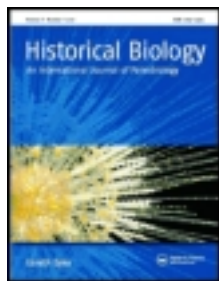


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Cranial anatomy and neuroanatomical features of a new specimen of Geosaurini (Crocodylomorpha: Metriorhynchidae) from west-central Argentina

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Fossil records of Geosaurini taxa in South American margins of the Eastern Pacific are scarce. We describe a new specimen of Geosaurini found in sedimentites of the Vaca Muerta Formation (*Substeueroceeras koeneni* Biozone, uppermost Tithonian–lowermost Berriasian) and referred it as *Dakosaurus* cf. *D. andiniensis*. The close stratigraphic association of this specimen with late Tithonian to early Berriasian ammonoids allows confirming with biostratigraphic accuracy that, up to date, the first known occurrence of the Geosaurini taxa in South America is in late Tithonian. The specimen consists of a partially preserved skull and a partially exposed natural endocast of the brain cavity. This work is the first detailed description of a natural endocast of a metriorhynchid. The conspicuous blood vessel fillings covering almost all the dorsal surface of the cerebral hemispheres suggest that the dural envelope of this region was thin and that the cerebral hemispheres filled most of the cavity. A large dorsal venous sinus that overlays the dorsal region of the hindbrain, a tube-like cavity connecting the cranioquadrate passage and an enlarged internal carotid canal, previously described for '*Metriorhynchus*' cf. '*M.* *westermanni*' and present in *Dakosaurus* cf. *D. andiniensis*, suggest that these features were more widely distributed within metriorhynchids.

Keywords: *Dakosaurus*; Thalattosuchia; Neuquén Basin; Tithonian; Berriasian

1. Introduction

The peculiar morphology of Metriorhynchidae, characterised by paddle-like forelimbs, hypocercal tail and loss of osteoderms, made this group to be recognised, since the middle of the nineteenth century up to the present, as a particularly distinctive crocodyliforms group (Fraas 1902; Andrews 1913). Studies performed in past years have increased our knowledge about this group. These studies include anatomical descriptions, nomination of new genus/species, physiological aspects, feeding ecologies and niche partitioning, among others (e.g. Fernández and Gasparini 2008; Pierce et al. 2009; Young, Brusatte, Andrade, et al. 2012; Young, Brusatte, Beatty, et al. 2012b; Young et al. 2013; Herrera et al. 2013a; Herrera, Gasparini, et al. 2013; Parrilla-Bel et al. 2013).

Due to the high rate of soft-tissue decay, the natural endocasts are not frequently recovered. Anatomical descriptions of natural or artificial cranial endocasts in extinct dinosaurs have been particularly abundant over the past few years (e.g. Chatterjee and Zheng 2002; Sanders and Smith 2005; Witmer et al. 2008; Evans et al. 2009; Knoll and Schwarz-Wings 2009; Witmer and Ridgely 2009; Paulina Carabajal 2011, 2012). Natural endocasts of crocodyliforms (Lemoine 1883; Edinger 1938; Yeh 1958; Hopson 1979; Storrs et al. 1983) and digital or latex

endocasts (e.g. Franzosa 2004; Witmer et al. 2008; Kawabe et al. 2009; Bona et al. 2013; Bona and Paulina Carabajal 2013) have also been described. Within Thalattosuchia, the information published on brain endocasts is relatively poor, and it corresponds to a partially preserved natural endocast of *Metriorhynchus superciliosus* (Wenz 1968), a latex endocast of a teleosaurid (Wharton 2000) and a digital cast of '*Metriorhynchus*' cf. '*M.* *westermanni*' (Fernández et al. 2011).

Based on the current state of knowledge about Patagonian metriorhynchids, only three species have been found so far in uppermost Tithonian–lowermost Berriasian beds of the Neuquén Basin: *Dakosaurus andiniensis* Vignaud and Gasparini, 1996; *Purranisaurus potens* Rusconi, 1948 and *Cricosaurus araucanensis* (de Gasparini and Dellapé, 1976). *Dakosaurus andiniensis* was found in northwestern Neuquén and southwestern Mendoza (Spalleti et al. 1999; Pol and Gasparini 2009). *Purranisaurus potens* comes from the south-east of Malargüe department, Mendoza Province, and *C. araucanensis* has been recovered from at least two localities of the Neuquén Province (Mallín Quemado, Yesera del Tromen-Pampa Tril; Spalleti et al. 1999; Herrera et al. 2013b). Although metriorhynchids natural endocasts of the pre-orbital region have been frequently recovered in several localities of the Neuquén Basin (west-central Argentina;

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Fernández and Gasparini 2000, 2008; Fernández and Herrera 2009; Herrera et al. 2013b), natural endocasts of the brain cavity have not yet been described.

