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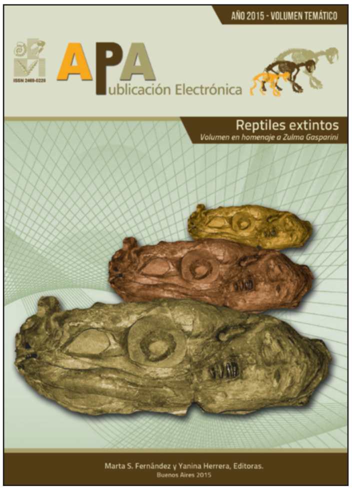

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Reptiles extintos

*Volumen en homenaje a Zulma Gasparini*

Marta S. Fernández y Yanina Herrera, Editoras.
Buenos Aires 2015

# METRIORHYNCHIDAE (CROCODYLOMORPHA: THALATTOSUCHIA) FROM UPPER JURASSIC–LOWER CRETACEOUS OF NEUQUÉN BASIN (ARGENTINA), WITH COMMENTS ON THE NATURAL CASTS OF THE BRAIN

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# METRIORHYNCHIDAE (CROCODYLOMORPHA: THALATTOSUCHIA) FROM UPPER JURASSIC–LOWER CRETACEOUS OF NEUQUÉN BASIN (ARGENTINA), WITH COMMENTS ON THE NATURAL CASTS OF THE BRAIN

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**Abstract.** Metriorhynchidae was the only Crocodylomorpha with a pelagic marine lifestyle. Related to this lifestyle, its peculiar body plan allows clearly differentiate them from others Crocodylomorpha. The fossil record of metriorhynchids from Tithonian–Berriasian levels of the Vaca Muerta Formation (Neuquén Basin, Argentina) is outstanding, in terms of quantitative and qualitative record. Its taxonomical diversity is composed by four taxa: *Cricosaurus araucanensis*, *Cricosaurus lithographicus*, *Dakosaurus andiniensis*, and *Purranisaurus potens*. This fossil record is also characterized by the tridimensional preservation of the materials and by the preservation of numerous natural endocasts of the skull cavities. Here, I made a description of the natural endocasts of the brain of *Cricosaurus araucanensis* together with a synthesis of the advances in the knowledge of these four taxa that were performed during the last years. The information that provides the endocasts, together with the quantity of endocasts, make of the Patagonian fossil record of metriorhynchids a key to the exploration and reconstruction of soft anatomy of these crocodylomorphs, and for the understanding of the physiological changes that accompanied the structural changes of the skeleton. Understanding these changes will allow defining the key innovations that allowed to the metriorhynchids conquer the pelagic environment, unparalleled among archosaurs.

**Key words.** *Cricosaurus*. *Dakosaurus*. *Purranisaurus*. Tithonian. Berriasian. Vaca Muerta Formation. Paleobiological aspects.

**Resumen.** METRIORHYNCHIDAE (CROCODYLOMORPHA: THALATTOSUCHIA) DEL JURÁSICO SUPERIOR–CRETÁCICO INFERIOR DE LA CUENCA NEUQUINA (ARGENTINA), CON COMENTARIOS SOBRE LOS MOLDES NATURALES DEL ENCÉFALO. Los Metriorhynchidae fueron los únicos Crocodylomorpha con un estilo de vida marino pelágico. Relacionado con este estilo de vida, su peculiar plan corporal permite diferenciarlos claramente de los demás Crocodylomorpha. El registro fósil de los metriorrínquidos titonienses–berriasienses de la Formación Vaca Muerta (Cuenca Neuquina, Argentina) es excepcional, tanto en términos cuantitativos como cualitativos. Su diversidad taxonómica está compuesta por cuatro taxones: *Cricosaurus araucanensis*, *Cricosaurus lithographicus*, *Dakosaurus andiniensis* y *Purranisaurus potens*. Este registro fósil también se caracteriza por la preservación tridimensional de los materiales y por la preservación de numerosos moldes naturales de las cavidades del cráneo. En este trabajo se presenta una descripción de los moldes naturales del encéfalo de *Cricosaurus araucanensis* junto con una síntesis de los avances en el conocimiento realizados, en los últimos años, sobre estos cuatro taxones argentinos. La calidad de la información que aporta los moldes naturales, sumado a la cantidad de moldes recuperados, hacen del registro patagónico una pieza clave para la exploración y reconstrucción de la anatomía blanda de estos crocodilomorfos, y para la comprensión de los cambios fisiológicos que acompañaron los cambios estructurales del esqueleto. La comprensión de estos cambios permitirá delimitar las innovaciones evolutivas claves que le permitieron a los metriorrínquidos la conquista, sin paralelo entre los arcosaurios, del medio pelágico.

**Palabras clave.** *Cricosaurus*. *Dakosaurus*. *Purranisaurus*. Titoniense. Berriasiense. Formación Vaca Muerta. Aspectos paleobiológicos.

THROUGHOUT the Neuquén Basin (west-central Argentina), several localities have yielded abundant and well-preserved Mesozoic marine reptiles remains. They come from Early Jurassic to Early Cretaceous levels and constitute the most diverse marine herpetofauna from Gondwana. This remarkable assemblage is mainly conformed by ichthyosaurs, pliosaurs, marine testudines, and metriorhynchids (Gasparini and Fernández, 2005, 2011).

Metriorhynchidae was a successful group of crocodylomorphs that differs from all other crocodylomorphs by: paddle-like forelimbs, hypocercal tail, osteoporotic-like bone tissue, loss of osteoderms (*e.g.*, Fraas, 1902; Andrews, 1913; Hua and Buffrénil, 1996; Young *et al.*, 2010), and enlarged external carotid foramen and canal, enlarged and highly vascularised nasal salt gland, preorbital fenestra related with the drainage of salt gland, and reduced olfactory tract and bulbs (Fernández and Gasparini, 2000, 2008; Fernández and Herrera, 2009; Pol and Gasparini, 2009; Fernández *et al.*, 2011; Herrera *et al.*, 2013a; Herrera and Vennari, 2015). Metriorhynchidae is a Middle Jurassic to Early Cretaceous group that mainly lived in the Tethys and Pacific oceans. Regarding South America, the oldest record of metriorhynchids from Argentina comes from upper Bathonian (Middle Jurassic) of Los Molles Formation (Gasparini *et al.*, 2005). However, the fossil record of metriorhynchids is particularly abundant, and well preserved, in Tithonian–Berriasian levels of the Vaca Muerta Formation.

