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ARTICLE

A METRIORHYNCHID CROCODYLIFORM BRAINCASE FROM NORTHERN CHILE

MARTA S. FERNÁNDEZ,*[,1] ARIANA PAULINA CARABAJAL,[2] ZULMA GASPARINI,[1]
and GUILLERMO CHONG DÍAZ[3]
[1]Departamento Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, La Plata 1900, Argentina, martafer@fcnym.unlp.edu.ar;
[2]Museo Carmen Funes, Av. Córdoba 55Plaza Huincul 8318, Neuquén, Argentina;
[3]Departamento de Ciencias Geológicas, Universidad Católica del NorteAngamos 0610, Antofagasta, Chile

ABSTRACT—A three-dimensionally preserved metriorhynchid braincase from the Oxfordian of northern Chile is described. The specimen is referred to the metriorhynchid *Metriorhynchus* cf. *M. westermanni*. The excellent preservation provides clear sutures and a detailed description, and X-ray computed tomographic (CT) scanning provides internal anatomical details. The general pattern of the orbitotemporal region is consistent with that of the basal thalattosuchian *Pelagosaurus typus* as described recently. The specimen from northern Chile shares with other metriorhynchids (e.g., *Cricosaurus araucanensis*, *Metriorhynchus westermanni*, *M. casamiquelai*, and *Dakosaurus andiniensis*) a dorsally exposed laterosphenoid, a laterosphenoid-prootic suture forming a blunt crest separating the supratemporal fenestra into two fossae for muscular attachment, and the quadrate incompletely sutured to the braincase. Thus, these features characterize not only basal but derived Thalattosuchia, as suggested by previous authors. The main difference in the orbitotemporal region is that in the specimen described herein, and in the other metriorhynchids examined, the trigeminal fossa is developed mainly caudal to the trigeminal foramen, whereas in *P. typus* the fossa is developed rostral and caudal to the trigeminal foramen. CT scanning indicates the presence of enlarged dorsal dural venous sinuses overlying the brain, as it has been described recently in *Steneosaurus pictaviensis*, and a well-developed sinus within the quadrate. The large foramen ventrolateral to the occipital condyle, which characterizes metriorhynchids, is confirmed as the entry for the internal carotid artery.

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INTRODUCTION

Metriorhynchids were a group of Mesozoic crocodyliforms completely adapted to a marine lifestyle. They are unique in several anatomical features, including a streamlined skull and body, loss of bony armor, short and paddle-like forelimbs, and hypocercal tail (Buffetaut, 1982), as well as in the acquisition of hypertrophied salt-secreting glands (Fernández and Gasparini, 2008). Although clearly recognized as a monophyletic group within Thalattosuchia, internal relationships of thalattosuchians as well as the phylogenetic position of this clade within Crocodyliformes are subject to debate. Some authors find support for thalattosuchians as basal mesoeucrocodilians (e.g., Buckley et al., 2000; Sereno et al., 2001; Tykoski et al., 2002; Larsson and Sues, 2007; Sereno and Larsson, 2009), whereas other authors find them nested within neosuchians and related to other longirostrine neosuchians such as pholidosaurs and dyrosaurids (Clark, 1994; Wu et al., 1997, 2001; Buckley and Brochu, 1999; Larsson and Gado, 2000; Brochu et al., 2002; Gasparini et al., 2006; Jouve, 2009; Pol and Gasparini, 2009). Although internal relationships of Thalattosuchia are controversial, in all cladistic analyses *Pelagosaurus typus* is consistently found as a basal thalattosuchian, and metriorhynchids are recovered as a well-supported clade of derived thalattosuchians (e.g., Mueller-Töwe, 2005; Young, 2006; Jouve, 2009; Pierce et al., 2009a; Young and Andrade, 2009). Morphological details of thalattosuchians have increased in recent years because of reexaminations of basal forms such as *P. typus* and *Teleosaurus cadomensis*, as well as cladistic and functional-morphological analyses of metriorhynchids (Pierce and Benton, 2006; Pierce et al., 2009b; Jouve, 2009; Young and Andrade, 2009). However, in the case of metriorhynchids, most of the anatomical knowledge corresponds to the external morphology and general shape of the skull.

Although there are a large number of metriorhynchid skulls, mainly from the Middle Jurassic Oxford Clay Formation of England, most are compressed, which prevents accurate braincase descriptions. A well-preserved, three-dimensional metriorhynchid crocodyliform braincase from the Oxfordian of northern Chile is described here. The specimen was subjected to X-ray computed tomographic (CT) scanning, which yielded good resolution, and for the first time allows an exploration of the internal anatomical details of a metriorhynchid braincase. Holliday and Witmer (2009) recently recognized major character transitions in the orbitotemporal region during crocodilian evolution, including a detailed description of *Pelagosaurus typus*. They characterize different arrangements of the crocodyliform cavum epiptericum and orbitotemporal region. Within this context, the specimen recovered from Chile represents an opportunity to test whether the arrangement present in basal thalattosuchians also characterizes advanced metriorhynchids. Based on morphology, we refer this specimen to *Metriorhynchus* cf. *M. westermanni*. *Metriorhynchus westermanni* is a metriorhynchid known from the Callovian of northern Chile (Gasparini, 1980; Gasparini et al., 2008).

Institutional Abbreviations—**BMNH**, Natural History Museum, London, U.K.; **MDA**, Museo del Desierto de Atacama, Antofagasta, Chile; **MGHF**, Museo Geológico Humberto Fuenzalida, Universidad Católica del Norte, Antofagasta, Chile; **MLP**, Museo de La Plata, Argentina; **MOZ**, Museo Olsacher, Zapala, Argentina.