Here, we describe in detail a partially preserved natural endocast of the brain cavity of a Metriorhynchidae found in sedimentites of the Vaca Muerta Formation, in the Vega de Escalone section, in northern Neuquén Province (Figure 1). Some cranial features present in the specimen described here, such as the inconspicuous basioccipital exposition on the occipital surface and the morphology of the basioccipital tubera, support its referral to *Dakosaurus* cf. *D. andiniensis*.

1.1 Institutional abbreviations

MJCM, Museo de Ciencias Naturales y Antropológicas ‘Juan Cornelio Moyano’, Mendoza, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MOZ, Museo Juan Augusto Olsacher de Zapala, Neuquén, Argentina.

2. Geological setting

The Vega de Escalone section (37°11’S; 69°48’W) is located in central west Argentina, in northern Neuquén Province. It is emplaced in the Pampa Tril area, about

70 km north of Chos Malal city, on a country road that forks westward from the national road 40 a few kilometres north of a Cenozoic basaltic neck (locally known as the Chihuido del Tril). This area is included within the region covered by the Neuquén Basin during the Mesozoic, a retroarc basin that holds a thick and almost uninterrupted mesozoic–cenozoic sedimentary column of marine and continental facies (Legarreta and Gulisano 1989). The sedimentation in the basin was mainly tectonically controlled (Ramos and Folguera 2005) and punctuated by eruptive events related to the activity of a discontinuous volcanic arc that allowed its connection with the Pacific Ocean to the west.

The studied locality lies over the eastern flank of the Yesera del Tromen anticline (Herrero Ducloux 1946) where a complete section of the Mendoza Group crops out. The specimen described here was found in rocks belonging to the Vaca Muerta Formation (Weaver 1931; enmend. Leanza 1972). The deposition of this sedimentary unit began after a sudden marine transgression in the Late Jurassic and extended up into the Early Cretaceous. The Vaca Muerta Formation includes calcareous and/or siliciclastic facies deposited over an homoclinal carbonate ramp to the eastern margin of the basin (Spalletti et al. 2000; Kietzmann et al. 2008) and over slope facies of a carbonate platform or a distally steepened carbonate ramp to the western margin of the basin (Spalletti et al. 2008; Kietzmann and Vennari 2013). The sedimentation was dominated by organic-rich black shales and marls intercalated with conspicuous calcareous beds and carbonate nodules intervals. The prevailing oxygen-deficient bottom conditions allowed the accumulation of large quantities of organic matter and favoured the preservation of abundant faunal remains (Doyle et al. 2005).

The measured section of the Vaca Muerta Formation is 482 m thick (Figure 2). It extends between the fluvial–lacustrine siltstones and sandstones of the Tordillo Formation and the transitional–marine siltstones and packstones of the Quintuco/Mulichinco Formation. In addition to the aforementioned lithological features, some ferruginous surfaces and thin fibrous calcite layers have been observed. Some of the last yielded ammonoid and bivalve impressions, in the way reported by Damborenea and Leanza (2004) in the Huncal area, central Neuquén. Ammonoid shells are abundant all along the section. They are usually recorded as well-preserved internal moulds or as impressions, being the last taphonomic mode more frequent to the top of the column. Aptichy, bivalves and gastropods shells and internal moulds, and scattered fish scales are also commonly found in the same beds that ammonoid remains.

The analysis of the ammonoid fauna resulted in the identification of all of the Late Jurassic–Early Cretaceous Andean ammonoid association biozones, in accordance

