. Sebecosuchia encompasses the clade that includes the most recent common ancestor of *Pehuenchesuchus* and *Baurusuchus*, and all its descendants [50] (see also [35]). This clade is included within Notosuchia [34,35,47,50, but see 29]. From here on, we reserve the informal name basal notosuchians for the strictly Cretaceous non-sebecosuchian notosuchians (excluding *Araripesuchus*; see below).

Baurusuchidae were defined as the common ancestors of *Baurusuchus* and *Stratiotosuchus* and all their descendants [13]. However, because a phylogenetic analysis of the family was not still performed, this definition seems to be provisional. We considered Baurusuchidae as composed by *Baurusuchus pachecoi*, *B. salgadoensis*, *Stratiotosuchus maxhechti*, *Cynodontosuchus rothi*, and *Pabwehshi pakistanensis*.

The phylogenetic placement of the *Araripesuchus* species is still controversial [34,49, contra 37]. In the text, they are informally called araripesuchids. We followed Gasparini et al. [21] for the taxonomic composition of Peirosauridae.

3. Institutional abbreviations

MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (N: Colección Neuquén, RN: Colección Río Negro) (Buenos Aires, Argentina); MLP: Museo de La Plata (La Plata, Argentina); MOZ: Museo 'Profesor-Dr. Juan A. Olsacher' (Zapala, Argentina).

4. Systematic palaeontology

Crocodyliformes Benton and Clark, 1988 [3]

Mesoeucrocodylia Whetstone and Whybrow, 1983

Baurusuchidae Price, 1945

Wargosuchus gen. nov.

Derivatio nominis: Warg in reference to a beast of J.R.R. Tolkien's mythology, and *suchus* from the Greek *Suchos* that refers to the Egyptian crocodile God.

Diagnosis. As for the type and only known species.

Type species. *W. australis*.

Wargosuchus australis sp. nov.

Holotype. MOZ-PV 6134, fragment of right premaxilla and maxilla, and portion of skull roof.

Derivatio nominis: Australis in reference to the southern geographical location of the holotype.

Locality, horizon, and age. MOZ-PV 6134 comes from the northern region of the Neuquén city, Neuquén Province. Bajo de La Carpa Formation, Río Colorado Subgroup, Neuquén Group, Santonian [6,25].

Diagnosis. *Wargosuchus* differs from other crocodyliforms in the association of the following features: deep median groove on the frontals (autapomorphy); extremely reduced contact between nasals and frontals with almost prefrontals touching one to each other at midline (autapomorphy); large depression for the olfactory bulbs; three large foramina surrounding the large, smooth perinarial depression; hypertrophied, conical, last premaxillary tooth followed by a large paracanine depression.

5. Description

The holotype, and only known specimen, consists of a right portion of the snout including part of the maxilla and most of the premaxilla, with the base of the penultimate tooth and the last premaxillary tooth almost complete (Fig. 1), and a portion of the skull roof including partial nasals, lachrymals, prefrontals, frontals, and left palpebral (Fig. 2).

5.1. Premaxilla

The right premaxilla is incomplete, lacking its rostral portion. It preserves the postero-ventral edge of the external naris, a large premaxillary-maxillary notch for the placement of a hypertrophied lower tooth, and the palatal process of the premaxilla. In lateral view, the facial exposure of the premaxilla is high, almost vertical, and slightly dorsoventrally convex (Fig. 1A). The dorsal contact with surrounding bones is not preserved. The alveolar border is strongly convex with the lowest point coincident with the placement of the largest premaxillary tooth, as seen in other mesoeucrocodylians (*Baurusuchus* and *Stratiotosuchus*; [11,13,38]). Ornamentation of the external surface exhibits disparities. The posterior half has deep, irregular grooves that continue over the maxilla; the rostral portion has a shallow ornamentation with small furrows and, just below the ventral edge of the external naris, there is a large, rounded depression that differs in texture from the remaining bone (Fig. 1). This depression, usually called perinarial area, is smooth and caudal-dorsally bordered by a relatively elevated rim that makes this region deeper. Dorsally, within the depression, there are two, relatively large, vascular foramina, as in *Baurusuchus*. This structure was possibly related to the soft tissue of the snout that would possibly regulate the opening and closure of the naris, as seen in some terrestrial crocodyliforms, in order to regulate the loss of water. This depression is also observed in other sebecosuchians such as *Iberosuchus* [1] and both species of *Baurusuchus* [13,38], in the basal notosuchian *Simosuchus* [7], and in peirosaurids such as *Uberabasuchus* [12] and *Stolokrosuchus* [28]. In several basal notosuchians, a perinarial region with the above-mentioned features is absent, showing only a small smooth area bordering the external naris, as observed in *Notosuchus* (MACN-PV-RN 1040). Immediately above the last premaxillary tooth, there are two large vascular foramina, and several irrigating vascular openings of small size.

In lateral view, the preserved border of the external naris is straight, with an acute angle between the caudal-dorsal and caudal-ventral rims. The shape and