Anatomical Abbreviations—**bo**, basioccipital; **bs**, basisphenoid; **bt**, basal tuber; **c?**, possible columella; **cqf**, cranioquadrate foramen; **cqp**, cranioquadrate passage; **cr B**, crest B; **ds**, dorsum sellae; **ec**, endocranial cavity; **eo**, exoccipital; **fm**, foramen magnum; **fo ept**, epipterygoid fossa; **fo mAMEP**, fossa for Musculus

*Corresponding author.

adductor mandibulae externus profundus; **fo mPSTs**, fossa for Musculus pseudotemporalis superficialis; **fo V**, trigeminal fossa; **fpt**, post-temporal foramen; **fv CM**, middle cerebral vein foramen; **gV1**, ophthalmic groove; **gV2**, maxillary groove; **ic**, internal carotid; **icc**, internal carotid canal; **ie**, inner ear; **if**, infundibular foramen; **ls**, laterosphenoid; **ls-pr**, laterosphenoid-prootic suture; **mec**, middle ear cavity; **mp**, most caudal portion of the median pharyngeal tube; **oc**, occipital condyle; **p**, parietal; **pf**, pituitary fossa; **pop**, paroccipital process; **pr**, prootic; **ps**, parasphenoid; **q**, quadrate; **so**, supraoccipital; **sq**, squamosal; **ss**, dorsal longitudinal venous sinus; **ve**, vestibular eminence; **III**, **V**, **VI**, **IX–XII**, cranial nerve foramina and/or passages; **1**, tube-like cavity communicating the cranioquadrate passage with the dorsal longitudinal venous sinus; **2**, cavity within the quadrate related dorsally with middle ear cavity and ventromedially with the Eustachian (= pharyngotympanic) tubes; **3**, small passage communicating middle ear cavity with the trigeminal fossa.

MATERIALS AND METHODS

The subject of this paper, MDA 2, was collected south of Cerro Laberinto (23°26′00″S, 69°21′02″W), Domeyko Cordillera, Caracoles area, Antofagasta, northern Chile. The specimen was found in a calcareous concretion in the Sierra El Cobre Formation, Cerro Amarillo Member (Ferraris and Di Biase, 1978), and associated with the Oxfordian ammonite *Perisphinctes andium*.

The braincase is nearly complete and lacks only the most rostral portion, skull roof, and ventral aspect of the basicranium (Figs. 1, 2A). This specimen is referred to Metriorhynchidae on the basis of a dorsally concave and posterolaterally directed posteromedial branch of squamosal and an enlarged foramen for the internal carotid artery. Based on morphology, we refer MDA 2 to *Metriorhynchus* cf. *M. westermanni* Gasparini, 1980. MDA 2 shares with *Metriorhynchus westermanni* Gasparini, 1980, holotype (MGHF 1-010199) and MDA 1 (Gasparini et al., 2008:fig. 2) the following combination of characters: horizontal sagittal frontoparietal crest, supraoccipital contributing to the foramen magnum, blunt exoccipital-supraoccipital suture, triangular prootic in lateral view, trigeminal fossa developed caudal to trigeminal foramen, vertical occiput, and basal tubera ventrally directed.

The thalattosuchian *Pelagosaurus typus* Bronn, 1841 (BMNH R32599), and the metriorhynchids *Metriorhynchus casamiquelai* Gasparini and Chong Díaz, 1977 (MGHF 1-08573), *Cricosaurus araucanensis* (Gasparini and Dellapé, 1976) Young and Andrade, 2009 (MLP 72-IV-7-1 and 72-IV-7-2), *Dakosaurus andiniensis* Vignaud and Gasparini, 1996 (MOZ 6146P), and *M. westermanni* Gasparini, 1980 (MGHF1-010199, MDA 1), were used for comparison. MDA 2 was mechanically prepared at the Departamento de Paleontología Vertebrados of the Museo de La Plata, Argentina. To explore internal anatomical details, MDA 2 was subjected to X-ray computed tomographic (CT) scanning at the Hospital Paroissien in La Matanza, Buenos Aires, Argentina. Slice thickness for MDA 2 is 1 mm. CT scanning provided good resolution between bone and rock matrix. Three-dimensional reconstructions of the endocranium and other cavities were reconstructed using the software Mimics (Version 13.1.2010; Materialise NV, Leuven, Belgium). The anatomical terminology used herein follows Holliday and Witmer (2009).

DESCRIPTION

General Form and Preservation

As with other metriorhynchids, the supratemporal fossae are enlarged. Most of the parietal-squamosal bars are preserved, missing only the most lateral portion of the squamosal. The good quality of preservation permits easily identifiable bone sutures.

Parietal—Externally the parietals are exposed as a single fused element, although internally paired pneumatic structures are observed, indicating the paired origin of this element (Figs. 1D, 3E). In rostral view the parietal has an isosceles triangle shape, with its base strongly convex and overlying the laterosphenoids (Fig. 1D). In dorsal view, the parietal sagittal bar is very narrow, but broadening caudally and forming a triangle. The base of this triangle is concave (Fig. 1A). Dorsally the parietal sagittal bar is narrow and partially eroded. Laterally the parietal is subvertical, as in *Metriorhynchus*, *Cricosaurus*, and *Dakosaurus* (Pol and Gasparini, 2009), and contacts the laterosphenoid and the prootic (Fig. 2A, B). The parietal contacts the squamosal caudolaterally, forming the medial and caudal sections of the supratemporal fossa. The lateral bar of the parietal is convex, and joins the squamosal through a V-shaped projection (Fig. 1B). The parietal forms part of the vertical occipital wall sitting on top of, and forming a M-shaped suture with the supraoccipital (Fig. 1C). The lateral branch of the parietal has a compressed rim that projects caudally overhanging the occipital wall (Fig. 1C), as observed in other metriorhynchids, but more conspicuously.

Squamosal—Both squamosals are incomplete, lacking the lateral process, which delimits the supratemporal fossa. Rostrally (Fig. 1D) and laterally (Fig. 2A), the squamosal contacts the pterygoid process of the quadrate. Caudally it forms with the parietal a conspicuous rim that overhangs the occipital wall (Fig. 1C). The parietal-squamosal bar is narrow and it is laterally expanded (Fig. 1A, C), as in *M. westermanni* and unlike *M. casamiquelai*, in which the parietal-squamosal bars are caudolaterally oriented (Gasparini and Chong Díaz, 1977:fig. 3A). The external and lateral tip of the right squamosal forms the dorsal border of the cranioquadrate foramen and overlies the pterygoid process of the quadrate.

