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Virtual reconstruction of the brain and sinuses of the early Jurassic marine crocodylomorph *Pelagosaurus typus* (Thalattosuchia)

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Thalattosuchians were highly specialised marine archosaurs of the Jurassic and Early Cretaceous, and represent a peak of aquatic adaptation among crocodylomorphs. Relatively little is known of their endocranial anatomy or its relevance for the evolution of sensory systems, physiology, and other aspects of biology. Nevertheless, such data have significance for two reasons: (1) thalattosuchians represent an important data point regarding adaptation to marine life in tetrapods; and (2) as early-diverging members of the crocodylian stem-lineage, thalattosuchians provide information on the evolutionary assembly of the brain and other endocranial structures in crocodylomorphs. Here we use μ CT data to virtually reconstruct the brain and sinuses of *Pelagosaurus typus*, an early thalattosuchian with plesiomorphic traits of relevance to the split between the two major subgroups: Teleosauroidea and Metriorhynchoidea. Interpreted in a phylogenetic context, these data indicate several endocranial features as likely synapomorphies of Thalattosuchia, including: a pyramidal morphology of the semicircular canals, the presence of an elongate cochlear duct that may indicate enhanced hearing ability, the presence of large, paired canals extending anteriorly from an enlarged pituitary fossa, a relatively straight brain (possibly due to the presence of large, laterally placed orbits) and an enlarged dorsal longitudinal sinus that is confluent with the paratympanic sinus system. Notably, we document a large expansion of the nasal cavity anterior to the orbits in *Pelagosaurus* as an osteological correlate of an enlarged salt gland previously only documented in Late Jurassic metriorhynchoids. This is the first direct evidence of this structure in early thalattosuchians. *Pelagosaurus* also shares the presence of paired olfactory tracts with metriorhynchoids, and shows an enlarged cerebrum, which may also be present in teleosauroids. Taken together, our findings indicate that physiological and sensory adaptations to marine life occurred early in thalattosuchians evolution, predating

the origins of flippers, tail flukes, and hydrodynamic body forms seen later in metriorhynchoids.

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[Short title: Endocranial anatomy of *Pelagosaurus*]

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ABSTRACT

Thalattosuchians were highly specialised marine archosaurs of the Jurassic and Early Cretaceous, and represent a peak of aquatic adaptation among crocodylomorphs. Relatively little is known of their endocranial anatomy or its relevance for the evolution of sensory systems, physiology, and other aspects of biology. Nevertheless, such data have significance for two reasons: (1) thalattosuchians represent an important data point regarding adaptation to marine life in tetrapods; and (2) as early-diverging members of the crocodylian stem-lineage, thalattosuchians provide information on the evolutionary assembly of the brain and other endocranial structures in crocodylomorphs. Here we use μ CT data to virtually reconstruct the brain and sinuses of *Pelagosaurus typus*, an early thalattosuchian with plesiomorphic traits of relevance to the split between the two major subgroups: Teleosauroidea and Metriorhynchoidea. Interpreted in a phylogenetic context, these data indicate several endocranial features as likely synapomorphies of Thalattosuchia, including: a pyramidal morphology of the semicircular canals, the presence of an elongate cochlear duct that may indicate enhanced hearing ability, the presence of large, paired canals extending anteriorly from an enlarged pituitary fossa, a relatively straight brain (possibly due to the presence of large, laterally placed orbits) and an enlarged dorsal longitudinal

sinus that is confluent with the paratympanic sinus system. Notably, we document a large expansion of the nasal cavity anterior to the orbits in *Pelagosaurus* as an osteological correlate of an enlarged salt gland previously only documented in Late Jurassic metriorhynchoids. This is the first direct evidence of this structure in early thalattosuchians. *Pelagosaurus* also shares the presence of paired olfactory tracts with metriorhynchoids, and shows an enlarged cerebrum, which may also be present in teleosauroids. Taken together, our findings indicate that physiological and sensory adaptations to marine life occurred early in thalattosuchians evolution, predating the origins of flippers, tail flukes, and hydrodynamic body forms seen later in metriorhynchoids.