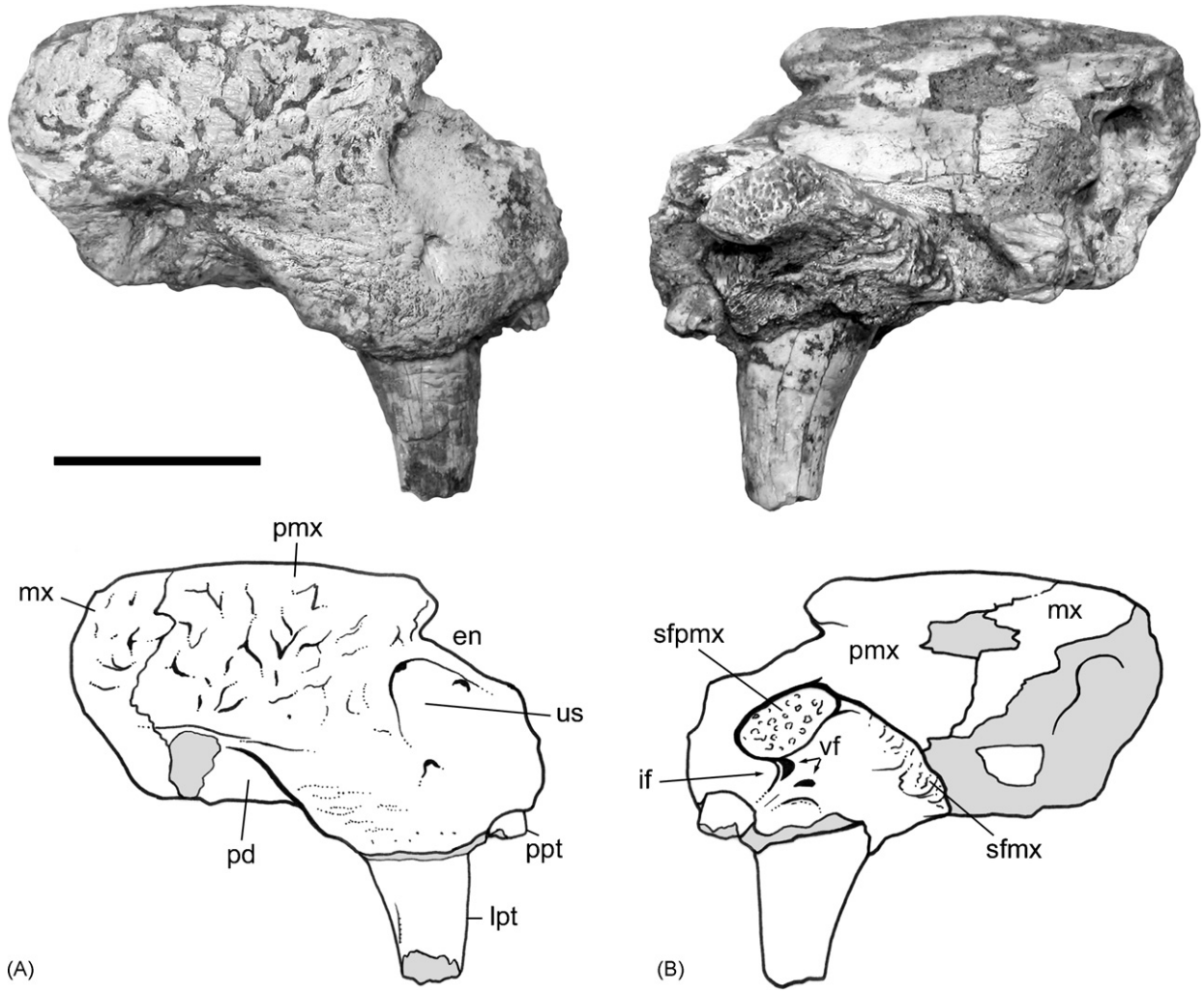

Fig. 1. *Wargosuchus australis* MOZ-PV 6134, fragment of right premaxilla and maxilla in lateral (**A**) and medial (**B**) views. Abbreviations: **en**, external naris; **lpt**, last premaxillary tooth; **mx**, maxilla; **pd**, paracanine depression; **pmx**, premaxilla; **ppt**, penultimate premaxillary tooth; **us**, unsculptured surface. Scale bar: 2 cm.

Fig. 1. *Wargosuchus australis* MOZ-PV 6134, fragment des prémaxillaire et maxillaire droits en vue latérale (**A**) et médiale (**B**). Abréviations : **en**, naris externe ; **lpt**, dernière dent du prémaxillaire ; **mx**, maxillaire ; **pd**, dépression paracanine ; **pmx**, prémaxillaire ; **ppt**, avant-dernière dent du prémaxillaire ; **us**, surface lisse. Échelle : 2 cm.

orientation of the ventral border of the external naris suggest that this opening was greatly laterally exposed. Despite the incomplete condition of the rostral portion of the premaxilla, the external naris seems to be relatively wide in rostral view, and elongated in lateral view.

The presence of a conspicuous paracanine depression located near the premaxilla–maxilla contact is widely spread among sebecosuchians, peirosaurids, trematochampsids, and in a few basal crocodyliforms (*Orthosuchus* [32]). In basal notosuchians and araripesuchids, this feature is absent.

In ventral view, the premaxilla preserves its palatal process, with a rough median surface to contact its left counterpart. This process is transversely narrow, suggesting that the rostrum, at the level of the hypertrophied tooth, was very narrow (Fig. 1B). The premaxilla palatal process is anteroposteriorly short, with two large vascular foramina and a small depression close to the rostral rim. This boundary, located at the level of the penultimate premaxillary tooth, is posteriorly concave and represents the border of the incisive foramen (or premaxillary fenestra), entirely enclosed into the premaxilla (Fig. 1B). In *Wargosuchus*, the incisive foramen and surrounding area seem to be highly vascularised. When observed anteriorly or dorsally, the palatal process of the premaxilla has a deep concave depression located posteriorly to the bor-