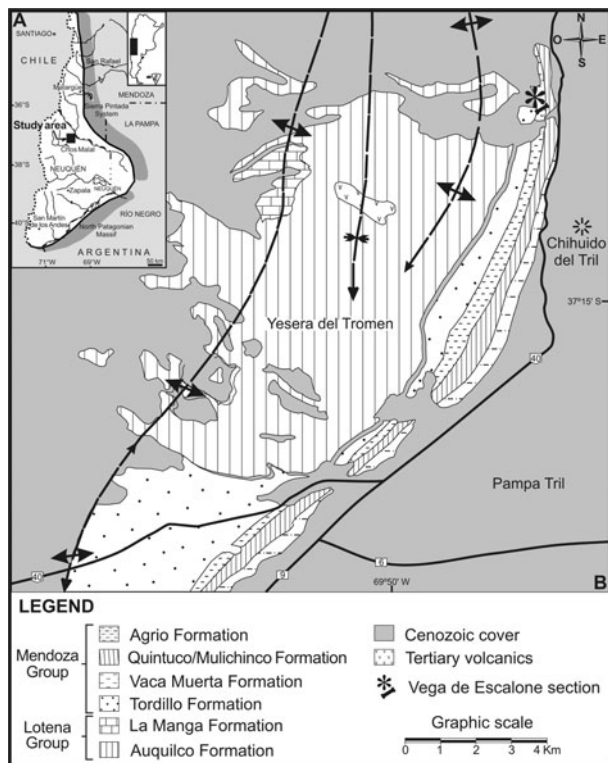


Figure 1. (A) Neuquén Basin situation with location of the study area and (B) geological map of the study area (modified from Gulisano and Gutiérrez-Pleimling 1994).

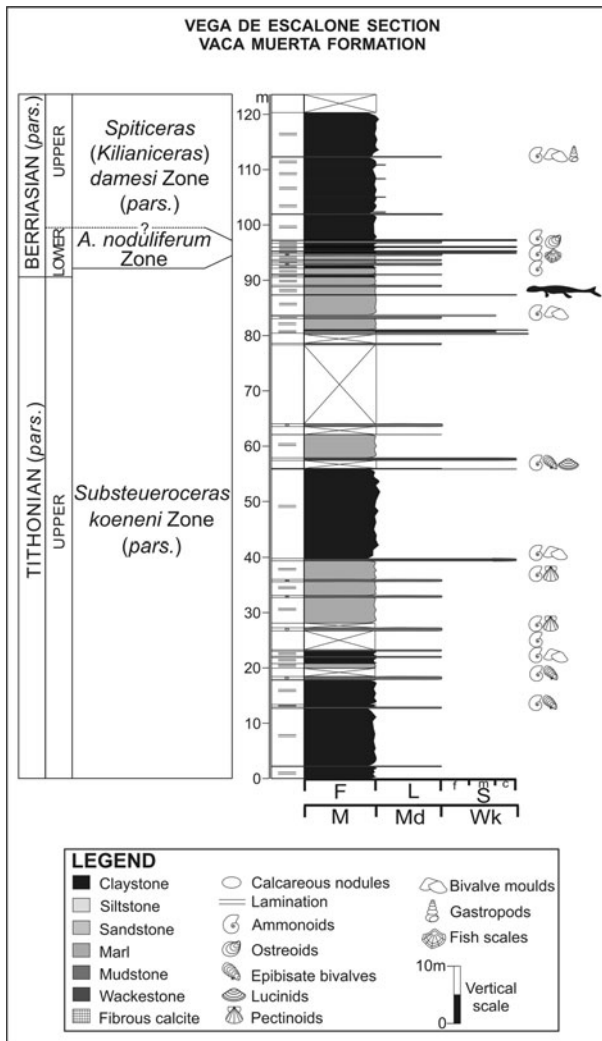


Figure 2. Detailed stratigraphic section of the Vega de Escalone Section (Vaca Muerta Formation) showing the positions of *Dakosaurus* cf. *D. andiniensis* (MOZ-PV 089) and associated ammonites in the uppermost Tithonian–lowermost Berriasian.

with the biostratigraphic schemes introduced by Leanza (1980, 1981) and Riccardi (1984, 1988), and their most recent refinements (Zeiss and Leanza 2008, 2010; Riccardi 2008; Riccardi et al. 2011; Vennari et al. 2013). Therefore, in the Vega de Escalone section, the Vaca Muerta Formation spans from the late Early Tithonian – *Virgatospinctes mendozanus* Biozone – to the Late Berriasian–Early most Valanginian – *Spiticeras (Kilianiceras) damesi* to *Neocomites wichmanni* Biozone. The specimen MOZ-PV 089 has been found in close association with the last beds included in the *Substeueroceras koeneni* Biozone (uppermost Tithonian to lowermost Berriasian), just below the first occurrence in the section of ammonoid remains ascribed to the *Argentinceras noduliferum* Biozone (lower Berriasian).

3. Materials and methods

The specimen MOZ-PV 089 is represented by the mid-posterior region of the skull that includes the orbital and post-orbital regions. The left side is partially complete; however, the supratemporal arch and the complete orbital margins are not preserved. At this side, a slightly deformed left scleral ring is completely preserved. On the right side, the braincase elements that surround the cranial cavity are incompletely preserved, leaving the natural endocast of the brain cavity, canal nerves and part of the pharyngotympanic system exposed. Measures were taken using a vernier calliper accurate to 0.1 mm.