Laterosphenoid—The laterosphenoid is incomplete. The preserved part of the body of the laterosphenoid is rostrocaudally long and it is dorsally exposed within the medial portion of the supratemporal fossa. The laterosphenoids form most of the lateral walls of the endocranial cavity. In rostral view, the endocranial cavity is subrhomboidal in outline (Figs. 1D, 3I). Caudally, the laterosphenoid contacts the prootic to form a blunt crest. As in *Pelagosaurus typus*, *M. casamiquelai*, *D. andiniensis*, and *C. araucanensis*, this crest separates the supratemporal fossa into rostral and caudal fossae. These fossae have been interpreted as the attachment areas of the M. pseudotemporalis superficialis and M. adductor mandibulae externus profundus, respectively (Holliday and Witmer, 2009).

In lateral view the body of the laterosphenoid is large (Fig. 2A). In *Metriorhynchus westermanni* (MDA 1), the laterosphenoid is almost complete except for a portion of the laterosphenoid postorbital process that has been damaged (Fig. 2C). Dorsal to the damaged area there is a subtle fossa rostroventral to the pseudotemporalis fossa, and caudomedially to the cotylar crest, in the same area where the epipterygoid fossa is developed in *P. typus*. Although no bone can be identified as an epipterygoid, we interpret this fossa as a remnant of the epipterygoid fossa (sensu Holliday and Witmer, 2009). In *M. westermanni* MDA 1, the laterosphenoid bears a robust postorbital process (Fig. 2C). On the ventral portion of the laterosphenoid, close to the suture to the basisphenoid, there is a groove and foramen interpreted to be for the oculomotor nerve (CN III) and associated vasculature. In *M. westermanni* MDA 1 (Fig. 2C) and in *M.* cf. *M. westermanni* MDA 2 (Fig. 2A), the laterosphenoid forms the rostral framework of the trigeminal fossa, within which an enlarged trigeminal foramen is located. The rostral border of the trigeminal foramen is convex.

A short conical groove is present on the lateral surface of the laterosphenoid body and the middle of the trigeminal fossa rim. This structure is interpreted as an osteological correlate of the exit of the ophthalmic division of the trigeminal nerve (CN V_1).

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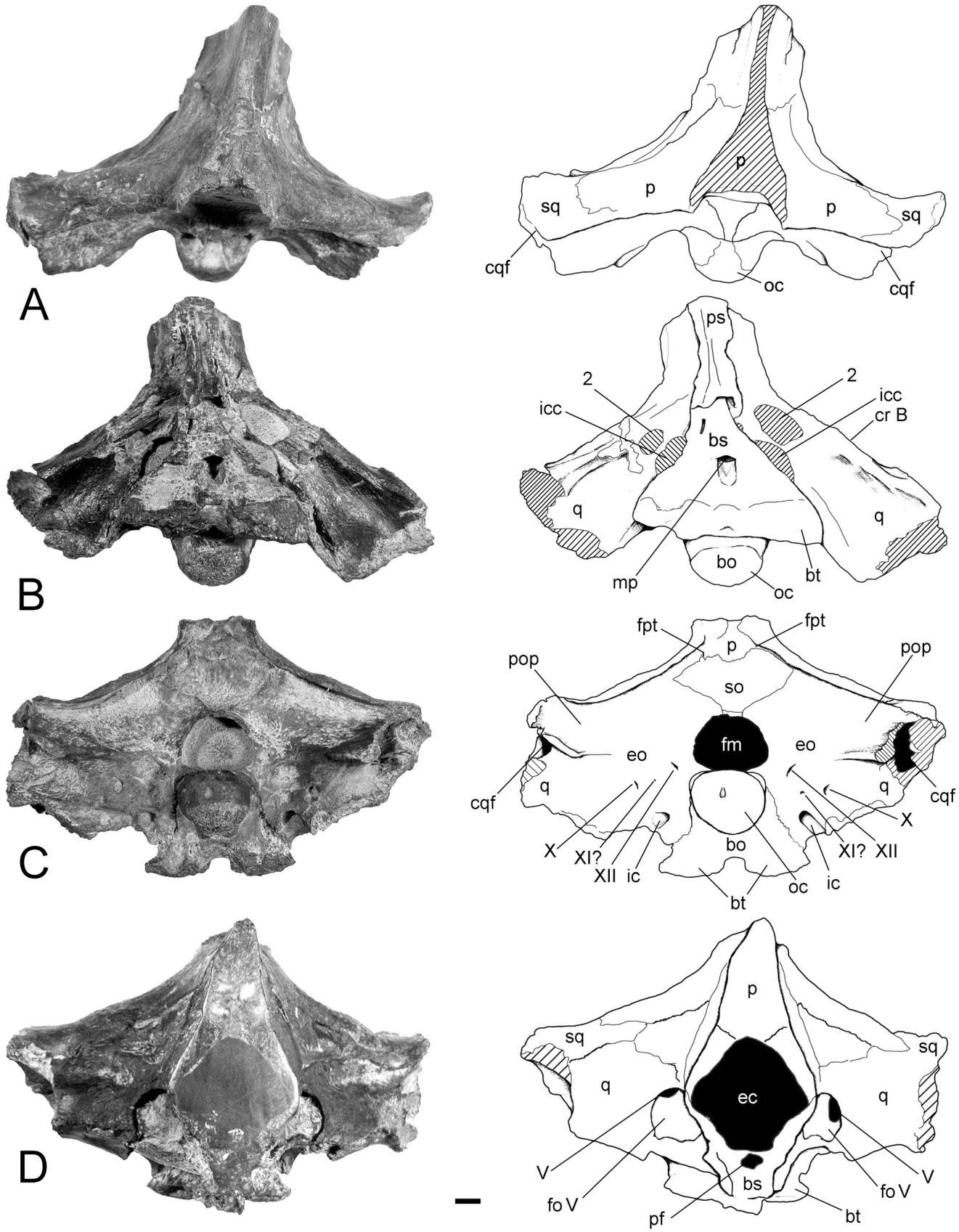

FIGURE 1. *Metriorhynchus* cf. *M. westermanni*, MDA 2. **A**, dorsal, **B**, ventral, **C**, caudal, and **D**, rostral views. Scale bar equals 1 cm.