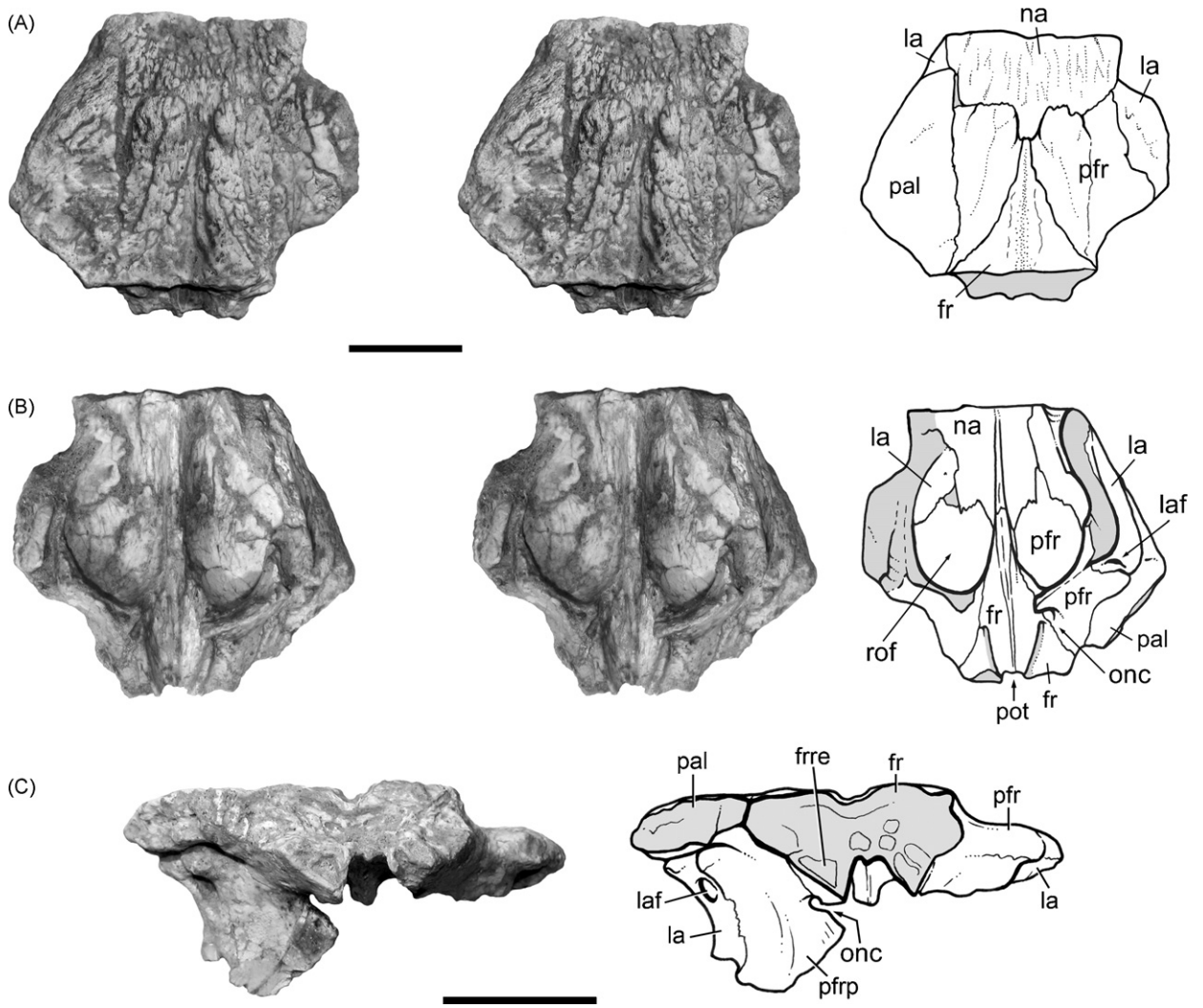

Fig. 2. *Wargosuchus australis* MOZ-PV 6134, fragment of skull roof in dorsal (**A**), ventral (**B**), and posterior (**C**) views. Abbreviations: **fr**, frontal; **frre**, frontal recess; **la**, lachrymal; **laf**, lachrymal foramen; **na**, nasal; **onc**, orbitonasal canal; **pal**, palpebral; **pfr**, prefrontal; **pfrp**, prefrontal pillar; **pot**, passage olfactory tract and associated vasculature; **rof**, recess for the olfactory bulb. Scale bar: 2 cm.

Fig. 2. *Wargosuchus australis* MOZ-PV 6134, fragment de la voûte crânienne en vue dorsale (**A**), ventrale (**B**) et postérieure (**C**). Abréviations : **fr**, frontal ; **frre**, repli frontal ; **la**, lacrymal ; **laf**, foramen lacrymal ; **na**, nasal ; **onc**, canal orbito-nasal ; **pal**, palpébral ; **pfr**, préfrontal ; **pfrp**, pilier préfrontal ; **pot**, conduite de l'appareil olfactif et vascularisation associée ; **rof**, repli pour le bulbe olfactif. Échelle : 2 cm.

der of the incisive foramen and immediately medial to the lower edge of the external naris. This fossa is directly associated with the narial passage and seems to represent the recess area for a gland, possibly related to the nasal epithelium.

5.2. Maxilla

In lateral view, the contact of the maxilla with the premaxilla is irregular, as shown in Fig. 1A, located close to the posterior edge of the paracanine depression. In the preserved portion, a foramen on the suture is not evidenced. In median view, part of the suture is evident at mid-height. In addition, just at the lower and mid-level of the paracanine depression, the premaxilla has a rough surface to accommodate the palatal process of the maxilla (Fig. 1B). Behind the diastematic paracanine depression, the maxilla alveolar border is partially broken; however, there is a rounded, large edge that may represent the mesial border of the alveolus for the first maxillary tooth.

The available portion of the skull roof includes part of nasals, fragments of the lachrymals, both prefrontals, a portion of the fused frontals, and the left palpebral

bone (Fig. 2). In dorsal aspect, the bones are deeply ornamented with deep, irregular grooves that become anastomozed in the nasals.