INTRODUCTION

Thalattosuchia is a radiation of marine crocodylomorphs that attained a worldwide distribution at low latitudes during the Early Jurassic – Early Cretaceous (Mannion et al., 2015). They are characterized by having a longirostrine skull morphology (long, narrow snout), although some taxa possessed relatively shorter and more robust snouts (e.g. *Dakosaurus*; Gasparini et al., 2006). The group is divided into two major clades, the teleosauroids, which were ‘gavial-like’ near shore predators, and the highly-derived pelagic metriorhynchoids, which exhibited modified flipper-like forelimbs, a crescentic fish-like tail, and loss of dermal armour. The morphology, phylogeny, and evolutionary dynamics of the Thalattosuchia has been under intense investigation over the past decade (e.g. Mueller-Töwe, 2005, 2006; Jouve, 2009; Pierce, Angielczyk & Rayfield, 2009a; Pol & Gasparini, 2009; Young & De Andrade, 2009; Young et al., 2010; Young, Bell & Brusatte, 2011; Marin & Vincent 2013; Stubbs et al., 2013; Cau, 2014; Martin et al., 2014; Jouve, 2016; Young et al., 2016) with some recent studies suggesting that thalattosuchians may be relatively early diverging members of the Crocodyliformes (e.g., Wilberg, 2015a). Moreover, there has been increasing interest in reconstructing their functional paleoecology, with studies focusing on feeding mechanics and niche partitioning (e.g., Pierce, Angielczyk & Rayfield, 2009b; De Andrade et al., 2010; Young et al., 2010; Stubbs et al., 2013; Young et al., 2013), as well as adaptations for aquatic locomotion (e.g., Hua, 1994; Hua & De Buffrenil, 1996; Hua, 2003; Molnar et al., 2015).

A further area of research has concentrated on thalattosuchian endocranial anatomy. Seeley (1880) provided one of the earliest neuroanatomical descriptions of a thalattosuchian by

longitudinally sectioning a teleosauroid braincase from the Whitby Lias (Early Jurassic of England); he noted that the brain “differed remarkably from that of living Crocodiles (p. 629)” and commented that it seemed to fill the cerebral cavity unlike other ‘reptiles’ and that more details were thus visible, including the median division of the cerebrum. This close appression of the brain to the endocranial cavity characterizes many extinct members of the archosaur total-group, including extant birds and their stem-lineage (e.g., Franzosa & Rowe, 2005) and members of the archosaurian stem-lineage (e.g., Sobral et al., 2016), but appears to have been lost in extant crocodylians, which have a thick dural envelope (Hopson, 1979). More than a century after Seeley’s (1880) work, Wharton (2000) described a three-dimensional (3D) reconstruction of a teleosauroid endocast. Making an endocranial silicone rubber mould from an acid prepared specimen of *Steneosaurus*, Wharton noted the presence of an enlarged longitudinal dorsal venous sinus as compared to the modern gharial. However, the endocast mould was susceptible to the degree of acid preparation and thus incomplete. More recently, Brusatte et al. (2016) presented the braincase endocast of a second *Steneosaurus* specimen, confirming some of Seeley (1880) and Wharton’s (2000) observations and documenting novel features such as the morphology of the endosseous labyrinth.

The endocranial characteristics of metriorhynchoids have also been investigated, with the majority of descriptions based on naturally preserved endocast. Most attention has been placed on the presence of a hypertrophied, lobate salt-section gland, which sits within the enlarged prefrontal area and appears to drain into the antorbital fenestra (Fernández & Gasparini, 2000; Gondola et al., 2006; Fernández & Gasparini, 2007; Fernández & Herrera, 2009; Herrera, Gasparini & Fernández, 2013). More recently, neuroanatomical features from a natural endocast have been detailed (Herrera & Vennari, 2015), in addition to the first virtual 3D reconstruction of the brain and sinuses in a thalattosuchian, *Cricosaurus araucanensis* (Herrera, Gasparini & Fernández, 2013). 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. 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 paratympanic sinus system (Fernández et al., 2011). Further, the 3D reconstruction exposed an expanded antorbital sinus and a paired

olfactory structure positioned between the salt-glands, features that appear, so far, to be unique to metriorhynchoids.

To further investigate endocranial anatomy in thalattosuchians, we examined a virtual 3D endocast of *Pelagosaurus typus*, a Toarcian (Early Jurassic) monotypic genus known from shallow marine sediments of Western Europe (Eudes-Deslongchamps, 1863, 1877; Westphal, 1961, 1962; Duffin, 1979; Pierce & Benton, 2006). The evolutionary affinity of *P. typus* has been a point of contention, with the species being diagnosed as both a teleosauroid (Eudes-Deslongchamps, 1863, 1877; Westphal, 1961, 1962; Duffin, 1979; Gasparini et al., 2006; Mueller-Towe, 2005, 2006; Sereno & Larsson, 2009; Wilberg, 2015b) and a metriorhynchoid (Buffetaut, 1980, 1982; Vignaud, 1995; Pol, Turner & Norell, 2009; Young et al., 2013; Adams, 2013; Parrilla-Bel et al., 2013; Wilberg, 2015a) or as the sister group to both clades (Benton & Clark, 1988; Clark, 1994; Buckley et al., 2000; Wu et al., 2001; Tykoski et al., 2002; Pol, 2003). *P. typus* was a small-bodied thalattosuchian (~1m in length) considered to be an adept aquatic pursuit predator, with a long streamlined snout ideal for snapping at fast moving prey (e.g. fish) and large, anterolaterally placed orbits for increased visual acuity (Pierce & Benton, 2006). Its overall gross morphology has been extensively documented (e.g. Pierce & Benton, 2006), but little is known about its soft-tissue anatomy. Here we extend our understanding of *P. typus* by illustrating its brain and associated sinuses and use this information to discuss potential functional paleoneurology, as well as endocranial evolution in thalattosuchians and crocodile-line archosaurs (pseudosuchians plus phytosaurs) more generally.

