

MUSEUM OF COMPARATIVE ZOOLOGY  
*The Agassiz Museum*



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5<sup>th</sup> February 2017

Dear Prof. Knoll,

We are very grateful for the thoughtful and detailed comments of the reviewers – Ariana Paulina Carabajal and Yanina Herrera. This review process has been incredibly professional and the expertise of the both reviewer's has greatly increased the quality of the manuscript.

After reading the reviews, we have modified the text and figures based on the recommendations. Most of these changes can be seen in the track-changes document. We have also attended to the technical changes required.

Our primary goal was to update the terminology used to reflect the paleoneurology literature more accurately. In keeping with this, we have modified our title by replacing 'brain and sinuses' with 'endocranial anatomy'. We have also attended to all anatomical identifications to ensure their accuracy and have added missing supporting literature to our reference list.

For ease of review, we have pulled out all major Review Comments and include either or Changed Text or a Reply.

Thank you for considering our manuscript.

Yours sincerely,

Stephanie E. Pierce

**Reviewer 1:**

**(1) Changed text:** The angle of the cephalic (forebrain-midbrain) and pontine (midbrain-hindbrain) flexure in *Pelagosaurus* is much greater (i.e. less acute) than most other pseudosuchians, indicating that the brain is relatively straight (Table 1).

**(2)** In terms of proportions, the olfactory tract (plus blubs) in *Pelagosaurus* is similar in size to other crocodile-line archosaurs, with the exception of phytosaurs and *Cricosaurus*, which have elongated olfactory tracts that form approximately half the length of the endocast (Table 2).

**Reply:**

**We chose to stick to the method here, as we cannot be 100% confident about the division between the blub and tract in our reconstruction or some of the other reference material.**

**Comment [PSE1]:**  
Reviewer 1 Comment:

I would recommend the use of forebrain, midbrain and hindbrain, and mention the angles formed between them. The cephalic and pontine flexures are terms usually used in embryology. Also, the presence of dorsal and ventral venous sinuses in reptile cranial endocasts obscures the real location of those flexures. Anyhow, the meaning is the same, and choosing the terminology is up to the author!

**Comment [PSE2]:**  
Reviewer 1 comment:

The Olfactory Ratio (Zelenitsky et al 2009) may be a better measure to compare the relative size of the olfactory bulbs in different taxa. It takes the longest diameter of the olfactory bulb and the longest diameter of the cerebral hemisphere



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(3) The dorsal surface of the cerebral cast bears a shallow, midline groove in *Pelagosaurus*, indicating the division between hemispheres by the cerebral longitudinal fissure, resulting in a heart-shaped cross-section (Fig. 5A). This groove is absent in *Gavialis* (Fig. 5D) and most other reptiles (Witmer & Ridgely, 2008; Witmer et al., 2008; Kley et al., 2010; Lautenschlager & Butler, 2016), including the metriorhynchoid *Cricosaurus* (Herrera, 2015) and the teleosauroid *Steneosaurus pictaviensis* (Wharton 2000).

**Reply:**

Unfortunately, the resolution of the scan is not high enough to determine if there was any vasculature present with any confidence.

(4) **Changed text:** The appearance of the division between the cerebral hemispheres in the brain endocast of *Pelagosaurus* (and potentially *Teleosaurus*) is therefore unusual among pseudosuchians studied so far, and may suggest that the dural envelope surrounding the cerebral hemispheres was relatively thin in this taxon. Such a morphology is common within some dinosaur clades (e.g. harosauroids) in which the cast of the cerebral hemispheres also bears vascular impressions (Evans, 2005).

(5) **Changed text:** In contrast to *Gavialis*, the cerebellum region in *Pelagosaurus* is characterized by two large, dorsally projecting rami, which are identified as branches of the dorsal longitudinal venous sinus (Figs. 5A, B). These branches, which presumably housed the caudal middle cerebral (head) vein (Witmer & Ridgely, 2009; Porter, 2015; Porter, Sedlmayr, & Witmer, 2016), connect the endocranial cavity with the paratympanic system (Fig. 3B, D).