The first detailed studies of metriorhynchids from Argentina (*e.g.*, Gasparini, 1973a; Gasparini and Dellapé, 1976) were originated from the doctoral thesis performed by Dr. Zulma Brandoni de Gasparini (Gasparini, 1973b). Later, she also conducted a series of studies about Chilean (*e.g.*, Gasparini and Chong Díaz, 1977; Gasparini *et al.*, 2000) and Cuban (*e.g.*, Gasparini and Iturralde-Vinent, 2001) metriorhynchids. For almost 30 years, her work was focused in the description of new taxa and the study of their paleobiogeographic relations with Tethys fauna (*e.g.*, Gasparini and Dellapé, 1976; Gasparini and Chong Díaz, 1977; Vignaud and Gasparini, 1996; Gasparini *et al.*, 2000). In the late 90s, the finding of some natural casts of the nasal salt gland of *Cricosaurus araucanensis* in the collection of the División Paleontología Vertebrados (Museo de La Plata) was the base of a series of works in which paleobiological aspects of Patagonian metriorhynchid began to be analyzed. Fernández and Gasparini (2000, 2008), Fernández and Herrera (2009), and Herrera *et al.* (2013a) described the natural casts of the preorbital region (*i.e.*, nasal gland, paranasal sinus system and related structures) of the skull.

The latest Patagonian metriorhynchids review was made by Pol and Gasparini (2007). Since that date a lot of progresses were made, mainly in some paleobiological aspects of the group. Here I review the advances in the knowledge of the group in Argentina for the four Late Jurassic–Early Cretaceous taxa found in several localities of the Vaca Muerta Formation (Neuquén Basin), which were previously studied by Zulma Gasparini. Additionally, and mostly based on the material found in the fieldtrips conduced in 2008–2011 in the Pampa Tril area (Vaca Muerta Formation), a description of the natural brain endocasts of *Cricosaurus araucanensis* is included.

***Institutional abbreviations*. MHNSR,** Museo de Historia Natural de San Rafael, San Rafael, Mendoza, Argentina; **MLP,** Museo de La Plata, La Plata, Buenos Aires, Argentina; **MJCM,** Museo de Ciencias Naturales y Antro-pológicas "Juan Cornelio Moyano", Mendoza, Argentina; **MOZ,** Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher", Zapala, Neuquén, Argentina.

## METRIORHYNCHIDS FROM VACA MUERTA FORMATION

Based on the supra-generic taxonomy of Metriorhynchoidea updated by Young and Andrade (2009), Young *et al.* (2010, 2011), and Cau and Fanti (2011), the Late Jurassic–Early Cretaceous Argentinean metriorhynchids are included in the Rhacheosaurini and Geosaurini tribes. Rhacheosaurini are mainly characterized by having gracile skulls with long and tubular snouts, and acute carinated teeth without true denticles in the carinae (*e.g.*, *Cricosaurus*), whereas Geosaurini have strong skull, bicarinated, large and robust teeth with a row of true denticles along the carinae (*e.g.*, *Dakosaurus*).

## SYSTEMATIC PALEONTOLOGY

Superorder CROCODYLOMORPHA Walker, 1970
Infraorder THALATTOSUCHIA Fraas, 1901
Family METRIORHYNCHIDAE Fitzinger, 1843 (*sensu* Young and Andrade, 2009)
Subfamily METRIORHYNCHINAE Fitzinger, 1843 (*sensu* Young and Andrade, 2009)
Tribe RHACHEOSAURINI Young, Bell and Brusatte, 2011