4. Systematic palaeontology

Crocodylomorpha Walker, 1970

Thalattosuchia Fraas, 1901

Metriorhynchidae Fitzinger, 1843

Geosaurinae Lydekker, 1889

Geosaurini Lydekker, 1889

Dakosaurus Quenstedt, 1856

Dakosaurus cf. *D. andiniensis*

(Figures 3, 4 and 5(A),(B),(E))

4.1 Specimen

MOZ-PV 089, skull incompletely preserved represented by the mid-posterior region of the skull that includes the orbital and post-orbital regions.

4.2 Locality

Vega de Escalone section (37°11'S; 69°48'W), northern Neuquén Province, central west Argentina.

4.3 Stratigraphic horizon

Vaca Muerta Formation, *Substeueroceras koeneni* Biozone (uppermost Tithonian to lowermost Berriasian).

4.4 Description

4.4.1 Skull

The material is weathered; so most of the sutures cannot be discriminated. In the dorsal view (Figure 3(A)), the medial and caudal margins of the supratemporal fossa are delimited. The anterior margin of the supratemporal fossa is partially preserved. Based on the preserved margins, the supratemporal fossa appears to be circular in outline. The left axial rib is identifiable as an impression over the matrix that fills the supratemporal fossa (Figure 3(A)).

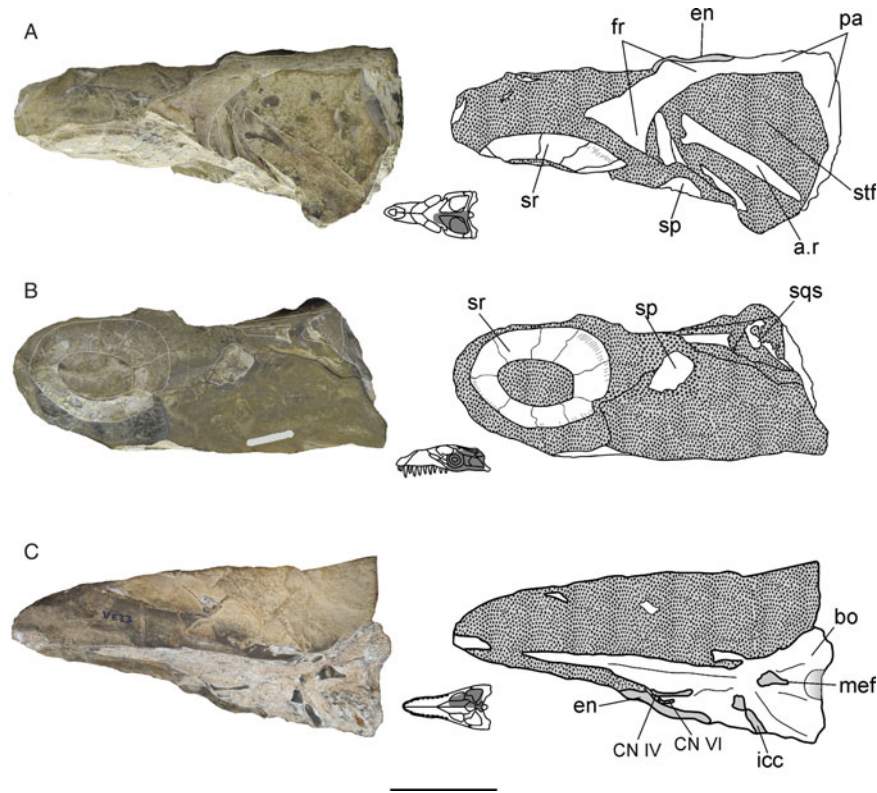


Figure 3. (Colour online) *Dakosaurus* cf. *D. andiniensis* (MOZ-PV 089): (A) dorsal view; (B) left lateral view; (C) ventral view. Small sketches show the region preserved and its orientation. a.r, axial rib; bo, basioccipital; icc, internal carotid canal; en, endocast; fr, frontal; mef, median eustachian foramen; pa, parietal; sp, scleral plate; sqs, squamosal flat surface; sr, scleral ring; stf, supratemporal fossa; CN IV, trochlear canal; CN VI, abducens canal. Scale bar: 50 mm.