(6) **Changed text:** The sinus that surrounds the caudal middle cerebral vein does not connect to the paratympanic sinus system in other crocodile-line archosaurs, including phytosaurs, but were recently described in the braincase of the metriorhynchoids "*Metriorhynchus*" cf. *westermanni* (Fernández et al., 2011), *Dakosaurus andiniensis* and *Cricosaurus anraucanensis* (Herrera, 2015), and similar dorsally directed branches extending from the cerebellum region have been described for the teleosauroid *Steneosaurus* (Wharton, 2000; Brusatte et al., 2016), suggesting this could represent a thalattosuchian synapomorphy.

(7) **Added text:** But similar large channels have been described extending anteriorly from the pituitary in the teleosauroids *Teleosaurus* (Seeley, 1880) and *Steneosaurus* (Wharton, 2000; Brusatte et al., 2016). These channels may therefore represent a thalattosuchian synapomorphy. Unfortunately, currently available data precludes us from assessing the character state in metriorhynchoids; however, such a feature may be present in *Cricosaurus anraucanensis* (pers. comm. A. Paulina Carabajal).

**Reply:**

Would Reviewer 1 be okay with us using a personal communication here?

**Comment [PSE3]:**

Reviewer 1 comment:

in most reptiles! This is indeed a striking character.  
It is possible to visualize any vascular impressions as well? The presence of those is supposed to be related to brains (or regions of the brain) full-filling endocranial cavities.

**Comment [PSE4]:**

Reviewer 1 comment:

at least at the area of the cerebral hemispheres. This is common within particular clades of dinosaurs (e.g. hadrosaurs) in which the cast of the cerebral hemispheres (not the mid and hindbrain) also bears vascular impressions (Evans, 2005).

**Comment [PSE5]:**

Reviewer 1 comment:

it seems to me that the protuberance is a cast of the dorsal longitudinal sinus (dorsal expansion, dural peak, in other papers). The cerebellum is indeed probably below that area, but I do not think the protuberance is reflecting the shape of the cerebellum itself. The lack of floccular process in crocodiles avoids proving the location...

**Comment [PSE6]:**

Reviewer 1 comment:

the dorsal sinus is a venous sinus. this "branches" are not branches of the sinus but passages connecting the pneumatic tube 1, with the endocranial cavity. The location indicates that the related blood vessel correspond probably to the caudal middle cerebral veins (=occipital veins, capitis dorsalis veins, etc in older papers).

**Comment [PSE7]:**

Reviewer 1 comment:

re-phrase to make clear the idea: the character that matters here are these tubes connecting the endocranial cavity with the paratympanic system, not the veins (which are commonly present in other reptiles).

**Comment [PSE8]:**

Reviewer 1 sent in an image of *Cricosaurus* which may also show the same feature.



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(8) The length of the endosseus cochlear duct (=lagenar recess) sensu Walsh et al. (2009) is proportionally much longer in *Pelagosaurus* than in *Gavialis* or most other crocodile-line archosaurs (Fig. 6; Table 2), or even those of early dinosaurs (e.g. cochlear duct length:labyrinth length = ~0.5 in both *Herrerasaurus* and *Massospondylus*; Sereno et al., 2007; Knoll et al., 2012).

**Reply:**

Our measurements follow those of Walsh et al. 2009 who measure the entire endosseus cochlear duct (ECD) from the end of the pars vestibularis. For consistency and comparison with this study and others (e.g. Brusatte et al. 2016) we have kept the measurement as is. It also allows us to make more measurements as the fenestra ovalis is not always discernible.

(9) **Changed text:** The 3D morphology of the paratympatic sinuses has been described in *Alligator mississippiensis* (Witmer & Ridgely, 2008; Dufau & Witmer, 2015) and *Crocodylus johnstoni* (Witmer et al., 2008); however, little is known about the system outside extant crocodylians (but see Bona, Degrange & Fernández, 2013).