Genus ***Cricosaurus*** Wagner, 1858

***Type species.*** *Steneosaurus* [sic] *elegans* Wagner, 1852. Early Tithonian, Mörnsheim Formation, Germany.

***Cricosaurus araucanensis*** (Gasparini and Dellapé, 1976)
Figures 1–2

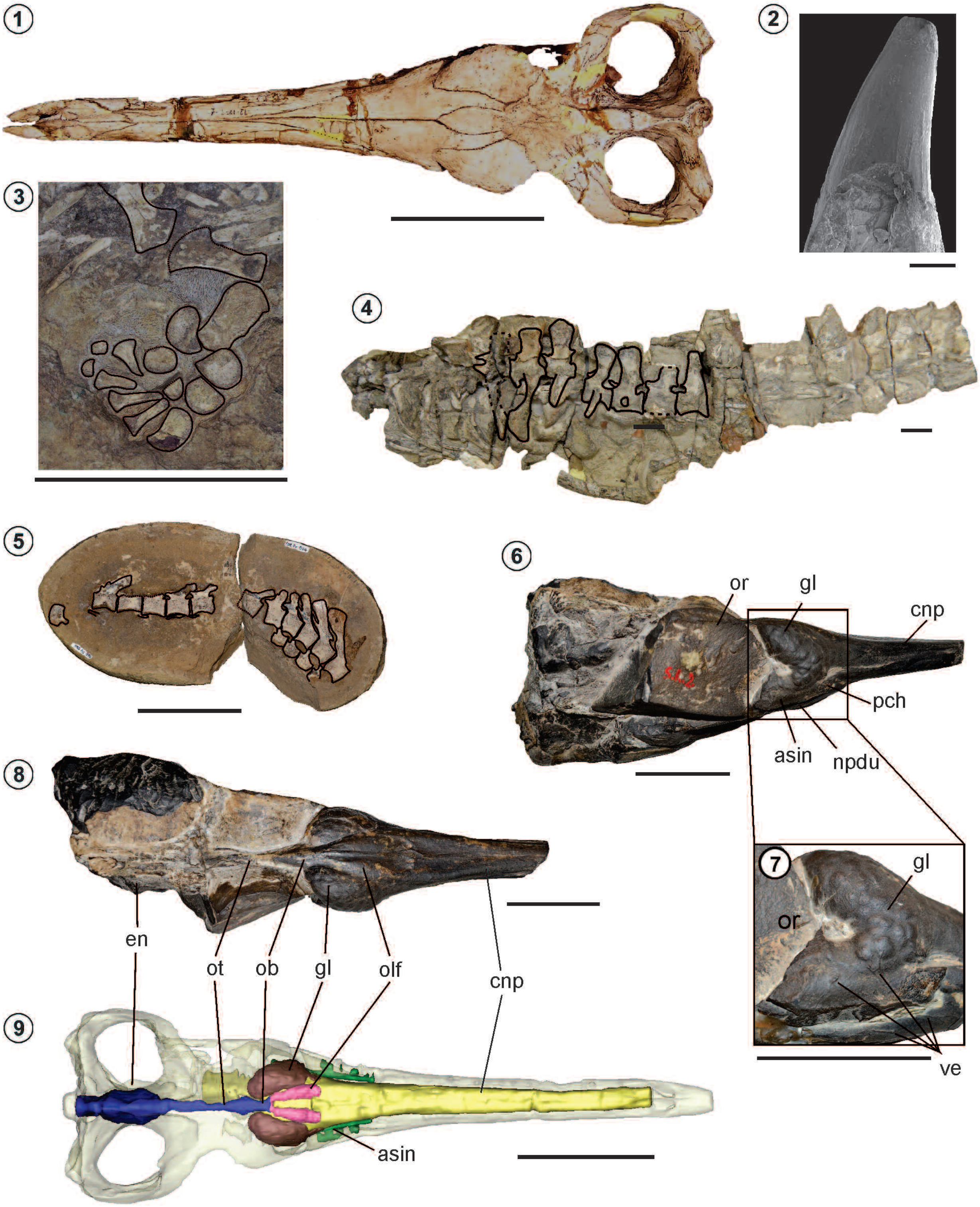

**Figure 1.** ***Cricosaurus araucanensis*****. 1, MLP 72-IV-7-1,** skull in dorsal view; **2, MLP 72-IV-7-4,** maxilar tooth in lingual view; **3, MLP 73-II-27-1,** left forelimb in ventral view; **4, MLP 73-II-27-6,** postcranial elements in left lateral view; **5, MOZ-PV 066,** caudal vertebrae in left lateral view showing the tail bend region; **6, MLP 76-XI-19-1,** natural endocast in right lateral view; **7,** detail of nasal salt gland in ventrolateral view; **8, MLP 76-XI-19-1,** natural endocast in dorsal view; **9, MLP 72-IV-27-1** reconstructed skull, paranasal sinuses and other cephalic components in dorsal view. Scale bars= 1, 5, 9, 100 mm; 2, 1 mm; 3, 6–8, 50 mm; 4, 30 mm. Abbreviations: **asin,** antorbital sinus; **cnp,** nasal cavity proper; **en,** endocast of brain cavity; **gl,** exocrine gland; **npdu,** nasopharyngeal duct; **ob,** olfactory bulb; **olf,** olfactory region of the nasal cavity; **or,** orbit; **ot,** olfactory tract; **pch,** primary choana; **ve,** vessel.

***Holotype.*** MLP 72-IV-7-1, complete skull and mandible, and postcranial elements comprised by five postaxial cervical vertebrae, 16 dorsal vertebrae, two sacral and four caudal vertebrae, ribs, gastralia, haemal arches, incomplete pectoral girdle and forelimbs, and incomplete pelvic girdle and hind limbs.

***Referred material.*** Specimens MPL 72-IV-7-2, MLP 72-IV-7-3, MLP 72-IV-7-4, MLP 72-IV-7-10, MLP 73-II-27-1, MLP 73-II-27-6, MLP 86-XI-5-7, MLP 86-XI-10-6*, MLP 86-XI-10-7, MLP 92-III-6-1*, MOZ-PV 066 are represented by skeletal elements (partially preserved skulls and/or postcranial elements, in a few cases [*] portions of natural endocasts are exposed), whereas the specimens MLP 73-II-27-3, MLP 76-XI-19-1, MLP 84-V-1-1, MOZ-PV 7201, MOZ-PV 7202, MOZ-PV 7204, MOZ-PV 7207, and MOZ-PV 7261 are natural endocasts of the skull cavities.

***Ocurrence.*** The holotype and the specimens MPL 72-IV-7-2, MLP 72-IV-7-3, MLP 72-IV-7-4, MLP 72-IV-7-10, MLP 86-XI-5-7, MLP 73-II-27-6, MLP 86-XI-10-6, and MLP 92-III-6-1 were found in Cerro Lotena (Portada Covunco Member, middle Tithonian). Specimens MLP 73-II-27-1, MLP 73-II-27-2, MLP 73-II-27-4, MLP 73-II-27-5, and MLP 73-II-27-3 came from Tithonian sediments of the Bosque Petrificado (about 7 km to southwest of Cerro Lotena). MLP 86-XI-10-7 was found in Cerro Granito (Tithonian). MOZ-PV 7202, MOZ-PV 7203, MOZ-PV 7204, MOZ-PV 7207 were found in Yesera del Tromen-Pampa Tril (Tithonian-Berriasian). All these sites are located in Neuquén Province. MLP 76-XI-19-1 and MLP 84-V-1-1 were found in Tithonian levels of Sierra de Reyes in Mendoza Province.

***Comments.*** Gasparini and Dellapé (1976) nominated the species as *Geosaurus araucanensis* and described an excellent three-dimensional preserved skull. More than 30 years after its nomination *Geosaurus araucanensis* was re-assigned to *Cricosaurus*, based on the proposal of Young and Andrade (2009). *Cricosaurus araucanensis* is one of the most complete and best-known taxon of the cosmopolitan genus *Cricosaurus*. In its original description, the authors mentioned the postcranial elements preservation associated to the skull but they did not describe them. Worldwide, the postcranial elements of metriorhynchids in general are poorly documented in comparison with their skulls. The postcranial description of *C. araucanensis* revealed that the deeply modified forelimbs transformed as paddles and its poor ossification, together with the delayed timing of neurocentral closure, which was observed in caudal vertebrae, are related with the occurrence of skeletal paedomorphosis, a widespread heterochronic process among secondarily adapted aquatic reptiles (Herrera *et al.*, 2009, 2013b; Herrera, 2012). The morphology of the caudal region with the transverse processes of the first caudal vertebrae ventrally deflected, and the reduction of the fourth trochanter, suggested a reduction of the hypaxial musculature allowing an increase in the epaxial musculature (Herrera *et al.*, 2013b). Additionally, the shape and the reduced size of the pelvic girdle of metriorhynchids indicate a reduction in available space for hind limb´s muscles and therefore a reduction of the musculature of the limb. This suggests that some movements of the hind limb were limited and probably do not allow to metriorhynchids to move in land (Herrera *et al.*, 2014a). According to the body length estimation (2.6 m) *Cricosaurus araucanensis* is the smallest metriorhynchid found in the Neuquén Basin, similar in body length to *Cricosaurus vignaudi* (Frey, Buchy, Stinnesbeck, and López-Oliva, 2002) and larger than *Cricosaurus elegans* (Wagner, 1852) (1.4 m) (Herrera, 2012).