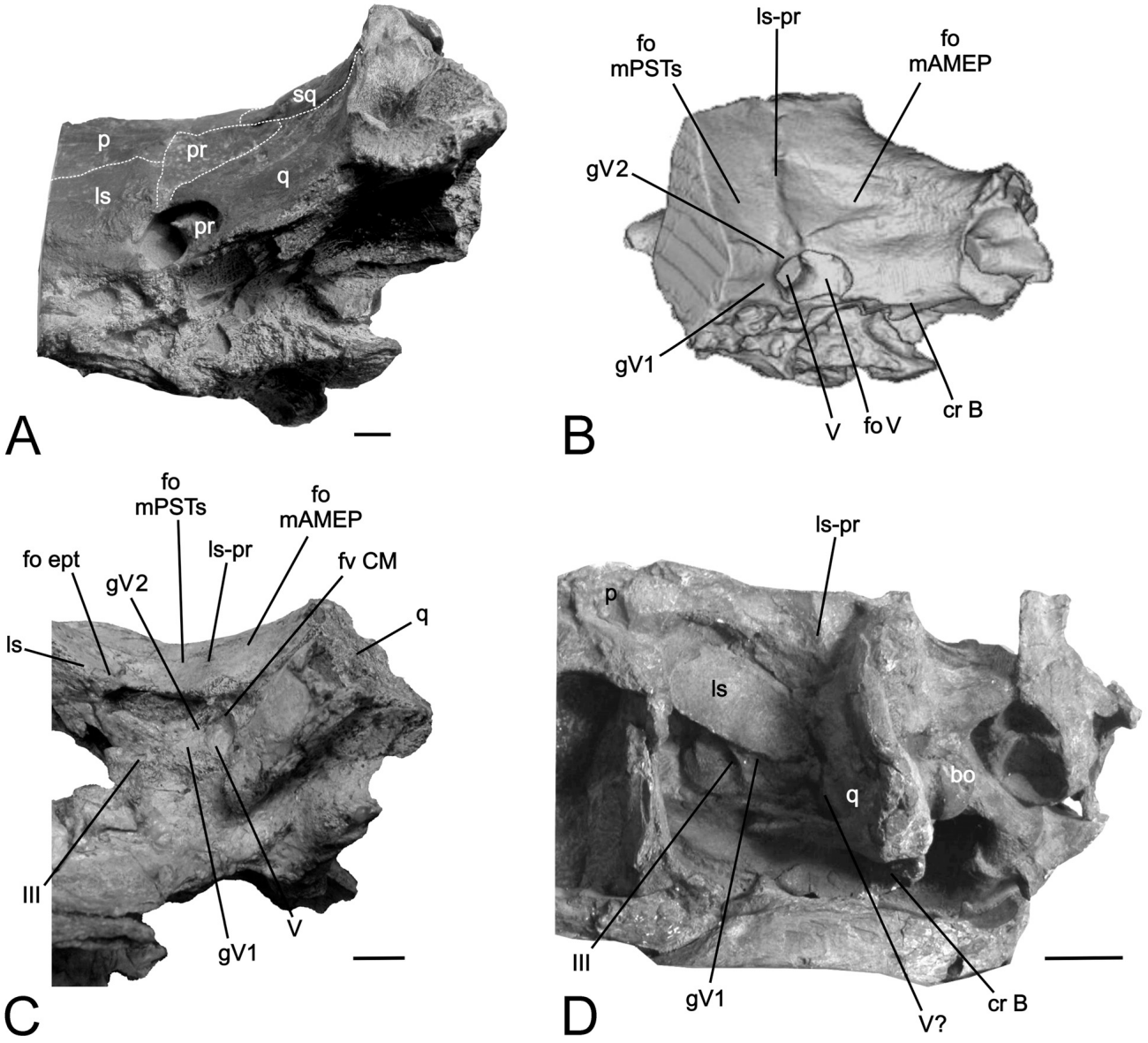

FIGURE 2. **A**–**B**, *Metriorhynchus* cf. *M. westermanni*, MDA 2. **A**, left lateral and slightly ventral view. **B**, CT-based surface in left lateral and slightly rostral view. Not to scale. **C**, caudal portion of the skull of *M. westermanni* (MDA 1) in left lateral view. **D**, caudal portion of the skull of *Dakosaurus andiniensis* (MOZ 6146P) in left lateral view. Scale bars equal 1 cm (**A**, **C**) and 5 cm (**D**).

In MDA 1 (*M. westermanni*), the conical fossa interpreted to be for the exit of V_1 is better defined than in MDA 2 (*Metriorhynchus* cf. *M. westermanni*), and continues rostrally as rostrodorsally directed groove. In both specimens, dorsal to this groove, there is a subtle groove on the rostrodorsal rim of the trigeminal fossa that is here interpreted to be for the exit of the maxillary division of the trigeminal nerve (V_2). This groove is better defined in MDA 1 (Fig. 2C). The pattern of neurovascular grooves that exit the trigeminal foramen and traverse the laterosphenoid rostrally in MDA 1 and MDA 2 is consistent with that of *P. typus* and we assume the homology and osteological correlates recently proposed by Holliday and Witmer (2009). The main difference between this basal thalattosuchian and the derived metriorhynchids described here is that in *P. typus* (BMNH R32599) the trigeminal fossa is developed rostrally and caudally to the trigeminal foramen, and the laterosphenoid is conspicuously recessed, whereas in MDA 1 and MDA 2 the fossa is mainly developed caudally to the trigeminal foramen (Fig. 2A–C). This condition is also present in *C. araucanensis*. In *D. andiniensis* the area of the trigeminal fossa is crushed. Another difference is that in *P. typus* the ophthalmic groove is more pronounced and dorsally bounded by an overhanging sharp crest, whereas in MDA 1 and MDA 2 the groove is dorsally bound by a subtle blunt crest. In *Dakosaurus andiniensis* (Fig. 2D), although the area surrounding the trigeminal fossa and foramen is badly preserved, the features observed on the laterosphenoid are consistent with those described in the other metriorhynchids used for comparison. The most conspicuous characteristic of *D. andiniensis* is the strong overhanging crest that dorsally borders the ophthalmic groove.