In the lateral view (Figure 3(B)), the subcircular, smooth and slightly concave surface formed by the squamosal, lateral to the distal end of the paroccipital process, is preserved as an impression over the matrix. This surface has been described for other metriorhynchids (Pol and Gasparini 2009; Herrera, Gasparini, et al. 2013; Parrilla-Bel et al. 2013). The well-ossified/developed scleral ring is preserved, formed by, at least, nine overlapped scleral plates, strongly imbricate, delimiting a ring with an oval outline. The antero-posterior diameter is approximately 76 mm and the dorso-ventral diameter is 57 mm. The internal aperture of the ring has a concave ventral margin, whereas the dorsal margin is flatter. This situation may be associated with a slightly post-mortem deformation. There is no *sulcus* at the scleral-corneal *limbus*, as in fishes, penguins, ichthyosaurs and marine turtles (McGowan 1973; Suburo and Scolaro 1990; Helfman et al. 1997; Kröger and Katzir 2008). One isolated scleral plate is preserved, exposed in an internal view, showing a slightly lateral curvature (Figure 3(B)). Unfortunately, the orbital margins are not completely preserved; however, delimitation of the dorsal, ventral and posterior margins of the orbit can be done based on some remains of frontal and palatal bones.

The basioccipital tubera are partially preserved and U-shaped in ventral and occipital views (Figures 3(C) and 4). These tubera are separated by a notch and are closer to each other, in contrast to *Purranisaurus potens* (MJCM PV 2060) where they are laterally expanded. Between the tubera, the basioccipital is anteroventrally–posterodorsally directed, as in *Dakosaurus andiniensis* (Pol and Gasparini 2009, Figure 9), unlike the most vertically orientation present in *P. potens*.

In the occipital view (Figure 4), a partially preserved exoccipital–supraoccipital suture suggests that the supraoccipital does not participate in the dorsal margin of the foramen magnum, a feature variable within metriorhynchids. Although the occipital condyle is not preserved, its margin can be inferred based on a subtle circular outline ventral to the foramen magnum. The exposition of the basioccipital on the occipital surface below the occipital condyle is inconspicuous (Figure 4), so the basioccipital surface is low, contrasting to the higher exposition present in *P. potens* (MJCM PV 2060).

4.4.2 Endocast of the brain cavity

The brain endocast of MOZ-PV 089 is incomplete, partially covered by surrounding bones and exposed in

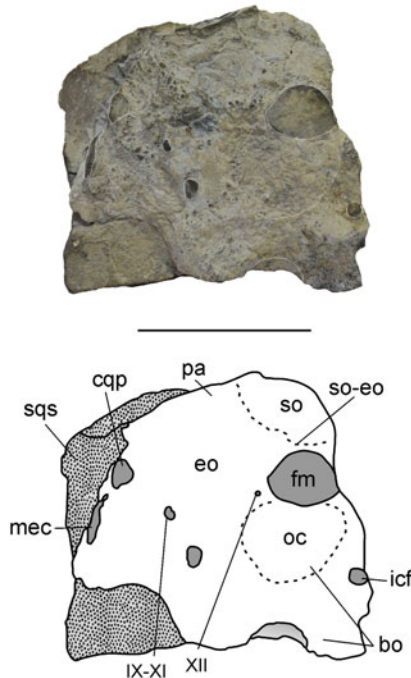


Figure 4. (Colour online) *Dacosaurus* cf. *D. andiniensis* (MOZ-PV 089) in occipital view. bo, basioccipital; cqp, cranioquadrate passage; eo, exoccipital; fm, foramen magnum; icf, internal carotid foramen; mec, middle ear cavity; oc, occipital condyle; pa, parietal; so, supraoccipital; so-eo, supraoccipital–exoccipital suture; sqs, squamosal flat surface; IX–XI, XII, cranial nerve foramina. Scale bar: 50 mm.

right lateral view. The general morphology indicates that the cephalic and pontine flexures are not well developed in comparison with extant crocodylians (Hopson 1979; Witmer et al. 2008; Bona and Paulina Carabajal 2013), as was described for ‘*Metriorhynchus*’ cf. ‘*M. westermanni*’ by Fernández et al. (2011). The endocast preserved measures are 96 mm from the foramen magnum to the base of the olfactory tract (Figure 5(A),(B)).