(10) **Changed text:** The most conspicuous feature of the paratympatic sinus system in *Pelagosaurus* and *Metriorhynchus* is that it is confluent with a cavity (Fig. 3B, D) that presumably carried the caudal middle cerebral (head) vein (Witmer & Ridgley, 2009; Porter, 2015; Porter, Sedlmayr, & Witmer, 2016).

(11) **Changed text:** As the caudal middle cerebral vein typically drains venous blood from the brain into the internal jugular, it is unclear what the functional implications of this morphology may be (i.e. why such a large volume of venous blood would drain through the paratympatic sinus). Further investigation of this morphology is encouraged, with higher resolution scans and in a broader range of thalattosuchians and crocodylomorphs.

**Reviewer 2:**

(1) Similar to observations of teleosauroids, these studies found that the dural envelope surrounding the cerebral hemispheres was thin in metriorhynchoids and that the cerebrum filled the majority of the cranial cavity (e.g., Herrera, 2015; Herrera & Vennari, 2015). Also, in keeping with Wharton (2000) and Brusatte et al. (2016), there appears to be an enlarged dorsal venous sinus overlying the dorsal region of the hindbrain that appears to connect with the paratympatic sinus system (Fernández et al., 2011; Herrera, 2015).

**Reply:**

We have added reference to the papers alluded to, but refrain from adding reference to Abstracts as anatomical features cannot be confirmed.

(2) **NOTE:** we have removed *Cricosaurus* from the measurements table.

**Comment [PSE9]:**  
Reviewer 1 comment:

The lagena needs to be measured below the fenestra ovalis (which marks the limit between the lagena and the vestibulum). In figure 6, I believe the fenestra ovalis is the enlarged area below the semicircular canals (the image is not very clear), and the lagena is the tubular projection, approximately 4.5 mm long. This seems to be relatively longer than *Gavialis* but is similar to most dinosaurs studied so far. Is it possible to determine the size and p location of the fenestra ovalis? Please check that you are measuring the length of the lagena only

**Comment [PSE10]:** Reviewer 1 comment:

Bona et al., 2012 described the paratympatic sinuses for *Mourasuchus*, an extinct crocodile

**Comment [PSE11]:**  
Reviewer 1 comment:

(used probably by the caudal middle cerebral vein to exit the endocranial cavity)

**Comment [PSE12]:**

Reviewer 1 comment:

The dorsal sinus is related -dorsally-to the middle cerebral vein system (rostral middle cerebral vein, dorsal head vein, caudal middle cerebral vein). See Sedlmayr, 2002; Witmer et al 2008; Witmer and Ridgely, 2009.

"caudal head vein" in the recently published work of Porter et al., 2016

**Comment [PSE13]:**  
Reviewer 2 comment:

We described these features (a thin dural envelope and a enlarged dorsal venous) for *Dakosaurus cf. D. andiniensis* (Herrera and Vennari, 2015). In Herrera et al. (2013) we only described the olfactory tract and bulbs of *C. araucanensis*. A more complete description of natural brain endocasts in *C. araucanensis* (and the proposal of a thin dural envelope and the tube-like 1 cavity) can be found in Herrera (2015).

Also, there are two abstracts with some information about the neuroanatomical features of thalattosuchians.

HERRERA Y. 2016. Comparative endocranial morphology of two thalattosuchian (Crocodylomorpha) species: *Steneosaurus bollensis* and *Cricosaurus araucanensis*. XIV Annual Meeting of the European Association ...



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(3) Immediately anterior to the endocast, the nasal passageway is expanded to form the olfactory region (dorsal region of the cavum nasi proprium; Parsons 1970) in both specimens (Fig. 3, 4; dark green).

**Reply:**

Olfactory region is not an usual term to use; it is common in the literature. But, we have now discussed this further at the end of the paragraph.