5.3. Nasal

The posteriormost portion of both nasals is the only preserved part. The median suture, with its counterpart, is not evident (possibly due to the strong ornamentation). The nasal has a wide contact with the prefrontal and a very small median contact with the acute rostral projection of the frontals (Fig. 2A). The suture of both nasals with the prefrontal bone is transversal and interdigited. The nasal is strongly, dorsally concave, forming a low surface with regard to the remaining portion of the skull roof. When observed laterally, the concavity of the nasals makes a notorious step in the dorsal profile of the skull, the skull roof (posterior to the level of the orbit) being more elevated than the snout.

In ventral view, the nasal is wedge-like, lying over the lachrymals and prefrontals. It has a median crest formed by the median joint of both nasals that runs posteriorly until the contact with the frontals. The frontals, in addition, form the remaining posterior portion of the crest. This crest, formed by the nasals and frontals, is deep and separates medially the olfactory depressions that would lodge the olfactory bulbs (see below).

5.4. Prefrontal

The prefrontals are the most notorious preserved bones, with a great dorsal exposure. In dorsal view, they are fairly rhomboidal, with two different surfaces. The medial surface is anteroposteriorly elongated and triangular. This portion of the bone is strongly ornamented, with a main deep groove diverging posteriorly and small furrows randomly distributed. The prefrontal contacts the frontal through a large, laterally concave suture. Both prefrontals converge rostrally, but they do not contact at midline; they are separated by a small cranial process of the frontals (Fig. 2A). The lateral surface of the prefrontal is separated from the rest of the skull roof by a step. This surface is large, almost unornamented, and provides support for the palpebral bone. The right palpebral is missing, exposing the dorsal surface of the lateral process of the prefrontal and its contact with the lachrymal (Fig. 2A).

In ventral view, the prefrontals also have a great exposure (Fig. 2A), forming most of the roof of the olfactory cavity. The left prefrontal is more complete, preserving part of the prefrontal pillar (i.e., descending process). The ventral flaring of the prefrontal pillar that would contact the palate (the palatine and the pterygoid) is not preserved. In the right side, the prefrontal pillar is broken, showing a hollow, subtriangular section that might represent the prefrontal recess [54]. The prefrontal pillar is a thin laminar bone, ventrally projected that separates the olfactory cavity from the orbital cavity. The prefrontal pillar has a rounded notch located near the medial contact with the frontal, just lateral to the space for the passage of the olfactory tract and associated vasculature, which constitute the posterolateral edge of the orbitonasal canal, for the passage of the nasal artery and vein [46,54] (Fig. 2B). In lateral and posteriorly views, the suture between the prefrontal pillar and the lachrymal descending process is observed, passing just posterior to the lachrymal foramen (Fig. 2C).

5.5. Frontal

The frontals only preserve their rostral portion. They are fused, triangular in shape, with an extremely sharp, acute angle that projects rostrally to meet the nasal through a very small suture. The frontals are ornamented as the remaining bones, but it is noteworthy that they have a deep and wide median groove that runs over all the length of the frontals until the beginning of the nasals, contrary to several notosuchians (*Comahuesuchus*, *Notosuchus*, and *Mariliasuchus*), where there is an axial ridge.

In ventral view, the frontals form the roof and walls of the constricted passage for the olfactory tract and associated vasculature that ends up at the olfactory cavity. The groove of the olfactory tract is laterally bordered by an acute descending process of the frontal, the *cristae cranii*, which would rostrally contact the prefrontal pillar and form the internal border of the orbitonasal canal (this contact and the internal border of the canal is not preserved in the holotype). At the level of the notch for the olfactory tract and associated vasculature, the frontals have a very low median crest that rostrally becomes more robust and tall. In posterior view, the broken profile of the skull roof exhibits a pneumatic frontal with notorious frontal recesses (Fig. 2C).

5.6. Lachrymal

The lachrymals are badly preserved. In the left side, it is nonetheless observed that the lachrymal, together with the prefrontal, supports the palpebral and that its ascending process contacts the prefrontal pillar. The lachrymal foramen is clearly observed in posterior view. The lachrymal canal runs rostrally parallel to the olfactory cavity, as evidenced by the endocast and the longitudi-

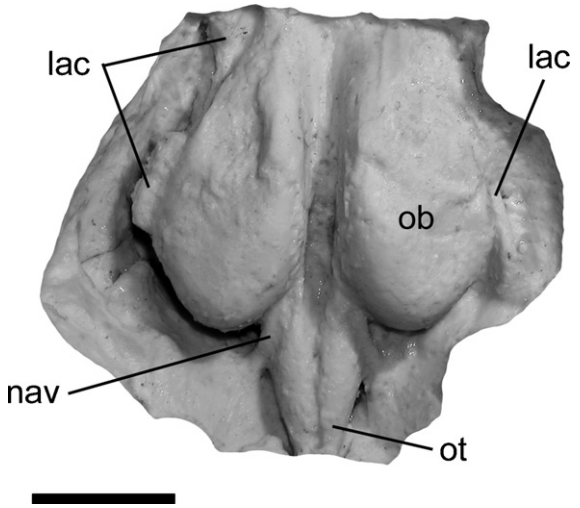

Fig. 3. *Wargosuchus australis* MOZ-PV 6134, plastic endocast of the internal side of the skull roof in dorsal view. Abbreviations: **lac**, nasolachrymal canal; **nav**, nasal artery and vein that run through the orbitonasal canal; **ob**, olfactory bulb; **ot**, olfactory tract and associated vasculature. Scale bar: 2 cm.
Fig. 3. *Wargosuchus australis* MOZ-PV 6134, moulage en plastique du côté interne de la voûte crânienne en vue dorsale. Abréviations : **lac**, canal nasolacrimal ; **nav**, artère et veine nasales sous le canal d'orbito-nasal ; **ob**, bulbe olfactif ; **ot**, appareil olfactif et vascularisation associée. Échelle : 2 cm.

nal fracture of the available portion of the skull. The lateral surface of the lachrymal is slightly concave and ornamented as the other skull bones.