In the lateral view, the forebrain is preserved by the right cerebral hemisphere and the proximal portion of the olfactory tract. The cerebral hemispheres are flat and anteroposteriorly elongated, contrary to the rounded shaped condition present in extant crocodylians. Conspicuous fillings of the blood vessels are preserved on the dorsal surface of the cerebral hemispheres and cover almost the entire surface of these structures. The major blood vessel infill is bifurcated; the two branches are projected anteroposteriorly. Dorsally to these branches, there are three small branches, anteroposteriorly directed, that converge posteriorly at a point. The trigeminal region is not completely preserved. Based on a subtle outline, the filling of the rostral middle cerebral vein is recognised. The blood vessels fillings that cover the dorsal surface of the cerebral hemispheres seem to connect to the rostral

middle cerebral vein (Figure 5(B)). In *C. araucanensis* (MLP 76-II-19-1), a small portion of the brain endocast, on the right side, is exposed (Figure 5(C),(D)). The trigeminal region of this specimen is represented by a bilobate filling, being the caudodorsal lobule smaller than the rostroventral lobule. The caudodorsal lobule corresponds to the filling of the rostral middle cerebral vein, whereas the rostroventral lobule is the filling of the trigeminal nerve (not preserved in MOZ-PV 089). In MLP 76-II-19-1, there is a bifurcated and conspicuous blood vessel filling, originating above the rostral middle cerebral vein. The longest branch is rostrocaudally directed above the cerebral hemisphere, whereas the shorter branch is dorsally directed (Figure 5(C),(D)). As in MOZ-PV 089, these fillings seem to be connected to the rostral middle cerebral vein.

Dorsoposteriorly to the cerebral hemispheres, the brain endocast is partially covered by bone. The parietal–prootic suture is preserved. On the dorsal-most region of the exposed brain endocast, a protuberance is preserved (Figure 5(B)). This structure corresponds to the medial-most portion of the tube-like cavity, named cavity 1 by Fernández et al. (2011). Due to the topology and the connection with cavity 1, the partially exposed region dorsocaudally to the cerebral hemispheres corresponds to the dorsal venous sinus that overlays the brain.

On the left side, the natural endocast of the brain cavity is not exposed although some fillings are preserved, delimited by the surrounding bones. The distal portion of the cavity 1 filling is preserved in connection with the craneoquadrate canal filling, as was described by Fernández et al. (2011). Cavity 1 filling is about half the size compared with the craneoquadrate canal filling. The cast of the middle ear cavity is exposed rostroventrally to the cavity 1/cranioquadrate canal filling, enclosed by the quadrate. It is oval in outline, being dorsoventrally longer than rostrocaudally (Figure 5(E)).

The pituitary fossa is covered by bone; however, posteriorly to the pituitary region, the filling of the well-developed internal carotid artery canal is preserved. Its diameter is about 7 mm, approximately the same diameter as that of the internal carotid foramen; feature shared with ‘*Metriorhynchus*’ cf. ‘*M. westermanni*’. Rostroventrally to the internal carotid artery canal, there is another filling, transversally orientated to the sagittal plane of the skull that is interpreted here as a portion of the pharyngotympanic recess (Figure 5(B)). In the ventral view, between and anteriorly to the basioccipital tubercles, the posterior ramus of the median Eustachian tube is preserved (Figure 3(C)). Both fillings, related to ventral pharyngotympanic system, have a diameter of approximately 7 mm.

The optic lobes and cerebellum are not discernible in the natural endocast because the dorsal venous sinus overlays this region. The posterior-most portion preserved corresponds to the medulla oblongata.