(4) **Changed text:** In many archosaurs, the paranasal sinus system perforates the lateral surface of the skull, forming a large antorbital fenestra between the maxilla, nasal and lacrimal (Witmer, 1997). Although the antorbital fenestra is closed in extant crocodylians such as *Gavialis*, the internal paranasal sinus is still well developed (Witmer, 1997). Unlike in crocodylians, the antorbital fenestra is small, but apparently present in *Pelagosaurus* (Witmer, 1997; Pierce & Benton, 2006). Witmer (1997) described *Pelagosaurus* as having a small, slit-like antorbital fenestra between the maxilla and lacrimal, with little or no surrounding external fossa, and this is evident in the specimen described here (Fig. 1A; and Pierce & Benton, 2006). This condition is similar to early teleosauroids, such as *Teleosaurus*, which also have an antorbital fenestra that is small, but nevertheless present (Jouve, 2009; the fenestra is closed in *Machimosaurus*, Martin & Vincent, 2013). A different morphology is present in metriorhynchoid thalattosuchians (reviewed by Leardi, Pol & Fernández, 2012: fig. 1), in which a larger, circular fenestra is present in this region, from which a broad groove extends anteriorly along the lateral surface of the snout, and which has been interpreted as being homologous with the antorbital fenestra of other archosaurs by most authors (e.g. Andrews, 1913; Witmer, 1997; Gasparini et al., 2006; Young & Andrade, 2009). Because of ambiguity over the homology of the ‘antorbital fenestra’ in thalattosuchians generally, and in metriorhynchoids specifically, Fernández & Herrera (2009) and Leardi, Pol & Fernández (2012) advocated use of the term ‘preorbital fenestra’ to describe this feature. In *Pelagosaurus*, this fenestra enters internally onto the dorsolateral surface of the olfactory recess anteriorly (the position of the antorbital fenestra is indicated by a star in Fig. 1A–B).

Although the preorbital fenestra of thalattosuchians has been identified as a reduced external antorbital fenestra by many authors (e.g. Witmer, 1997), Fernández & Herrera (2009) proposed an alternative hypothesis. Based on the observed association of this external opening with the internal recess for a salt gland (labeled here as ‘olfactory region’; Fig. 4), Fernández & Herrera (2009) suggested that the external opening of the antorbital fenestra was closed in metriorhynchids, and their external opening instead represented a neomorphic exit for the salt gland. This hypothesis was supported by dynamic homology analyses by Leardi Pol & Fernández (2012) for metiorhynchids, but not for other thalattosuchians. The analysis of Leardi Pol & Fernández (2012) requires reassessment in light of the topological similarity of structures associated with the preorbital fenestra (or antorbital fenestra) in *Pelagosaurus* to those of metiorhynchids. This raises the possibility that our ‘antorbital fenestra’ instead represents an external opening of the salt gland. For now, we denote the external opening as the antorbital fenestra here. In reconciliation of these hypotheses, we see no reason why the internal recess (‘olfactory’ region) might not have housed an enlarged salt gland, alongside olfactory epithelia and portions of the internal paranasal sinus, or

**Comment [PSE14]:**

Reviewer 2 comment:

Although the authors say that the olfactory region is used here in a loose sense, I think that use “olfactory recesses” to do reference to the osteological correlates of the salt gland is not proper and is confusing, I strongly suggest the use of other term (e.g. antorbital recesses, prefrontal recesses). Also, I suggest replacing narial cavity by nasal cavity, narial passage by nasal cavity proper or nasopharyngeal duct when appropriate (e.g. line 210. narial passage should be replaced by nasopharyngeal duct ).