Prootic—In lateral view the prootic is triangular and its surface is slightly concave (Fig. 2A, B), forming the fossa interpreted for the attachment for M. adductor mandibulae externus profundus

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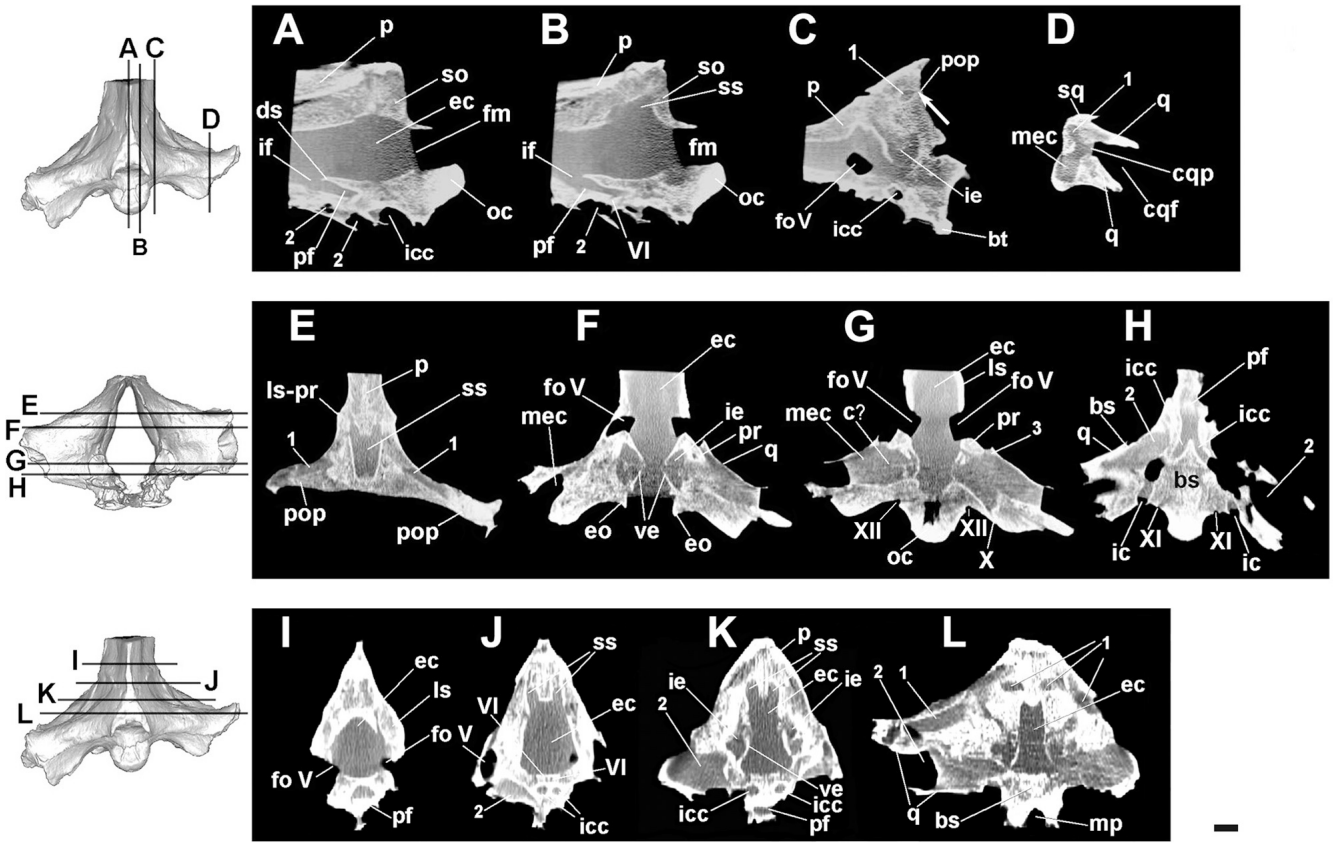

FIGURE 3. *Metriorhynchus* cf. *M. westermanni*, MDA 2, illustrated with CT data. Selected CT-slice images in **A**–**D**, sagittal, **E**–**H**, horizontal, and **I**–**L**, coronal planes. Arrow in C indicates short canal connecting cavity 1 with the post-temporal foramen. Scale bar equals 1 cm.

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(Holliday and Witmer, 2009). The prootic forms the caudal and ventral margins of the trigeminal foramen, which is bounded by a wide trigeminal fossa. The floor of the trigeminal fossa is formed by the prootic only and is developed principally caudal to the trigeminal foramen (Fig. 2A, B), a trait shared with other metriorhynchids such as *M. casamiquelai*, *M. westermanni* (Fig. 2C), and *C. araucanensis*. On the caudal rim of the trigeminal fossa lies a rostral projection of the prootic, with a bilobate outline dividing the trigeminal foramen in two portions: a smaller caudodorsally directed dorsal lobule interpreted as the foramen for the middle cerebral veinand a large semicircular ventral portion interpreted as the exit for the branches of the trigeminal nerve.

Supraoccipital—In caudal view the supraoccipital has a subhexagonal shape and is vertical, except for the portion participating in the rim of the foramen magnum (Fig. 1C). The supraoccipital contacts the parietal dorsolaterally and the exoccipital laterally in a blunt suture. The post-temporal foramen is reduced on both sides and is located on the dorsal portion of the lateral suture of the supraoccipital. In other metriorhynchids this foramen can be reduced or absent (Wenz, 1968). Obliteration or reduction of the post-temporal foramen can be variable within species, such as *Cricosaurus araucanensis* (MLP 72-IV-7-1; 71-IV-7-2; 71-IV-7-4).

Exoccipital—The exoccipital is the bone most widely exposed on the occipital wall. It forms, together with the supraocipital, the foramen magnum. The dorsal section is laterally expanded, with a marked caudolateral crest that forms the ventral border of the paroccipital process (Fig. 1C). This crest is subhorizontal, and is similar to that in *Metriorhynchus casamiquelai* (Gasparini and Chong Díaz, 1977:fig. 4) and *M. westermanni* (Gasparini et al., 2008:fig. 2C). The ventral section of the exoccipital also participates in the boundary of the foramen magnum, laying on the basioccipital but not participating in the occipital condyle. In caudal view, there are two defined areas on the ventral portion of the exoccipital: one medial, vertically oriented, and related to the foramen magnum and the basioccipital; the other a wide lateral area that forms the caudal margin of the cranioquadrate foramen. This foramen is bounded by the squamosal dorsally, the quadrate rostrally, and the exoccipital caudally. Internally this foramen continues into the cranioquadrate canal, which is completely ossified and is separated from the external auditory opening. This condition is similar to that in *Metriorhynchus*, *Cricosaurus*, and *Dakosaurus*, but differs from that in *Teleosaurus cadomensis*, in which the cranioquadrate canal is incompletely separated from the external auditory opening by a thin ventral lamina of the exoccipital and is not closed dorsally (Jouve, 2009).