5.7. Palpebral

In the left side of the skull, the palpebral is in natural position. It is very large and deep, even with its posterior border broken off. The ornamentation of the palpebral consists of small furrows, mainly distributed on its medial half. In dorsal view, the procumbent palpebral hides the lateral surface of the lachrymal by means of a robust shelf. With the evidence at hand, we cannot assume about the presence/absence of an additional palpebral bone (i.e., posterior palpebral).

5.8. Endocast

A plastic endocast was done with the skull fragment of MOZ-PV 6134 (Fig. 3) offering an opportunity to explore the internal structure of the posteriormost portion of the nasal cavity of *Wargosuchus*. Furthermore, it could be a useful tool to obtain characters to reconstruct the phylogenetic relationships among mesoeucrocodylians, at the time when these internal traits become available in the literature.

The plastic endocast shows the presence of large olfactory bulbs (Fig. 3), even much more prominent than in *Sebecus* [14]. Apparently, they are medially divided by an axial bony septum. In the endocranial cast of *Sebecus*, the olfactory bulbs seem to be more elongated anteroposteriorly and narrower transversely, lacking both a clear median division and an abrupt bulkiness just passing the frontal notch for the passage of the olfactory tract. In extant crocodylians, the olfactory bulbs are relatively smaller [14,43], and in the skull roof, the depression for these bulbs are shallow.

The large size of the depressions for the olfactory bulbs suggests a well-developed olfactory system [15]. Data on the size and shape of the olfactory bulbs is poorly documented in extinct mesoeucrocodylians. In *Wargosuchus* and *Notosuchus* (MACN-PV N 106), the olfactory bulbs are greatly developed, even more than in *Sebecus*, suggesting a specialized adaptation for useful smell. This inference agrees with the terrestrial mode of life of these notosuchians in contrast to extant eusuchians that have a poorly developed olfactory system related to the semiaquatic mode of life.

Other features observed in the endocast of *Wargosuchus* are the orbitonasal passage for the nasal artery and vein that runs close to the olfactory tract, and the nasolachrymal canal that runs from the nasolachrymal foramen to the olfactory bulbs (Fig. 3). The canals of both sides, in addition, run parallel, although separated by a thin wall.

5.9. Dentition

There are only two teeth preserved in the posterior portion of the premaxilla. Rostrally, this bone is broken off; thus, the precise number of premaxillary teeth remains uncertain. The two posterior premaxillary teeth differ considerably in size between them. The penultimate tooth has a basal circular cross-section, which is less than half the size of the last tooth. Most of the crown of this tooth is broken off, but apparently, it was slightly procumbent anteroventrally. The basal surface of the crown presents neither indication of serrated carinae nor texture enamel.

The last premaxillary tooth is large and caniniform in shape, even lacking its apex. It possible overhangs the lower jaw. It is robust, sub-conical, and slightly curved backward. In lateral view, the mesial border is straight, whereas the distal border is slightly concave. A poorly preserved minute carina with minuscule denticles is present on the disto-labial surface of this tooth. Additionally, the size of the paracanine depression indicates the presence of, at least, one

hypertrophied lower tooth, as commonly found among baurusuchids.

6. Discussion

Wargosuchus differs from *Notosuchus* and *Comahuesuchus* by the presence of a hypertrophied last premaxillary tooth followed by a deep and laterally opened paracanine depression. In *Notosuchus*, the last premaxillary tooth is also the largest [6,16], but its relative size with regard to the remaining teeth randomly varies among the specimens (MACN-RN 1040, which may represents a juvenile, is one of the most variable example).

In *Notosuchus*, in addition, the paracanine depression is absent. In *Comahuesuchus*, the third maxillary tooth is the largest, while the remaining teeth, including those of the premaxilla, are small [31]. *Comahuesuchus* has also a paracanine fossa, which is dorsally opened and located entirely in the maxilla, behind the hypertrophied tooth. In addition, in lateral view, the external nares are deeper in *Notosuchus* and *Comahuesuchus* than in *Wargosuchus*. The latter taxon has the posterior rims of the external nares forming a more acute angle than that observed in the two above-mentioned taxa.

The exact geographical and stratigraphical provenance of the holotype of *Cynodontosuchus rothi* (MLP 64-IV-16-25 (205)) is uncertain, but, because of its association with *Notosuchus*, it was assumed that *C. rothi* comes from the Bajo de la Carpa Formation [18], as *Wargosuchus* does. *Wargosuchus* differs from *Cynodontosuchus* in several features: in *Cynodontosuchus*, the premaxilla–maxilla suture is not observed, but it was inferred to be placed on the paracanine depression, where a lower tooth rests [17]. This hypothesis suggests that *Cynodontosuchus* has three premaxillary teeth, all small, of similar size, and circular in cross-section [17], clearly differing from the cases of *Wargosuchus*, in which the last premaxillary tooth is hypertrophied, and of other baurusuchids, which have heterodont premaxillary teeth. If the interpretation of the premaxilla–maxilla suture is wrong in *Cynodontosuchus*, and the suture should be in turn located more caudally or cranially, then, the relationship between the largest tooth and the paracanine depression is also notably different from the situation seen in *Wargosuchus*.

In *Baurusuchus pachecoi* and *B. salgadoensis*, there are four premaxillary teeth, the third being the hypertrophied one, whereas *Pabwehshi pakistanensis* [53] and *Stratiotosuchus maxhechti* have only three premaxillary teeth, the last one being the largest. In *Iberosuchus*, there are five premaxillary teeth, the three caudal teeth being larger than the first two ones [1]. In *Ilchunaia* [17,45], there are four premaxillary teeth, the second and the third ones being larger than the fourth one [45] (nevertheless, the latter tooth could be erupting). In *Sebecus*, *Aylusuchus*, and *Bretesuchus*, there are four premaxillary teeth, all similar in size [14,19,22]. In *Hamadasuchus*, there are four premaxillary teeth, the third one being the largest [29]. The relative size of the last two premaxillary teeth of *Wargosuchus* is similar to those of *Pabwehshi* and *Stratiotosuchus*, among sebecosuchians. Furthermore, the shape of the premaxilla and the edge of the external nares suggest that the number of premaxillary teeth in *Wargosuchus* should be three or four, but possibly no more.