**Comment [PSE15]:** Reviewer 2 comment:

Related to the antorbital fenestra, the authors go for the classical point of view (i.e. *Pelagosaurus typus* has antorbital fenestra). However, Witmer (1997), and Jouve (2009) proposed that basal thalattosuchians have an internalized antorbital fenestra. The authors did not discuss about this interpretation. Based on the description and figure 3, my opinion is also that in *Pelagosaurus typus* the antorbital fenestra is internalized. The morphology and the topographic relationships of the structures in the dark green region resemble the morphology present in *Cricosaurus araucanensis* (i.e., the antorbital sinus is ventral to the salt gland, and tapers anteriorly along the length of the snout, the antorbital sinus is lateral to the primary choana and, apparently, the ostium is directly opposite to the it), which has an internalized antorbital fenestra. I am not able to distinguish/understand the participation of the antorbital sinus to the osteological correlate of the salt gland, as the authors described. But, if so, I believe that is not enough evidence (or it is not properly described) to assume the presence of antorbital fenestra because there are more evidences to hypothesized the absence of external antorbital fenestra. Leardi et al. (2012) proposed, based on a dynamic homology approach, that the fenestra in basal thalattosuchians is interpreted as homologous to the antorbital fenestra of other archosaurs. As noted, there are many sources of information related to this topic that should be discussed as I think that it is an important topic for understand the evolution of thalattosuchians and I feel that the authors did not take the opportunity to describe and discuss it properly.



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why the external opening might not have provided an exit for the salt gland as well as being homologous with the antorbital fenestra of other archosaurs.

**Reply:**

We have done our best to add a considered discussion of this other hypothesis. Note when reading this that neither Jouve 2009 nor Witmer 1997 stated that the external opening of the antorbital recess (i.e. antorbital fenestra) was lost in teleosauroids. Their descriptions mirror ours in saying that the external opening was reduced. Other than semantically, this does not differ from the referee's statement that the antorbital fenestra was 'internalised'. The internal portion of the recess houses the internal paranasal sinus and we discuss it as such.

(5) **Changed text:** In both *Pelagosaurus* and *Gavialis*, the hypothesized antorbital sinus (i.e. the hypothesized internal recess for the major portion of the paranasal sinus) is confluent anteriorly with elongate internal canals that extend longitudinally along the length of the snout (Figs. 3, 4; dark pink). Despite the confluence of these recesses, we identify the tapering anterior portions as neurovascular canals rather than being the anterior portion of the antorbital sinuses. In particular, we identify it as the dorsal alveolar canal for the maxillary branch of the trigeminal nerve and maxillary vein and artery. As added evidence of these, we have observed smaller canals that branch off and enter the bases of the maxillary and premaxillary alveoli, indicating a neurovascular function.

**Comment [PSE16]:**  
Reviewer 2 comment:

according to the authors the antorbital sinus exits through the antorbital fenestra but also enters to the maxilla (through the internalized antorbital fenestra)?

(6) **Changed text:** A straight brain is shared with the metriorhynchoids *Dakosaurus* cf. *andiniensis* (Herrera and Vennari, 2015), and *Metriorhynchus* cf. *westermanni* (Fernández et al., 2011), and the teleosauroid *Steneosaurus* cf. *gracilirostris* (Table 1); the sectioned braincase of the teleosauroid *Teleosaurus eucephalus* also appears more straight in outline (Seeley, 1880).

**Comment [PSE17]:** Reviewer 2 comment:

Fernández et al. (2011) described a reduction of the flexures in 'Metriorhynchus' cf. 'M.' westermanni. Herrera and Vennari (2015) in *Dakosaurus* cf. *D. andiniensis* and Herrera (2015) in *Cricosaurus araucanensis*.

(7) The pituitary is also characterized by two distinct anterodorsally projecting channels (see further below), and large posterolaterally projecting channels that housed the two branches of the internal carotid artery (Fig. 5B, D);

**Reply:**

Based on the scan data that we have, we were unable to reconstruct them further. We had the same problem in *Gavialis*, perhaps due to low resolution.

**Comment [PSE18]:**  
Reviewer 2 comment:

Are not the canals for the internal carotid completely ossified? or why are not completely reconstructed?

(8) These branches, which presumably housed the caudal middle cerebral (head) vein (Witmer & Ridgely, 2009; Porter, 2015; Porter, Sedlmayr, & Witmer, 2016), connect the endocranial cavity with the paratympatic system (Fig. 3B, D).

**Comment [PSE19]:**  
Reviewer 2 comment:

How the authors determined the extension of the branches of the dorsal sinus and the extension of the PTS1?