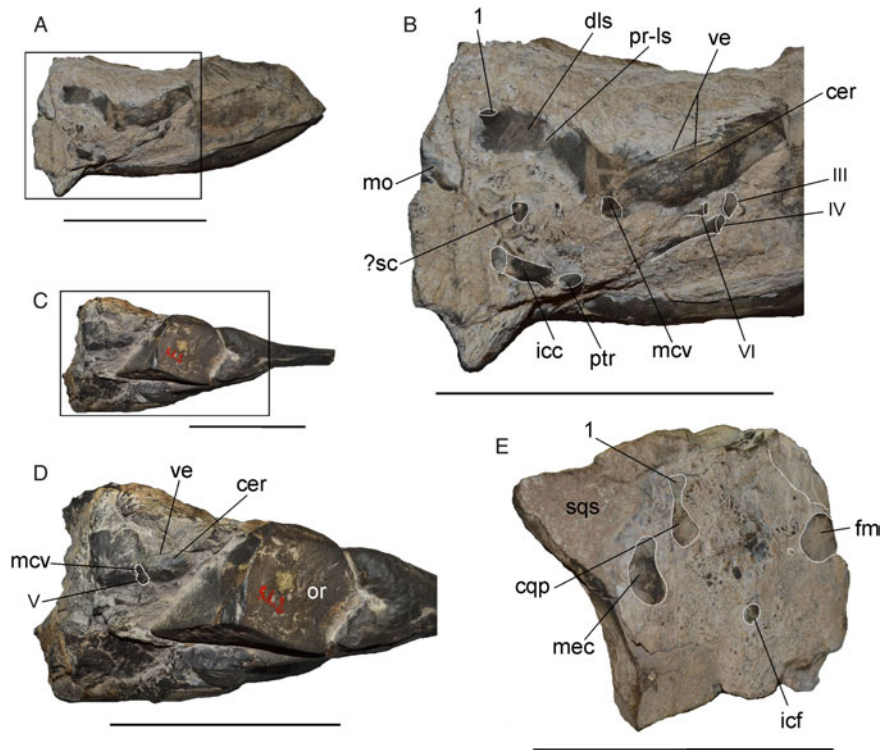


Figure 5. (Colour online) (A) *Dakosaurus* cf. *D. andiniensis* (MOZ-PV 089) in right lateral view showing the region of interest; (B) detail of endocast; (C) *C. araucanensis* (MLP 76-II-19-1) in right lateral view showing the region of interest; (D) detail of endocast; (E) *Dakosaurus* cf. *D. andiniensis* (MOZ-PV 089) in left latero-occipital view. 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; mo, medulla oblongata; or, orbit; pr-ls, prootic–laterosphenoid suture; ptr, pharyngotympanic recess; ?sc, semicircular canal; sqs, squamosal flat surface; ve, vessel; 1, tube-like cavity; III, IV, V, VI, cranial nerves foramen and/or canals. Scale bars: 100 mm.

4.4.3 Inner ear and nerves

Ventrolaterally to the cerebral hemispheres, the fillings of the three canals of cranial nerves are preserved. The largest filling has a diameter of approximately 6.5 mm. It is positioned laterally to the sagittal plane of the skull and more medial and dorsally than the other two casts. It is interpreted here as the canal of the oculomotor nerve (CN III). The medium-size filling (ca 5 mm of diameter) is lateroventral to CN III, and the smallest filling (ca 3.5 mm) is lateral to the CN III. The medium-size cast is interpreted as the canal of the trochlear nerve (CN IV), and the smallest cast as the canal of the abducens nerve (CN VI). Canals for CN III and CN IV are closer to each other, whereas the distance between these canals and canal for CN VI is larger than the distance between CN III and CN IV (Figure 5(B)).

Posteriorly to the middle cerebral vein, there are two other fillings. The anterior-most cast has a diameter of approximately 1 mm, whereas the posterior cast, and largest, is about 4.5 mm in diameter. These fillings are particularly difficult to identify. The largest may correspond to a part of the semicircular canal of the inner ear (Figure 5(B)).

In occipital view, ventrolateral to the foramen magnum and aligned with the foramen magnum–occipital condyle boundary, the foramen with the filling of hypoglossal nerve (CN XII) is preserved. Ventrolateral to the foramen magnum and dorsolateral to the internal carotid foramen, we find the metotic foramen (CN IX–XI). The last foramen is larger than the former, and both of them are smaller than the internal carotid foramen, as in all metriorhynchids (Figure 4).

5. Discussion

The affinities of MOZ-PV 089 can be explored as it preserves some morphological diagnostic features of the skull. On the basis of a well-developed supratemporal fossa as well as an enlarged foramen for the internal carotid artery, we referred the specimen MOZ-PV 089 to Metriorhynchidae. This specimen is referred to Geosaurini on the basis of the parietal–squamosal bar, which is projected slightly caudoventrally, feature only present in the two known Argentinean Geosaurini, *Dakosaurus andiniensis* (Pol and Gasparini 2009; Vignaud and Gasparini 1996) and *Purranisaurus potens* (Rusconi

1948), and contrasting with *Cricosaurus araucanensis*, where this bar is much ventrally projected (per. obs.). The inconspicuous basioccipital exposition on the occipital surface and the morphology of the basioccipital tubera resemble *D. andiniensis* and not *P. potens*. As the most conspicuous features present in *D. andiniensis* cannot be observed in this specimen, we refer the specimen to *Dakosaurus* cf. *D. andiniensis*.