Lateral to the foramen magnum and occipital condyle, the exoccipital is pierced by three small foramina corresponding to cranial nerves XII, XI, and X, and a large ventral opening for the internal carotid artery (Fig. 1C). The foramen magnum is wider than tall and is delimited dorsally by a marked caudal projection of the supraoccipital, and exoccipitals, and ventrally by the basioccipital.

Basioccipital—The basioccipital forms the occipital condyle. The neck of the condyle is short and the main body has a central pit (Fig. 1C). The basioccipital is vertical in caudal view. The basal tubera are separated by a transverse, convex bony bridge and ventrally directed. In other longirostrine forms, such as dyrosaurids, these expansions are rostroventrally oriented (Brochu et al., 2002; Jouve, 2005).

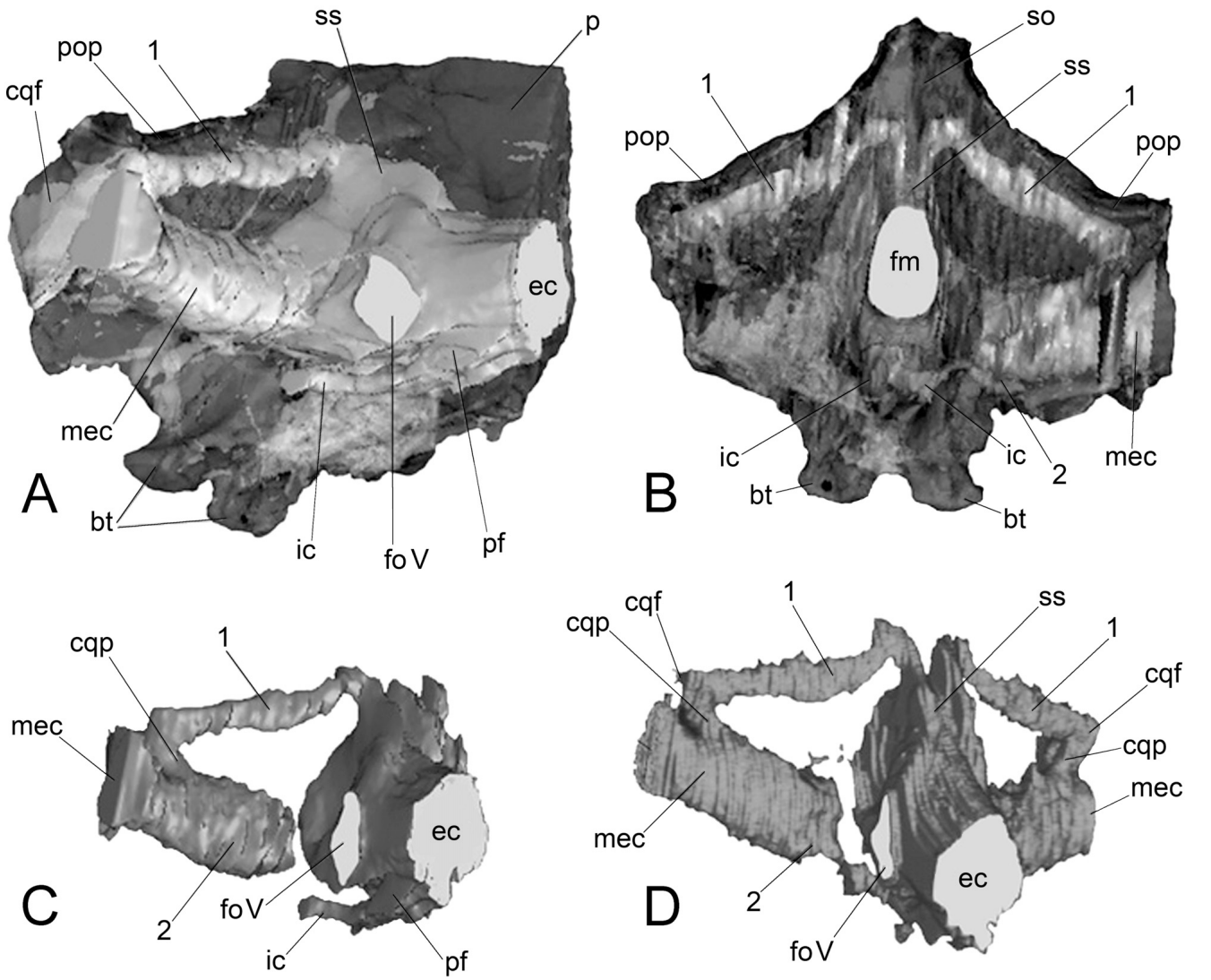

FIGURE 4. *Metriorhynchus* cf. *M. westermanni*, MDA 2. **A**, ventrolateral and **B**, rostral views of the braincase and endocranial cavities. **C**, rostroventrolateral and **D**, rostrolateral views of isolated cavities. Not to scale.

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Basisphenoid—In rostral view, the fractured braincase reveals the basisphenoid forming the floor of the endocranial cavity (Fig. 1D). It is triangular, with two projections caudolaterally directed. In ventral view, the basisphenoid is eroded, which has exposed a large median foramen that corresponds to the most caudal portion of the median pharyngeal system (Fig. 1B).

Parasphenoid—The parasphenoid is incompletely preserved and is a long and narrow bar with a dorsal medial crest and two longitudinal lateral depressions (Fig. 1B). The morphology of this bone is similar to the one figured by Andrews (1913:plate XIII 4) for *Metriorhynchus durobrivensis*.

Quadrate—Both quadrates are incomplete. Although most of the orbital process of the quadrate has not been preserved, its caudal portion projects laterally, indicating that, as in *P. typus*, *M. westermanni*, *C. araucanensis*, and *D. andiniensis*, the rostromedial surface of the orbital process of the MDA 2 remains free of bony attachment (Fig. 2A, B). The quadrate forms the walls of a large middle ear cavity.