The first description of a metriorhynchid natural endocast corresponds to the description of the nasal salt gland of *Cricosaurus araucanensis* made by Fernández and Gasparini (2000). In 2008, Fernández and Gasparini proposed that the hypertrophied salt gland of *C. araucanensis* had a high excretory capability and that *C. araucanensis* represents an advanced stage of the basic physiological model to marine adaptations in reptiles. Fernández and Herrera (2009) described the natural snout endocasts and proposed that the modifications of the paranasal sinus system were associated with the internalization of the antorbital cavity and the development of a neomorphic opening for salt glands drainage (*i.e.*, preorbital opening and fossa). The more recent study of the natural snout endocasts includes the construction of a digital cast based on CT scan of the holotype (Herrera *et al.*, 2013a). This study indicates that the skeletal changes of metriorhynchids were coupled with changes in the soft anatomy of cephalic structures. The comparison between the natural and digital cast showed that both data are congruent, and they can be combined to generate an accurate reconstruction, which improves our knowledge of the preorbital anatomy of metriorhynchids. Based on this study the authors proposed that the nasal salt glands were structures highly vascularised, and the reduction of the olfactory bulbs and tract indicates that the aerial olfaction was not well developed in this group.

A significant number of well-preserved natural casts of the brain of *Cricosaurus araucanensis* (Fig. 2) were recently exhumed in Tithonian levels of the Vaca Muerta Formation, in the Pampa Tril area (Herrera *et al.*, 2014b). Only in the

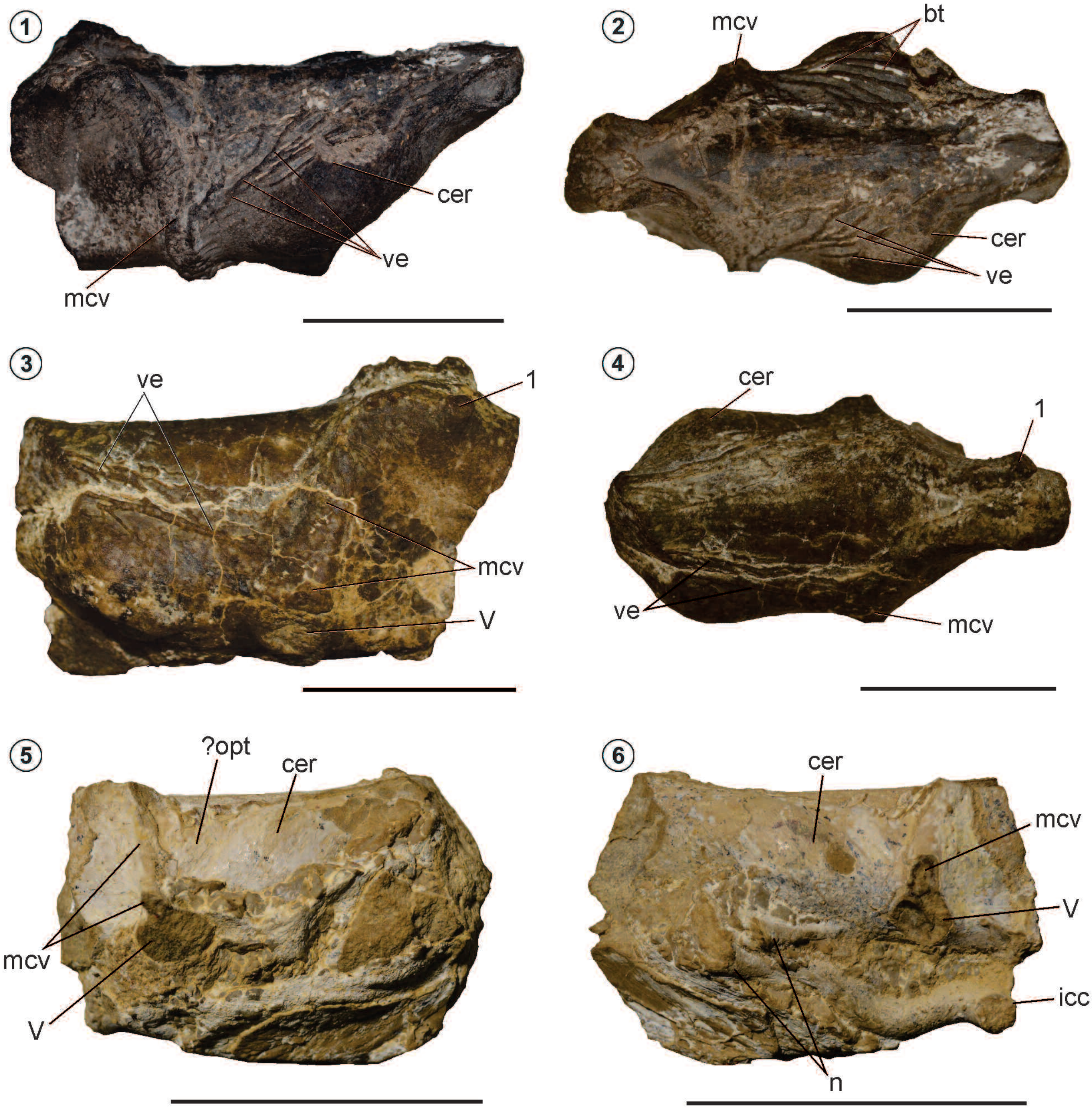

**Figure 2.** *Cricosaurus araucanensis* natural brain endocast. **1–2, MOZ-PV 7201; 1,** right lateral view; **2,** dorsal view; **3–4, MOZ-PV 7261; 3,** left lateral view; **4,** dorsal view; **5–6, MLP 73-II-27-3; 5,** right lateral view; **6,** left lateral view. Scale bars= 1–4, 25 mm; 5–6, 100 mm. Abbreviations: **bt,** bone tissue; **cer,** cerebral hemisphere; **icc,** internal carotid canal; **mcv,** middle cerebral vein; **n,** cranial nerves canals; **?opt,** optic lobe; **ve,** vessel; **1,** tube-like cavity; **V,** cranial nerve foramen and/or canal.