The *Substeueroceras koeneni* Biozone was traditionally ascribed to the upper Tithonian, but its position experienced some fluctuations over the last decades (see Riccardi et al. 2011) on the basis of arguments that are beyond the scope of this paper. However, in a recent study conducted by Vennari et al. (2013), the authors extended this biozone to the earliest Berriasian. *Dakosaurus* cf. *D. andiniensis* has been found in close association with the last beds included in the *Substeueroceras koeneni* Biozone (uppermost Tithonian to lowermost Berriasian). Records of Geosaurini taxa in South American margins of the Eastern Pacific are scarce. To date, only four specimens are known: three of them correspond to *D. andiniensis* and one to *P. potens*. The new material is quite significant for three main reasons: first, it adds a new specimen to the record of the South American Geosaurini; second, it can be related to a precise biostratigraphic framework, based on ammonites and third, it has the natural endocast of the brain cavity exposed and well preserved. The specimen MOZ-PV 089 makes it possible to confirm that, to date, the first known occurrence of the Geosaurini taxa in South American margins of the Eastern Pacific is late Tithonian, contrary to European Geosaurini taxa, whose first occurrence takes place in the middle Oxfordian (Young 2013).

A relevant feature of the *Dakosaurus* cf. *D. andiniensis* (MOZ-PV 089) is the well-developed and almost complete scleral ring that allows comparing it with that of *D. andiniensis* (MOZ-PV 6146). In *D. andiniensis* (MOZ-PV 6146), the scleral ring filled about 65% of the orbit, while in the specimen described herein it seems obvious that the proportion filled with the scleral ring is significantly smaller than in *D. andiniensis*. Although a reliable measure cannot be taken, the dorsal, ventral and posterior orbital margins of *Dakosaurus* cf. *D. andiniensis* can be inferred based on the remains of preserved bones. The external diameter of the scleral ring (measured anteroposteriorly) is 80 mm in *D. andiniensis* and 76 mm in *Dakosaurus* cf. *D. andiniensis*. Fernández et al. (2005) suggested that the scleral ring of juvenile parvipelvian ichthyosaur filled the orbit almost completely, whereas in adults the percentage is lower. The different proportions of scleral ring filling the orbit in both specimens, and the different skull sizes of *Dakosaurus* cf. *D. andiniensis* and *D. andiniensis* support the contention that, in metriorhynchids, a similar relationship could happen.

The general morphology of the natural endocast of *Dakosaurus* cf. *D. andiniensis* is characterised by reduced cephalic and pontine flexures, well-developed flat and

anteroposteriorly cerebral hemispheres, a conspicuous blood vessel pattern above the dorsal surface of the cerebral hemispheres and a conspicuous cast of the canal of the oculomotor nerve (III).

In many reptiles, the dural envelope that covers the cerebral hemispheres is relatively thin and the endocast is a good proxy for the brain size and shape (Hopson 1979; Witmer et al. 2008). Vascular impressions on the internal surface of the frontals and parietals have been described for many dinosaurs (Osmolka 2004; Evans 2005; Witmer and Ridgely 2009) and they were interpreted as regions where the dural envelope was thin and, in consequence, the endocranium closely reflected brain morphology. In *Dakosaurus* cf. *D. andiniensis*, the pattern of conspicuous blood vessel fillings, anteroposteriorly projected over the dorsal surface of the cerebral hemispheres, allows us to suggest that, in metriorhynchids, the dural envelope of this region was thin and that the cerebral hemispheres filled most of the cavity.

The most evident fillings of the cranial nerves canals preserved are related to the extrinsic ocular muscles (cranial nerves III, IV and VI). In extant crocodylians and birds, the cranial nerve foramina transmit cranial nerves as well as associated vasculature (Witmer et al. 2008). In this sense, the diameter of the foramen does not reflect the diameter of the nerve. The cast interpreted as the canal of the oculomotor nerve described in *Dakosaurus* cf. *D. andiniensis* may reflect the preservation of cranial nerve as well as associated veins. However, the diameter of the oculomotor nerve of *Dakosaurus* cf. *D. andiniensis* is exaggeratedly larger than that of *Gavialis gangeticus* (MLP 602). Judging from the diameter of the oculomotor, as well as the trochlear and abducens nerves canals, the eyeball of metriorhynchids might have had a great mobility and, consequently, a great visual range. Nevertheless, this hypothesis needs to be evaluated.

Several of the internal features described for '*Metriorhynchus*' cf. '*M. westermanni*' by Fernández et al. (2011), based on CT images and three-dimensional reconstruction, such as a large dorsal venous sinus that overlays the dorsal region of the hindbrain, a tube-like cavity connecting the cranioquadrate passage and an enlarged internal carotid canal, are present in the endocast of *Dakosaurus* cf. *D. andiniensis*. These features, together with the same orientation of the rostral middle cerebral vein and its relation with the blood vessel pattern that covers the dorsal surface of the cerebral hemispheres, shared with *C. araucanensis*, were widely distributed within metriorhynchids.

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