The pterygoid branch of the quadrate is strongly concave ventrally with a sharply ridged rostral border. A sharp crest ('crest B' of Iordansky, 1973) extends parallel to this border. In ventral view, the medial rostral portion of the quadrate is eroded and has exposed two large, oval hollows: the medial one corresponds to the large internal carotid canal, and the most external one as a pneumatic cavity (cavity 2; see below) that is confluent with the middle ear cavity (Fig. 1B).

Endocranial and Other Braincase Internal Cavities

A digital three-dimensional reconstruction of the cranial endocast and associated pneumatic cavities is shown in Figure 4. The endocranium of MDA 2 is incomplete, lacking the rostral part of the cavity occupied by the forebrain. The endocranial cavity is subrhomboidal in coronal view at the level of laterosphenoid-prootic contact. In sagittal view, and in comparison to extant crocodylians, the shape of the cavity indicates that the cephalic and pontine flexures of the brain were only slightly developed. The natural endocast of a pholidosaur described by Edinger (1938) and Hopson (1979), as well as a braincase of a teleosaurid described by Seeley (1880), also indicates that flexures are not

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well demarked, but in MDA 2 this condition is more extreme. The floor of the medullary fossa, between the foramen magnum and the infundibular foramen, is slightly concave. The dorsum sellae is not projected dorsally, and instead is almost continuous with the floor of the endocranial cavity (Fig. 3B). The infundibular foramen opens rostrally to the dorsum sellae, communicating ventrally with the pituitary fossa, which is low and rostrocaudally developed (Fig. 3A, B). In the floor of the medullary fossa, caudal to the dorsum sellae, are two foramina through which the abducens nerves would have exited the endocranial cavity by rostrally piercing the basisphenoid to the pituitary fossa.

The internal cranial carotid canals are well ossified and have been preserved almost completely. These canals enter the pituitary fossa caudally through two separate foramina (Fig. 3H). The diameter of these canals (ca. 4 mm) is large along their lengths and it is approximately the same as the diameter of the external opening on the exoccipitals. An enlarged external opening for the internal carotid canal has been considered a synapomorphy of metriorhynchids (Pol and Gasparini, 2009). It is not possible to determine if the cranial carotid canals were ossified along all their entire lengths or if, as in extant *Alligator mississippiensis* (Sedlmayr, 2002), portions of the canal were cartilaginous tubes, because the region where the canals course through the rostral middle ear space has been eroded ventrally (Figs. 1B, 3H).

The medial wall of the vestibular eminence is well ossified and, as in extant crocodylians (Witmer et al., 2008), is a relatively simple, triangular structure that projects into the endocranial cavity (Fig. 3C, F, K). Three cavities can be recognized within the vestibular eminence, but CT scan data do not permit confident reconstructions of the labyrinth of the inner ear.

Caudodorsally the endocranial cavity is enlarged, indicating well-developed dural venous sinuses would have overlain the brain. The cavity housing the dural venous sinuses is rostrodorsally divided by a sagittal septum from the parietal (Fig. 3J, K). Wharton (2000) described a similar enlarged longitudinal dorsal venous sinus, above the junction of the midbrain and hindbrain, in *Steneosaurus pictaviensis.*

Other Internal Cavities

Based on CT scan data there are two main paired cavities that could be traced with confidence. These cavities will be named 1 and 2 for descriptive purposes. Cavity 1 is a tube with a maximum diameter of 6 mm that connects the cranioquadrate canal with the longitudinal dorsal dural venous sinus that had overlain the brain (Fig. 4). From the dorsal longitudinal sinus, cavity 1 is parallel to its counterpart and rises caudodorsally. At its dorsal extent, cavity 1 curves ventrolaterally and projects along the dorsal portion of the paroccipital process ending at the cranioquadrate canal. A short canal, interpreted to be for the caudal middle cerebral vein (Sampson and Witmer, 2007; Witmer and Ridgely, 2009), links cavity 1 to the post-temporal foramen (Fig. 3C).

The other paired cavities (cavity 2) are in the quadrate and are interpreted as pneumatic. Cavity 2 is, apart from the middle ear cavity, the largest of all the preserved cavities pneumatizing the braincase (Figs. 3H, J; 4). Dorsally, cavity 2 is broadly confluent with the large middle ear cavity. A short rostromedially oriented canal, probably for the tympanic branch of the trigeminal nerve (Witmer et al., 2008; Holliday and Witmer, 2009), connects the middle ear cavity with the trigeminal fossa (Fig. 3G).

Erosion to the ventral surface of the basioccipital and part of the basisphenoid has exposed the most caudal portion of the median pharyngeal system (Witmer et al., 2008) (= median Eustachian tube, Owen, 1850; Colbert, 1946; Iordansky, 1973). The basisphenoid is pneumatized by a sinus that branches rostrally into right and left portions. Each branch enters the quadrate ventral to the pituitary fossa (Fig. 3J).

Braincase Cranial Nerves

The ventrolateral flange of the exoccipital of MDA 2 is pierced by four foramina (Fig. 1C). The cranial foramen located more dorsally and closest to the occipital condyle corresponds to the hypoglossal nerve (CN XII). CT scan data show that, on each side, this foramen connects a single short canal directed medially and opening as a small foramen on the medial endocranial wall close to the foramen magnum (Fig. 3G, H).

Ventral to the foramen for CN XII (Fig. 1C) lie two smaller foramina. The CT scan data show that the more laterally located foramen is connected to a long, curved canal directed anteromedially, which opens at a foramen located caudal to the vestibular eminence and interpreted to have housed CN X (Fig. 3G).

The more medially positioned foramen connects to a canal that extends rostrally and opens into the caudolateral portion of the middle ear cavity (Fig. 3H). This communication with the middle ear cavity and the location of the canal are equivalent to the canal described by Iordansky (1973) for the passage of the ramus comunicans of N. sympathicus in extant crocodylians, or as the canal for the tympanic branch of the glossopharyngeal (CN IX) and vagus nerves (CN X) by Witmer et al. (2008).

The fourth foramen, located ventrolateral to the occipital condyle, corresponds to the external opening of the osseous cranial carotid canal. This opening, as in other metriorhynchids, is remarkably large in comparison with that of most crocodyliforms (Pol and Gasparini, 2009; Young and Andrade, 2009).