Peirosaurids usually have five teeth in the premaxilla [12,21,39], with the penultimate tooth being the largest, differing, thus, from the case of *Wargosuchus*. Another difference is the relationships of the antero-posterior length of the premaxilla with the placement of the hypertrophied premaxillary tooth. In peirosaurids, and also trematochampsids [8,12,39], the antero-posterior length between the external nares and the last premaxillary tooth is larger than in notosuchians. In this way, the facial elongation of the premaxilla produces a more rostral placement of the external naris openings in comparison with the position of the last premaxillary tooth. Similar to most notosuchians, *Wargosuchus* exhibits a short premaxilla.

In *Wargosuchus*, the prefrontals are placed extremely close to each other, with only a minuscule contact between nasals and frontals. This situation is very different from that of most crocodyliforms (protosuchians, araripesuchids, basal notosuchians, *Sebecus*, *Iberosuchus* [Ortega, pers. comm.], peirosaurids, and neosuchians, excepting alligatorids; [26]) in which there is a relatively transverse, wide, nasal-frontal contact separating the prefrontals from the axial line of the skull. Noteworthy, a median contact between prefrontals, excluding the nasal-frontal contact, is recognized in *Baurusuchus salgadoensis* [13,51], which is quite similar to the case of *Wargosuchus*. In other baurusuchids, this region is unknown or poorly preserved. In *Stratiotosuchus,* the dorsal cranial bones are extremely sculptured and sutures appear to be difficult to recognize [11]. A detailed description of the skull of *Stratiotosuchus* was made by Riff [41], but unfortunately the relationships of the prefrontals with the surrounding bones are unclear. In *Stratiotosuchus*, the sutures of the prefrontals with the surrounding bones (e.g., nasal and frontal) are uncertain. For this reason, we prefer to be careful in evaluating the prefrontal relationships in *Stratiotosuchus*, which perhaps exhibits a situation similar to that of *Baurusuchus*.

The extremely close axially prefrontals (in contact in *B. salgadoensis*) should be taken in consideration because it would be a potential synapomorphy of Baurusuchidae.

The ornamentation of *Wargosuchus* resembles that of several notosuchians in having irregular grooves [6,36], whereas the pattern present in peirosaurids, araripesuchids, and other mesoeucrocodylians consists of deep and relatively regular pits and fossae [21,34].

Albeit the incompleteness of *Wargosuchus*, the comparisons suggest that it represents a new burly-built crocodyliform, with high and narrow rostrum, bearing heterodont teeth with at least one upper and one lower (inferred by the paracanine depression) robust caniniform tooth, as typically found among baurusuchids.

7. Conclusion

The new crocodyliform described, albeit based on a fragmentary specimen, indicates the occurrence of a new genus and species in the Santonian Bajo de la Carpa Formation, in Neuquén Province. In this unit, at the moment, five mesoeucrocodylian have been reported: *Notosuchus terrestris* [6,18,55], *Comahuesuchus brachybuccalis* [6,31], *Cynodontosuchus rothi* [16,55], *Lomasuchus palpebrosus*, and *Peirosaurus torminni* [21]. Largely, *Notosuchus* is the most frequent crocodyliform recovered from the Bajo de la Carpa Formation, especially in the localities of Paso Córdova (Río Negro Province) and Neuquén (Neuquén Province). The remaining species are sparser than *Notosuchus*, being *Cynodontosuchus*, *Wargosuchus*, *Lomasuchus*, and the Argentinean *Peirosaurus* based only on single specimens. The crocodyliform assemblage of the Bajo de la Carpa Formation represents one of the most taxonomically diverse in Argentina.

The finding of *Wargosuchus* in Patagonia, a taxon with a strong resemblance to Brazilian baurusuchids, reinforces the hypothesis of a similar biota in both regions by the Late Cretaceous. Besides, in our view, *Wargosuchus* and *Cynodontosuchus* represent the only Argentinean mesoeucrocodylians to be included within Baurusuchidae. This family is constituted by highly specialized terrestrial predators, which were more diverse and abundant in the Cretaceous of Brazil. Baurusuchids played apparently, in this land, the role of medium to large carnivores, because of the virtual absence of medium-to-large theropod dinosaurs. In Argentina, in contrast, the situation seems to be reversed, and theropods were the dominant medium-to-large carnivores in terrestrial ecosystems.

Acknowledgments

We thank J.F. Bonaparte for permitting us to study the specimen MOZ-PV 6134, A. Kramarz, S. Bargo, and M. Reguero for the access to the specimens under their care, S. Cocca for his help in identifying the catalogued number of *Wargosuchus*, F. Ortega for providing us with unpublished data on *Iberosuchus*, and D. Riff on *Stratiotosuchus*, and A. Forasiepi for comment on a draft of the manuscript. Also, we benefited from D. Pol's comments. Finally, we thank the editor P. Taquet and two anonymous reviewers.