specimen MLP 76-XI-19-1 the endocast is completely preserved, from the olfactory bulbs to the medulla oblongata, but is it not completely exposed (Fig. 1.6, 8). In most of the specimens the olfactory tract and bulbs are not preserved. The endocasts are elongated and the angles formed by the hindbrain, midbrain and forebrain are not developed, and the cerebral hemisphere are laterally extended (Figs. 1.6, 2). Conspicuous blood vessel fillings cover almost all the dorsal surface of the cerebral hemispheres (Fig. 2.1–4). In some specimens, between these blood vessel fillings, there is bone tissue preserved (Fig. 2.2). In the lateral view of the endocasts there is a bilobate filling with the posterodorsal lobule much smaller than the anteroventral one. The small lobule corresponds to the middle cerebral vein and the large to the trigeminal nerve/ganglion (Fig. 2.). In MOZ PV 7201 (Fig. 2.2) the blood vessel fillings that cover the cerebral hemispheres are connected to the middle cerebral vein. In MLP 73-II-27-3, between the cerebral hemispheres and the middle cerebral vein, a small protuberance is recognized. This structure would correspond to the optic lobe (Fig. 2.5). In MLP 73-II-27-3 conspicuous filling of cranial nerves are preserved (Fig. 2.6). The proximal portion of cavity 1 of Fernández *et al.* (2011), cavity that connects the dorsal longitudinal venous sinus with the cranio-quadrate foramen, was identified in both sides of MOZ-PV 7261 (Fig. 2.3–4), and in the digital cast of the holotype of *Cricosaurus araucanensis* (Herrera *et al.*, in progress). In MOZ-PV 7261 the proximal portion of the cavity 1 is preserved as a protuberance in the dorsoposterior region of the brain (Fig. 2.3–4).

### ***Cricosaurus lithographicus*** Herrera, Gasparini and Fernández, 2013
### Figure 3

***Holotype.*** MOZ-PV 5787, complete skull with articulated lower jaws, postcranium composed by cervical, dorsal, sacral and caudal vertebrae, an isolated pectoral girdle element, incomplete forelimb and hind limb, pelvic girdle elements.

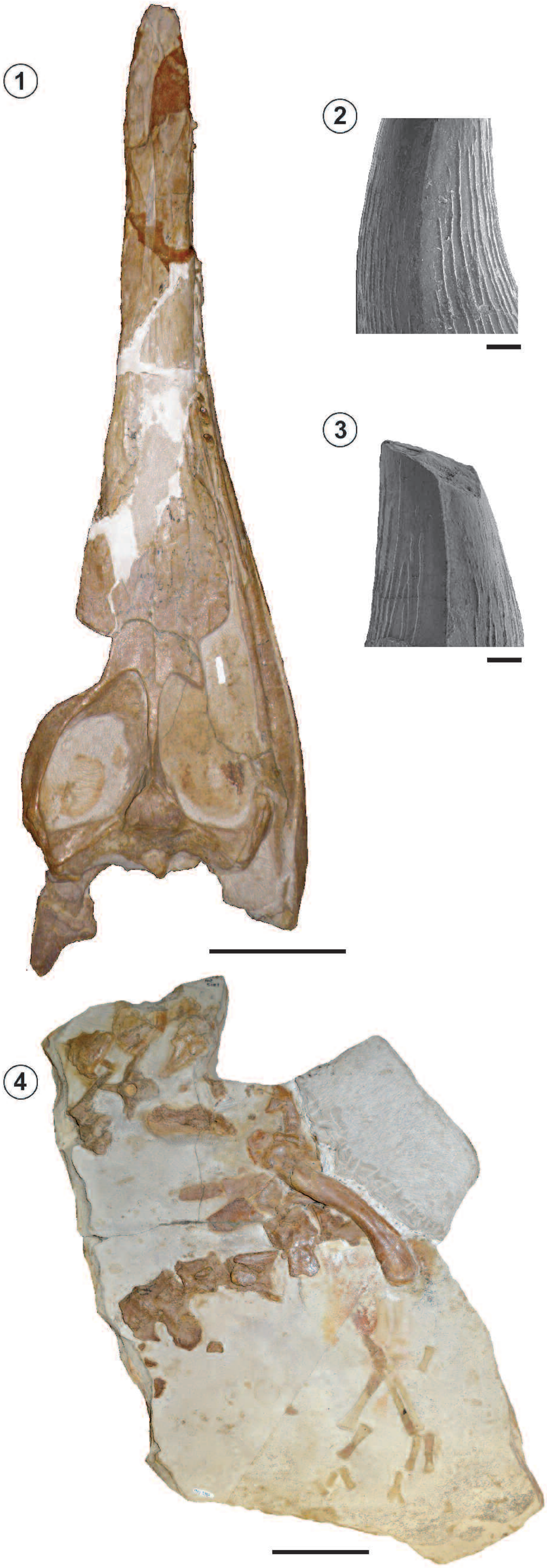

**Figure 3.** ***Cricosaurus lithographicus*, MOZ-PV 5787. 1,** skull in dorsal view; **2–3,** posterior dentary tooth; **2,** carina in distal view; **3,** carina in mesial view; **4,** postcranial elements. Scale bars= 1, 4, 100 mm; 2–3, 1 mm.

***Ocurrence.*** Upper lower–middle upper Tithonian levels of El Ministerio quarry, Los Catutos Member (Neuquén Province).
***Comments.*** *Cricosaurus lithographicus* was the second species of *Cricosaurus* described for the Neuquén Basin. The material designated as *Cricosaurus lithographicus* by Herrera *et al*. (2013c) had previously been briefly mentioned and illustrated (*e.g.*, Gasparini *et al*., 1995; Gasparini and Fernández, 2005, 2011). This species, with a body length of approximately 3.36 m (Herrera, 2012), is the largest Rhacheosaurini from the Vaca Muerta Formation. The main difference between *C. lithographicus* and *C. araucanensis* lies in the dentition. Both species have bicarinated teeth with a smooth carina on the mesial and distal margin. In *C. lithographicus*, the number of maxillary teeth is fewer and the interalveolar spaces are larger than in *C. araucanensis*. Also, in the former taxon, the teeth have conspicuous, but not continuous, longitudinal ridges that run along the crown, except in the apical region that is smooth (Fig. 3.2–3), whereas in *C. araucanensis* the teeth have fine longitudinal ridges (Fig. 1.2) only visible under high magnification (*e.g.*, SEM analysis).