(9) Nevertheless, the labyrinth varies among extant crocodylians (Brusatte et al., 2016) and some taxa have a pyramidal labyrinth morphology similar to those of *Pelagosaurus* and *Steneosaurus*,



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especially *Crocodylus johnstoni* (Fig. 7; redrawn from Brusatte et al., 2016), indicating homoplasy in this trait. Nevertheless, the labyrinth varies among extant crocodylians (Brusatte et al., 2016) and some taxa have a pyramidal labyrinth morphology similar to those of *Pelagosaurus* and *Steneosaurus*, especially *Crocodylus johnstoni* (Fig. 7; redrawn from Brusatte et al., 2016), indicating homoplasy in this trait.

**Reply:**

Has been adjusted

**(10) Changed text:** Based on our 3D endocranial reconstructions of the thalattosuchian *Pelagosaurus typus* and of the extant crocodylian *Gavialis gangeticus*, and making use of existing knowledge of the relationships of these taxa, we are able to clarify the phylogenetic distributions of key soft-tissue features of thalattosuchians, including....

**Reply:**

Individual characters can be mapped to a phylogeny by observing their distributions regardless of whether that phylogeny was constructed in the present study or not. Nonetheless, we have changed the wording.

**(11) Changed text:** Below, we propose functional interpretations relevant to the construction of the snout in longirostrine pseudosuchians, thalattosuchian salt excretion and regulation, as well as neuroanatomical and sensory adaptations in some of the earliest diverging members of the Crocodylomorpha.

**(12) Changed text:** Further, the large, laterally placed orbits in thalattosuchians, and particular *Pelagosaurus*, may indicate these animals were highly visual predators (Pierce & Benton, 2006) and relied less on auditory signals. Although the cranial nerves were not distinguishable here, Herrera and Vennari (2015) described enlarged oculomotor nerves (CN III) in the braincase of the metriorhynchid *Dakosaurus* that may have functioned to control finer-scale eye movements.

**(13) Changed text:** Previous workers have suggested that enlarged nasal salt glands are a derived feature of the highly-specialized metriorhynchoids, enabling them to maintain constant plasma osmolality (Fernández & Gasparini, 2000, 2008). Although Fernández and Gasparini (2008) predicted the presence of salt glands in teleosauroids, they suggested it would have been small with low secretory capability. (text continues)

**Comment [PSE20]:**

Reviewer 2 comment:

to me the redrawing of cochlea duct in *C. johnstoni* does not look like the figure 8G of Brusatte et al. (2016). The cochlea duct in *C. johnstoni* (Fig. 7) looks shorter than in Brusatte et al. (2016)

**Comment [PSE21]:**

Reviewer 2 comment:

I believe that it cannot be a conclusion. I think that the proposal of synapomorphies has to be done together with a phylogenetic analysis, and it is not the case. Also, three of these features (1, 2 and 3) are unknown for metriorhynchids, so maybe are not characteristics for all thalattosuchians

**Comment [PSE22]:**

Reviewer 2 comment:

It is not discussed. The authors identified the osteological correlate of the salt gland, and based on it reconstructed the gland in *Pelagosaurus* and propose salt-excretion capabilities in earliest thalattosuchians, that was previously proposed by Brusatte et al. (2016). But there is not a discussion about the evolutionary origins of salt excretion and regulation

**Comment [PSE23]:**

Reviewer 2 comment:

Also Herrera and Vennari (2015) described and enlarged CN III for *Dakosaurus cf. D. andiniensis* and related this with the movements of the eyeball.

**Comment [PSE24]:**

Reviewer 2 Comment:

Fernández and Gasparini (2008) said that: "Thus, teleosaurids would have represented the third stage of Dunson and Mazzotti's (1989) model, i.e. an osmoregulation strategy based on small salt glands of low secretory capacity ..... If the model of Dunson and Mazzotti (1989) is applicable to secondary adaptation of crocodyliforms to marine life during the Mesozoic, then no particular 'bony signatures' of salt glands should be expected in teleosaurids."

They said that teleosaurids would have had small salt glands