DISCUSSION

The most conspicuous modifications of metriorhynchid skeleton include hydrofoil-like forelimbs, a hypocercal tail, and loss of dermal armor (Buffetaut, 1982). Within the skull, features of metriorhynchids include broad prefrontals orientated transversely and overhanging the orbit, lateralization of the orbits, internalization of the antorbital cavity, and a neomorphic preorbital opening for the exit of salt-gland ducts (Fernández and Herrera, 2009). Metriorhynchids, as well as all other thalattosuchians and dyrosaurids, share enlarged supratemporal fenestrae. Although these marine crocodyliforms have conspicuous modifications in the orbitotemporal region, the evolutionary and morphological patterns of this region of the skull have been poorly understood not only in thalattosuchians, but also in crocodyliforms. However, a recent comprehensive analysis by Holliday and Witmer (2009) has helped to shed light on this issue, especially their detailed description and reconstruction of this region in *P. typus*. Examination of the orbitotemporal region of the *Metriorhynchus* cf. *M. westermanni* and other three-dimensionally well-preserved metriorhynchid skulls (*M. westermanni*, *M. casamiquelai*, *Cricosaurus araucanensis*, and *Dakosaurus andiniensis*) show strong similarities between the orbitotemporal region of metriorhynchids with that of *P. typus* described by Holliday and Witmer (2009). Those authors recognized four different arrangements of the cavum epiptericum and orbitotemporal region within mesoeucrocodylians: columnar, waisted, overlapping, and isolated, all based on epipterygoid morphology. *Pelagosaurus* possesses the overlapping morphology. Although the epipterigoid is not preserved in MDA 2, a subtle fossa on the laterosphenoid, rostroventral to the pseudotemporalis fossa in *M. westermanni* (MDA 1) and in the holotype of *C. araucanensis*, suggests that these metriorhynchids also possess an overlapping epipterigoid. In all metriorhynchids examined, the laterosphenoid is dorsally exposed. The pattern of neurovascular grooves on the lateral wall of the laterosphenoid of these metriorhynchids is also consistent with that of *P. typus* in exhibiting a rostrolaterally directed V_2 (Holliday and Witmer, 2009:fig. 6B, E). *Pelagosaurus typus*, *Metriorhynchus* cf. *M. westermanni*, *M. westermanni*, *M. casamiquelai*, *C. araucanesis*, and *D. andiniensis* also share two distinct fossae for muscular

attachments in the supratemporal fossa. The rostral fossa is interpreted to be for the M. pseudotemporalis superficialis.

Another feature shared by *Pelagosaurus* and metriorhynchids is the presence of an orbital process of the quadrate that remains free of bony attachments. Thus, both main features of the orbitotemporal region of *P. typus* pointed out by Holliday and Witmer (2009), i.e., quadrate incompletely sutured to the braincase and two muscle-attachment areas in the supratemporal fossa, seem to characterize Thalattosuchia.

The main differences between the metriorhynchids examined and *P. typus* is that in the latter a trigeminal fossa is excavated rostrally and caudally to the trigeminal foramen. The condition in *Metriorhynchus* cf. *M. westermanni*, *M. westermanni*, and *C. araucanesis* is more restricted, with the trigeminal fossa mainly developed only caudally to the trigeminal foramen (Fig. 2A–C). Although not all metriorhychids were sampled here, it is noteworthy to point out many of those, such as *D. andiniensis* and *C. araucanensis*, represent extreme known endpoints in metriorhynchid morphological diversity (Pierce et al., 2009b).

Internal exploration of the braincase of *Metriorhynchus* cf. *M. westermanni* revealed the presence of a well-developed pneumatic system with an expanded cavity within the quadrate confluent to the middle ear cavity. Another conspicuous feature is the presence of paired, tube-like cavity (cavity 1) connecting the dural venous sinuses overlaying the brain and the cranioquadrate canal, which also connects the middle ear cavity. Cavity 1 is interpreted to have housed neurovascular elements, as indicated by its relationship with the dorsal longitudinal dural sinus, the canal for the caudal middle cerebral vein, and the cranioquadrate passage. However, its connection with the middle ear cavity suggests that cavity 1 could be related to the paratympanic pneumatic system. Clearly, additional CT data of other thalattosuchian taxa are needed to address this issue.

CT data also confirm that, as previously proposed by other authors (e.g., Wenz, 1968; Pierce and Benton, 2006; Pol and Gasparini, 2009; Young and Andrade, 2009), the enlarged foramen located ventrolateral to the occipital condyle corresponds to the entry foramen for the internal carotid artery. This foramen is connected to an osseous cranial canal that ends at the pituitary fossa and has the same course as the one described for the passage of the internal carotid artery in extant crocodiles (Sedlmayr, 2002). These internal braincase morphologies have not been described for other thalattosuchians, so we cannot discern if the morphologies of *Metriorhynchus* cf. *M. westermanni* are autapomorphic, shared with other metriorhynchids, or shared with all thalattosuchians.

CONCLUSIONS

Examination of three-dimensionally preserved skulls of metriorhynchids revealed a consistent orbitotemporal pattern within this clade that is congruent with that described by Holliday and Witmer (2009) for the basal thalattosuchian *Pelagosaurus typus*. The main difference between *P. typus* and metriorhynchids is a caudally restricted trigeminal fossa. The presence of a subtle fossa on the laterosphenoid of *Metriorhynchus* cf. *M. westermanni* (MDA 2) suggests the presence of an overlapping epipterygoid, as it has been described by Holliday and Witmer (2009) for *P. typus*. CT-scan data of the braincase of *Metriorhynchus* cf. *M. westermanni*, allowed for the first time the description of internal anatomy of the skull in a metriorhynchid. The most conspicuous internal features are an enlarged cavity interpreted to be for large dural venous sinuses covering much of the brain dorsally (similar to the one in *P. typus* described by Wharton, 2000); an expanded sinus within the quadrate confluent with the middle ear cavity; and a paired tube-like cavities connecting the cranioquadrate passage to the dorsal dural venous sinus. CT data also allow us to confirm that the enlarged foramen located ventrolateral to the occipital condyle in metriorhynchids likely accommodated the internal carotid artery.

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