Herrera *et al*. (2013c) found *C. lithographicus* nested with *Cricosaurus macrospondylus* (Koken, 1883) and *Cricosaurus araucanensis* in a polytomy. More recently, *Cricosaurus lithographicus* was found as the sister taxon of *C. macrospondylus*, with *Cricosaurus araucanensis* as the sister taxa of this clade (Herrera *et al*., 2015).

### Subfamily Geosaurinae Lydekker, 1889 (*sensu* Young and Andrade, 2009)

### Tribe Geosaurini Lydekker, 1889 (*sensu* Cau and Fanti, 2011)

### Genus ***Dakosaurus*** Quenstedt, 1856

***Type species.*** *Geosaurus maximus* Plieninger, 1846. Upper Kimmeridgian, Staufenbei Giengen, Baden-Württemberg, Germany.

### ***Dakosaurus andiniensis*** Vignaud and Gasparini, 1996

Figure 4.1

***Holotype.*** MHNSR PV 344, an isolated rostrum slightly eroded.
***Referred material.*** MOZ-PV 026, anterior region of the snout and preorbital natural endocast; MOZ-PV 6140, anterior mandibular fragment; MOZ-PV 6146, skull with articulated lower jaws and fragmentary postcranial remains.
***Ocurrence.*** The holotype was found in Tithonian–Berriasian levels of the Catan Lil, Barranca River (Malargüe, Mendoza Province). Specimen MOZ-PV 026 was found in Tithonian levels of Mallín Quemado area (Neuquén Province), MOZ-PV 6140 and MOZ-PV 6146 were found in Yesera del Tromen-Pampa Tril area (Neuquén Province), in Berriasian and Tithonian levels respectively.
***Comments.*** In 2009, Pol and Gasparini made a comprehensive description of the an almost complete and three dimensionally preserved skull and lower jaws of *Dakosaurus andiniensis* (MOZ-PV 6146), which is characterized by a short and high snout with ziphodont dentition. Phylogenetic analyses showed that *Dakosaurus andiniensis* is the sister taxon of *D. maximus*, a form of the Jurassic of Europe (Pol and Gasparini, 2009; Young *et al*., 2012; Herrera *et al*., 2015; Wilberg, 2015). Based on skull length of MOZ-PV 6146, the body length estimation is 4.20 m (Herrera, 2012). In 2010, in the Mallín Quemado area, one skull of *D. andiniensis* that includes the natural endocasts of the snout was found (Fernández *et al*., 2010, 2012). The natural endocast reveals the presence of enlarged salt gland, the internalization of the antorbital cavity, and probably the presence of the suborbital diverticula (Fernández *et al*., 2012), however deeper studies are necessary and are being performed by Fernández *et al*. Also, in the same level, was found a quite articulated hind limb, probably referable to the same taxon (Fernández *et al*., 2012).

### ***Dakosaurus*** cf. ***D. andiniensis***

Figure 4.2–4

***Referred material.*** MOZ-PV 089, skull incompletely preserved that includes the orbital and post-orbital regions as well as the exposed natural endocast of the brain cavity.
***Ocurrence.*** Vega de Escalone locality (Neuquén Province) in the uppermost Tithonian levels (*Substeueroceras koeneni* Biozone-uppermost Tithonian to lowermost Berriasian).
***Comments.*** Based on the absent of diagnostic features, a more accurate determination could not be done (Herrera and Vennari, 2015). However, its description constituted the first detailed report of the brain endocast morphology and cranial nerves of a metriorhynchid.

The endocast has an anteroposteriorly elongated cerebral hemispheres and conspicuous blood vessel fillings covering almost all the dorsal surface of the hemispheres (Fig. 4.3). The bone tissue preserved between the blood vessel fillings, suggested that the dural envelope of this region was thin and that the cerebral hemispheres filled most of the cavity (Herrera and Vennari, 2015). The infilling of the cranial nerves III, IV and VI were identified (Fig. 4.3). One of them (CN III) is markedly enlarged (in diameter and compared with *Gavialis gangeticus*) and, based on this, was proposed that the eyeball of metriorhynchids might have had a great mobility and a great visual range (Herrera and Vennari, 2015). On the other hand, the distal portion of cavity 1, and an enlarged internal carotid canal were recognized in the natural endocast (Fig. 4.3–4). These structures were previously identified in a digital cast of the Chilean metriorhynchid *'Metriorhynchus'* cf. *'M'. westermanni* by Fernández *et al.* (2011).