References

[1] M.T. Antunes, *Iberosuchus*, crocodile sébécosuchien nouveau, l'éocene ibérique au nord de la Chaine centrale, et l'origine du canyon de Nazare, Com. Serv. Geol. Portugal 59 (1975) 285–330.
[2] J.T. Arruda, I.S. Carvalho, F.M. Vasconcellos, Baurusuquídeos da Bacia Bauru (Cretáceo Superior, Brasil), An. Inst. Geocienc. 27 (2004) 65–75.
[3] M.J. Benton, J.M. Clark, Archosaur phylogeny and the relationships of the Crocodylia, in: M.J. Benton (Ed.), The Phylogeny and Classification of the Tetrapods, 1, Clarendon Press, Oxford, UK, 1988, pp. 295–338.
[4] D. Berg, Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*? Aus dem Eozän von Messel bei Darmstadt/Hessen, Abh. Hess. Land. Bod. 52 (1966) 1–105.
[5] R.J. Bertini, F.F. Manzini, M. Brandt Neto, Novas ocorrências de Baurusuchidae (Sebecosuchia: Crocodylomorpha) na região de General Salgado, Formação Adamantina (Cretáceo Superior) do Grupo Bauru na região noroeste do Estado de São Paulo, Acta Geol. Leopold. 49 (1999) 29–38.
[6] J.F. Bonaparte, Los vertebrados fósiles de la Formación Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico Superior, Argentina, Rev. Mus. Arg. Cns. Nat. Paleontol. 4 (1991) 17–123.
[7] G. Buckley, C. Brochu, D. Krause, D. Pol, A pug-nosed crocodyliform from the Late Cretaceous of Madagascar, Nature 405 (2000) 941–944.
[8] E. Buffetaut, Ostéologue et affinities de *Trematochampsa taqueti* (Crocodylia, Mesosuchia) du Sénonien inférieur d'in Beceten (république du Niger), Geobios 9 (1976) 143–198.
[9] E. Buffetaut, Radiation évolutive, paléoécologie et biogéographie des crocodiliens mésosuchiens, Mem. Soc. geol. France 142 (1982) 1–88.
[10] C.R. Candeiro, A.G. Martinelli, Paleogeographical and chronostratigraphical distribution of mesoeucrocodylian species from the Upper Cretaceous beds from Bauru (Brazil) and Neuquén (Argentina) Groups, Southern South America, J. South Am. Earth Sci. 22 (2006) 116–129.
[11] D.A. Campos, J.M. Suarez, D. Riff, A.W.A. Kellner, Short note on a new Baurusuchidae (Crocodyliformes, Metasuchia) from Upper Cretaceous of Brazil, Bol. Mus. Nac., Ser. Geol. 57 (2001) 1–7.
[12] I.S. Carvalho, L.C.B. Ribeiro, L.S. Avilla, *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil, Gond. Res. 7 (2004) 975–1002.
[13] I.S. Carvalho, A.C.A. Campos, P.H. Nobre, *Baurusuchus salgadoensis*, a new Crocodylomorpha (Cretaceous), Brazil, Gond. Res. 8 (2005) 11–30.