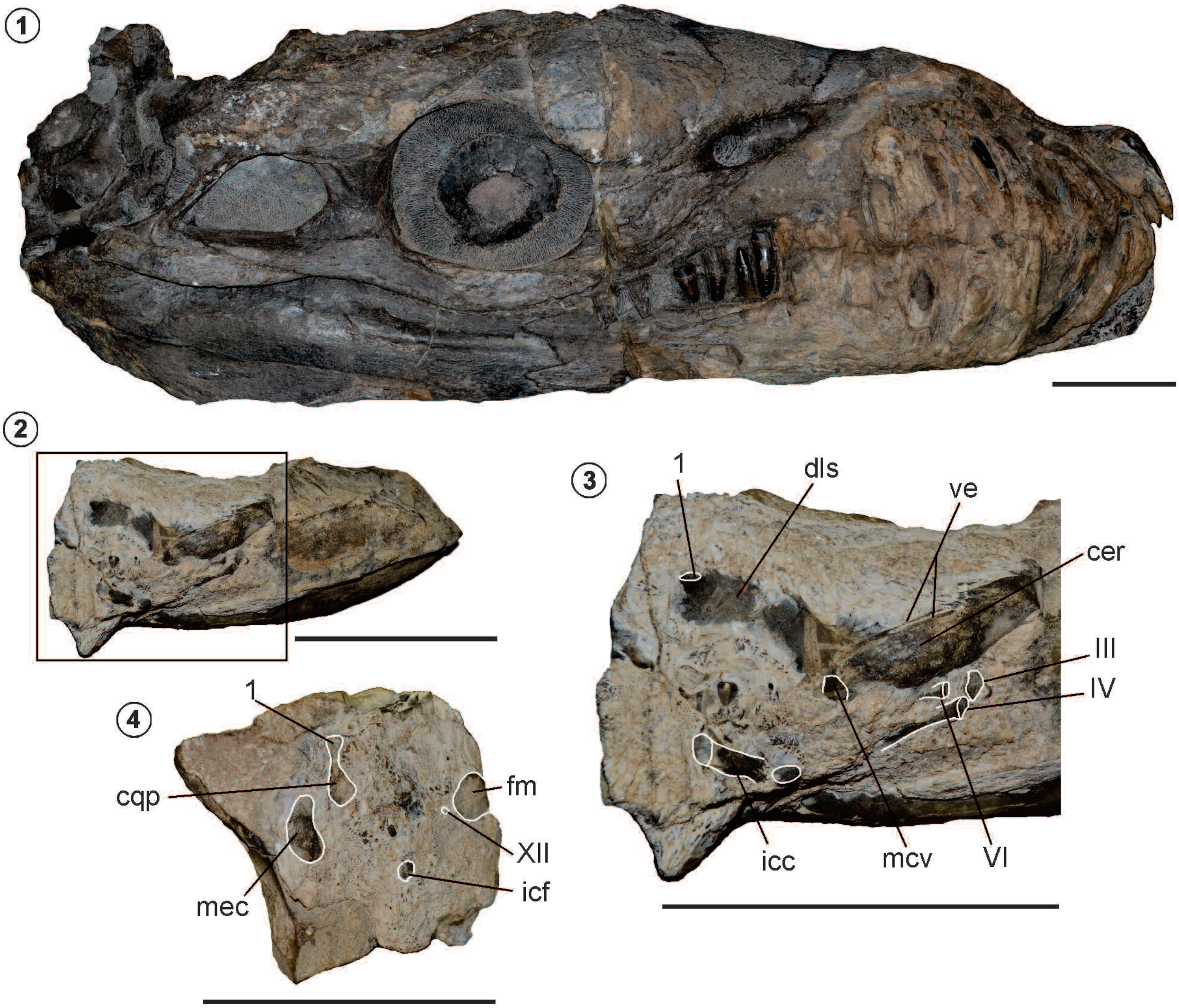

**Figure 4. 1,** ***Dakosaurus andiniensis*****, MOZ-PV 6146,** skull in right lateral view; **2–4,** *Dakosaurus* cf. *D. andiniensis*, **MOZ-PV 089; 2,** right lateral view showing the region of interest; **3,** detail of endocast; **4,** left latero-occipital view. Scale bars= 100 mm. Abbreviations: **cer,** cerebral hemisphere; **cqp,** cranioquadrate passage; **dls,** dorsal longitudinal sinus; **fm,** foramen magnum; **icc,** internal carotid canal; **icf,** internal carotid foramen; **mec,** middle ear cavity; **mcv,** middle cerebral vein; **ve,** vessel; **1,** tube-like cavity; **III, IV, VI, XII,** cranial nerves foramen and/or canals.

Genus ***Purranisaurus*** Rusconi, 1948a

Figure 5

***Type species.*** *Purranisaurus potens* Rusconi, 1948a. Arroyo del Cajón Grande, southwest of Malargüe Department, Mendoza Province. Upper Tithonian–lower Berriasian of Vaca Muerta Formation (biozone of *Substeueroceras koeneni*, Vennari *et al.*, 2014).

***Holotype.*** MJCM PV 2060, skull incompletely preserved without the most anterior portion; incomplete left lower jaw.

***Comments.*** This taxon corresponds to the first metriorhynchid skull described in Argentina, although it was originally described as a plesiosaur (Rusconi, 1948a,b) and then reassigned to Nothosauria (Rusconi, 1967). Years later, some authors placed *Purranisaurus potens* in 'Crocodylia' or 'Metriorhynchidae?' (*e.g.*, Romer, 1956; Kuhn, 1968; Gasparini, 1973a). During decades the systematic status of *P. potens* has been debated (see Gasparini, 1973a, 1985; Buffetaut, 1982; Vignaud, 1995; Pol and Gasparini, 2007; Young *et al.*, 2010; among others) but the poor preparation of this specimen precluded its determination. A recent preparation of the material allowed its redescription as well as the exploration of its phylogenetic relationships (see Herrera *et al.*, 2015). Hitherto *Purranisaurus* is a monotypic genus for South America, and *P. potens* is the second Geosaurini genus described for Argentina. The skull is incompletely preserved, thus an estimation of body length can not be made.

## DISCUSSION

The Upper Jurassic and Lower Cretaceous fossil record of Patagonian metriorhynchids is outstanding, both in quantity and quality, although taxonomical diversity is lower than that of the reported for the Tethys. In the South American margins of the Eastern Pacific no metriorhynchid have been collected from Oxfordian and Kimmeridgian levels, while in the Tethys and Hispanic Corridor (Mexico and Cuba) several taxa have been found (*e.g.*, Gasparini and Iturralde-Vinent, 2001; Buchy *et al.*, 2007; Buchy, 2008; Young *et al.*, 2012, 2013). In Patagonia, Oxfordian–Early Kimmeridgian marine levels are restricted to marine platform limestones (La Manga Formation) and evaporites (Auquilco Formation) without evidences of vertebrates, whereas the Kimmeridgian is represented by continental (Tordillo Formation) and volcanics (Río Damas Formation) deposits (A.C. Garrido, pers. comm.). During the Tithonian–Berriasian the diversity of Patagonia metriorhynchids is also lower than in the Tethys however, this could be due to uneven collecting efforts. The major taxonomic diversity of Patagonian metriorhynchids have been collected in upper Tithonian–lower Berriasian levels of the Vaca Muerta Formation, and includes at least three different taxa: *Dakosaurus andiniensis*, *Cricosaurus araucanensis* and *Purranisaurus potens*. *Dakosaurus* sp. and *Cricosaurus* sp. have also been recorded in the Hispanic Corridor. Based on the exhaustive systematic revisions performed by Young and Andrade (2009) and Young *et al.* (2012) and what we know so far, both western Tethys and Eastern Pacific probably had endemics genera for the Tithonian–Berriasian such as: *Plesiosuchus*, *Geosaurus*, *Rhacheosaurus* (for the western Tethys), and *Purranisaurus* for Patagonia. No endemic genera of metriorhynchids are recognized for the Hispanic Corridor.

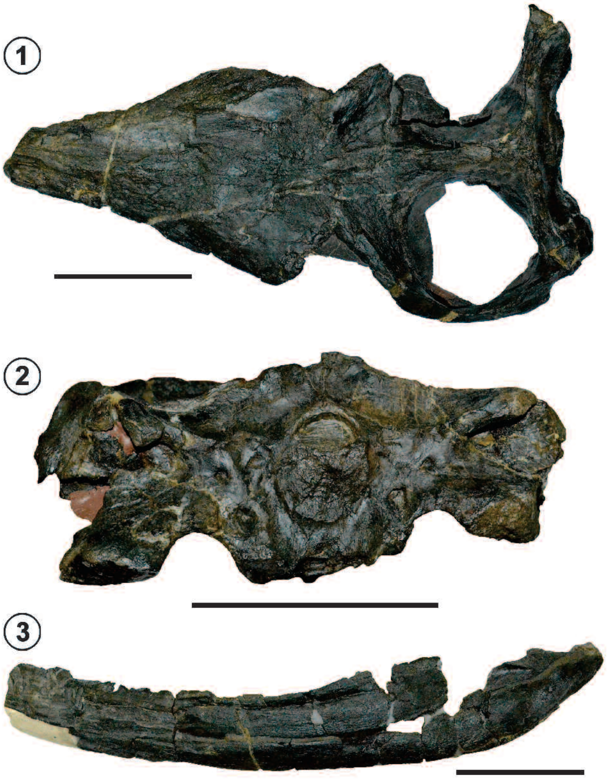

**Figure 5.** ***Purranisaurus potens*, MJCM PV 2060. 1,** skull in dorsal view; **2,** skull in occipital view; **3,** left mandibular ramus in lateral view. Scale bars= 100 mm.

Some undescribed Patagonian specimens need to be described. These new materials, as well as paleontological prospections of poorly sampled areas of Patagonia, will help to test whether the differences in the evolutionary scenarios between the western Tethys and Eastern Pacific faunas are due to uneven fossil sampling or not.

### *Natural casts of the brain*

The information on natural and/or artificial brain casts of thalattosuchians in general, and metriorhynchids in particular, is scarce. In this way, the description of the Geosaurini brain endocast of *Dakosaurus* cf. *D. andiniensis* improved the scarce knowledge of the neuroanatomy of metriorhynchids.

Based on the available information, in *Cricosaurus araucanenis*, *Dakosaurus* cf. *D. andiniensis*, as well as in a teleosaurid (Seeley, 1880), *Steneosaurus pictaviensis* (Wharton, 2000), and *'Metriorhynchus'* cf. *'M'. westermanni* (Fernández *et al.*, 2011) the angles formed by the hindbrain, midbrain and forebrain are much less developed than in extant crocodiles (*e.g.*, *Caiman crocodylus*, Hopson, 1979: fig. 1B; *Crocodylus johnstoni*, Witmer *et al.*, 2008: fig. 6.3A; *Caiman yacare*, Bona and Paulina Carabajal, 2013: fig. 6B) and less developed than in some extinct crocodyliforms (*e.g.*, *Pholidosaurus meyeri*, Hopson, 1979: fig. 10; *Caiman gasparinae*, Bona and Paulina Carabajal, 2013: fig. 6A). In the mosasaur *Platecarpus* (Hopson, 1979: fig. 8) and in an ichthyosaur (Marek *et al.*, 2015: fig. 11A–B) the brain casts seems to be much flexed than in metriorhynchids. In comparison with other marine reptiles, metriorhynchids brain endocast are elongated, as in nothosaurs, plesiosaurs and ichthyosaurus, and the cerebral hemispheres are somewhat enlarged as in an ichthyosaur (Marek *et al.*, 2015). If the identification of the optic lobe in *Cricosaurus araucanensis* is correct, this structure is small in comparison with that of ichthyosaurs (Marek *et al.*, 2015: fig. 10). Seeley (1880) described a deep excavation in the posterodorsal region of the braincase of a teleosaurid, and he interpreted this cavitity as for the optic lobe. However, this cavity probably corresponds to a part of the cavity 1 or a part of a venous sinus, and not to the cavity for the optic lobe. As in *Cricosaurus araucanensis*, in *Steneosaurus pictaviensis* the optic lobe appears to be small (Wharton, 2000: fig. 1a).

Based on the current knowledge, metriorhynchids endocasts (*'Metriorhynchus'* cf. *'M'. westermanni*, *Dakosaurus* cf. *D. andiniensis*, and *Cricosaurus araucanensis*) share the following features: conspicuous blood vessel fillings that cover almost all the dorsal surface of the cerebral hemispheres, an enlarged internal carotid canal, conspicuous filling of cranial nerves III, IV and XI, and the cavity that connects the dorsal longitudinal venous sinus with the cranio-quadrate foramen. However, fine details (as the blood vessel fillings and nerves) are only recognized in the endocasts, a similar situation was described for the natural and digital cast of the preorbital region of *Cricosaurus araucanensis* (Herrera *et al.*, 2013a). The presence of the same endocasts features in Geosaurini and Rhacheosaurini tribes suggests that they were widely distributed within metriorhynchids, and that could be related with adaptations to a pelagic lifestyle.

A more exhaustive analysis of the metriorhynchid endocasts (natural and digital) is fundamental to determine if the identification of the optic lobe is correct, as well as to understand the biological/functional significance of the poor developed flexures in the brain of metriorhynchids, and the brain vascular system, among other features. Improving the knowledge of these topics is essential to understand the secondary adaptation of the metriorhynchids to the pelagic environment, adaptation unique among Archosauria.

### *Future perspectives of the study of Patagonian metriorhynchids*

The most remarkable peculiarities of the Patagonian metriorhynchid fossil records are the excellent preservation of their skeletons (in most cases the specimens are tridimensionally preserved) and the preservation of the natural endocasts of the skull cavities. These oustanding fossil records would allow us to continue exploring interesting paleobiological aspects such as the analyse of sensory capabilities (vision, olfaction and hearing) and their relationships with physiological and behavioural attributes. The current evidence suggests that the soft anatomy of the brain in metriorhynchids seems to be as modified and could be coupled with skeletal changes (as the soft anatomy of the snout, and the postcranium), in relation of their pelagic lifestyle. Ongoing contributions will allow determining detailed information regarding these modifications and their significance in the secondary adaptation of metriorhynchids to the pelagic environment.

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