[14] E.H. Colbert, *Sebecus*, representative of a peculiar Suborder of fossil Crocodilia from Patagonia, Bull. Am. Mus. Nat. Hist. 87 (1946) 221–270.
[15] D.C. Evans, Nasal cavity homologies and cranial crest function in lambeosaurine dinosaurs, Paleobiology 32 (2006) 109–125.
[16] Z.B. Gasparini, Los Notosuchia del Cretácico de América del Sur como un nuevo infraorden de los Mesosuchia (Crocodylia), Ameghiniana 8 (1971) 83–103.
[17] Z.B. Gasparini, Los Sebecosuchia (Crocodylia) del territorio Argentino. Consideraciones sobre su "status" taxonómico, Ameghiniana 9 (1972) 23–34.
[18] Z.B. Gasparini, Los Crocodylia fósiles de Argentina, Ameghiniana 18 (1981) 177–205.
[19] Z.B. Gasparini, New Tertiary Sebecosuchia (Crocodylia: Mesosuchia) from Argentina, J. Vertebr. Paleontol. 4 (1984) 85–95.
[20] Z.B. Gasparini, Biogeographic evolution of the South American crocodilians, in: G. Arratia (Ed.), Contribution of sourthern South America to Vertebrate Paleontology, Muench. Geowiss. Abh. A (1996) 159–184.
[21] Z.B. Gasparini, L. Chiappe, M. Fernandez, A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American crocodylians, J. Vertebr. Paleontol. 17 (1991) 316–333.
[22] Z.B. Gasparini, M. Fernandéz, J. Powell, New Tertiary sebecosuchians (Crocodylomorpha) from South America: Phylogenetic Implications, Hist. Biol. 7 (1993) 1–19.
[23] E.M. Gomani, A crocodyliform from the Early Cretaceous dinosaur beds, Northern Malawi, J. Vertebr. Paleontol. 17 (1997) 280–294.
[24] M. Hecht, M. Archer, Presence of ziphodont crocodilians in the Tertiary and Pleistocene of Australia, Alcheringa 1 (1977) 383–385.
[25] C.A. Hugo, H.A. Leanza, Hoja Geológica 3969-IV, General Roca. Provincias de Río Negro y Neuquén, Bol. Serv. Geol. Min. Arg., Inst. Geol. Rec. Min. 308 (2001) 1–65.
[26] N.N. Iordansky, The skull of the Crocodilia, in: C. Gans, T.S. Parsons (Eds.), Biology of Reptilia, 4, Academic Press, New York, 1973, pp. 201–261.
[27] W. Langston Jr., The Sebecosuchia: Cosmopolitan crocodilians? Am. J. Sci. 254 (1956) 605–614.
[28] H.C.E. Larsson, B. Gado, A new Early Cretaceous crocodyliform from Niger, Neues Jahrb. Geol. Palaeontol. Abh. 217 (2000) 131–141.
[29] H.C.E. Larsson, H.-D. Sues, Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco, Zool. J. Linn. Soc. 149 (2007) 533–567.
[30] F.F. Manzini, M. Brandt Neto, L.D. Vizotto, Cintura pélvica de *Baurusuchus pachecoi* Price, 1945, em sedimentos da Formação Adamantina (Grupo Bauru, Cretáceo Superior), IVo Simp. Cretác, Brasil (Rio Claro), Abstracts, 1996, pp. 273–276.
[31] A.G. Martinelli, New cranial remains of the bizarre notosuchid *Comahuesuchus brachybuccalis* (Archosauria, Crocodyliformes) from the Late Cretaceous of Río Negro Province (Argentina), Ameghiniana 40 (2003) 559–572.
[32] D. Nash, The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho, Ann. S. Afr. Mus. 67 (1975) 227–329.
[33] F. Ortega, A.D. Buscalioni, Z.B. Gasparini, Reinterpretacion and new denomination of *Atacisaurus crassiproratus* (Middle Eocene; Issel, France) as cf. *Iberosuchus* (Crocodylomorpha, Metasuchia), Geobios 29 (1996) 353–364.
[34] F. Ortega, Z.B. Gasparini, A. Buscalioni, J. Calvo, A new species of *Araripesuchus* (Crocodylimorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina), J. Vertebr. Paleontol. 20 (2000) 57–76.
[35] A. Paolillo, O.J. Linares, Nuevos cocodrilos Sebecosuchia del Cenozoico suramericano (Mesosuchia: Crocodylia), Paleobiol. Neotrop. 3 (2007) 1–25.
[36] D. Pol, New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil, J. Vertebr. Paleontol. 23 (2003) 817–831.
[37] D. Pol, S. Apesteguía, New *Araripesuchus* remains from the early Late Cretaceous (Cenomanian–Turonian) of Patagonia, Am. Mus. Nov. 3490 (2005) 1–38.
[38] L.I. Price, A new reptile from the Upper Cretaceous of Brazil, Serv. Geol. Min. 25 (1945) 1–8.
[39] L.I. Price, Novos crocodilideos dos Arenitos da Série Bauru, Cretáceo do Estado de Minas Gerais, An. Acad. Bras. Cienc. 27 (1955) 487–498.
[40] L.I. Price, Sobre um crocodilideo notosúquido do Cretáceo Brasileiro, Bol. Div. Geol. Min. Rio de Janeiro 188 (1959) 1–55.
[41] D. Riff, Descrição morfológica do crânio e mandíbula de *Stratiotosuchus maxhechti* (Crocodylomorpha, Cretáceo Superior do Brasil) e seu posicionamento filogenético. Dissertação (Mestrado), UFRJ/Museu Nacional/Programa de Pós-graduação em Ciências Biológicas (Zoologia), 2003, p. 173.
[42] D. Riff, A.W.A. Kellner, On the dentition of *Baurusuchus pachecoi* Price (Crocodyliformes, Metasuchia) from the Upper Cretaceous of Brazil, Bol. Mus. Nac., Sér. Geol. 59 (2001) 1–15.
[43] A.S. Romer, Osteology of the Reptiles, University of Chicago Press, Chicago, 1956 (772 p.).
[44] C. Rusconi, Sobre reptiles Cretácicos del Uruguay (*Uruguaysuchus aznarezi* n.g.sp.) y sus relaciones con los notosúquidos de Patagonia, Inst. Geol. Perforac., Bol. 19 (1933) 3–63.
[45] C. Rusconi, Ave y reptil oligocenos de Mendoza, Bol. Paleontol. (Buenos Aires) 21 (1946) 1–3.
[46] J.C. Sedlmayr, Anatomy, evolution and functional significance of cephalic vasculature in Archosauria, PhD thesis, Ohio University, 2002 (398 p.).
[47] P.C. Sereno, H.C. Larsson, C.A. Sidor, B. Gado, The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa, Science 294 (2001) 1516–1519.
[48] P.C. Sereno, C.A. Sidor, H.C. Larsson, B. Gado, A new notosuchian from the Early Cretaceous of Niger, J. Vertebr. Paleontol. 23 (2003) 477–482.
[49] A.H. Turner, Osteology and phylogeny of a new species of *Araripesuchus* (Crocodyliformes: Mesoeucrocodylia) from the Late Cretaceous of Madagascar, Hist. Biol. (2006) 1–115.
[50] A.H. Turner, J.O. Calvo, A new sebecosuchian crocodyliform from the Late Cretaceous of Patagonia, J. Vertebr. Paleontol. 25 (2005) 84–95.
[51] F.M. Vasconcellos, I.S. Carvalho, Cranial features of *Baurusuchus salgadoensis* Carvalho, Campos, Nobre 2005, a Baurusuchidae (Mesoeucrocodylia) from the Adamantina Formation, Bauru Basin, Brazil: paleoichonological, taxonomic and systematics implications, in: I.S. Carvalho, et al. (Eds.), Paleontologia: Cenários de Vida, Editora Interciência, Rio de Janeiro, 2007, pp. 319–332.
[52] K.N. Whetstone, P. Whybrow, A 'cursorial' crocodilian from the Triassic of Lesotho (Basutoloand), southern Africa, Pap. Mus. Nat. Hist. Univ. Kansas 106 (1983) 1–37.
[53] J.A. Wilson, M.M. Malkani, P.D. Gingerich, New crocodyliform (Reptilia, Mesoeucrocodylia) from the Upper Cretaceous

Pab Formation of Vitakri, Balochistan (Pakistan), Contrib. Mus. Paleontol. Univ. Mich. 30 (2001) 321–336.

[54] L.M. Witmer, Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae, J. Morphol. 225 (1995) 269–327.

[55] A.S. Woodward, On two Mesozoic crocodilians *Notosuchus* (genus novum) and *Cynodontosuchus* (genus novum) from the Red Sandstones of the Territory of Neuquén (Argentina Republic), An. Mus. de La Plata, Paleontol. 4 (1896) 1–20.