MATERIAL AND METHODS

We reconstructed the brain and sinus cavities of a three-dimensionally preserved skull of *Pelagosaurus typus* (specimen M1413) from the Charles Moore Collection housed in the Bath Royal Literary and Scientific Institute (BRLSI) (Fig. 1 A, B; see Supplementary Fig. 1 for interactive 3D reconstruction). The specimen comes from Strawberry Bank, north of Ilminster, Somerset England, is geologically from the lower part of the Upper Lias (Toarcian; Early Jurassic), and is preserved in a limestone nodule providing excellent 3D preservation with minimal taphonomic distortion. The external surface has been manually prepared, but the internal cavities are still infilled with limestone. As the geological setting and the external skull morphology of this specimen has been described in detail by Pierce & Benton (2006), we focus

solely on endocranial morphology here. For comparison, we also reconstructed the brain and sinus cavities of the extant crocodylian, *Gavialis gangeticus* (specimen R5792, University Museum of Zoology, Cambridge or UMZC) (Fig. 1 C, D; see Supplementary Fig. 1 for interactive 3D reconstruction). We chose *Gavialis* because out of all extant crocodylian species its skull morphology (longirostrine) and ecology (aquatic, piscivorous) are most analogous to that of *Pelagosaurus*. Furthermore, no detailed 3D endocranial reconstruction of a gharial is currently available in the literature (except for the vestibular system; Georgi & Sipla, 2008; Brusatte et al., 2016), so in addition to being a comparison for this study, it also provides valuable information about extant crocodylian internal skull morphology.

To get at the internal morphology of the specimens, the *Pelagosaurus* specimen M1413 was μ CT scanned at the University of Texas at Austin's High-Resolution X-ray CT Facility in two parts: the rostrum, which has a natural break about 2/3 from the tip of the snout and the posterior part of the skull which contains the braincase. When the two pieces are fit together the total skull length (from tip of snout to end of parietal table) is 270 mm. Resolution of each image is 1024 x 1024 pixels with an isotropic voxel size of 0.156 mm. Scan data for *Pelagosaurus* is stored on DigiMorph (http://digimorph.org/specimens/Pelagosaurus_typus/whole/). The *Gavialis* specimen R5792 was a large adult male (skull length = 645 mm) and scanned on a medical CT scanner at The Royal Veterinary College, London. Resolution of each image is 512 x 512 pixels, the pixel width and height is 0.791 mm, and the voxel depth is 0.625 mm. Scan data for the gharial is stored at the UMZC. All data can be made available through the repositories or authors by request. Finally, 3D reconstructions of the brain and sinus cavities was done in Materialise Mimics® Research edition version 19 and rendered in Autodesk® 3ds Max 2015.

In addition to details of gross morphology of the endocranium, we also captured morphometric data (Fig. 2; Table 1) on the endocasts of *Pelagosaurus*, *Gavialis*, and a selection of documented pseudosuchians (including phytosaurs) from the literature, including: the phytosaurs *Ebrachosaurus neukami* (Lautenschlager & Butler, 2016), *Parasuchus* (= *Paleorhinus*) *angustifrons* (Lautenschlager & Butler, 2016), and *Machaeroprotopus* (= *Pseudopalatus*) *mccauleyi* (Holloway, Claeson & O'Keefe, 2013); the aetosaur *Desmatosuchus spurensis* (Hopson, 1979); the teleosauroid *Steneosaurus* cf. *gracilirostris* (Brusatte et al., 2016); the metriorhynchoid *Cricosaurus* (= *Geosaurus*) *araucanensis* (Herrera, Gasparini & Fernández, 2013); the notosuchian *Simosuchus clarki* (Kley et al., 2010); the

sebecid *Sebecus icaeorhinus* (Colbert, 1946; Hopson, 1979); the pholidosaur *Pholidosaurus meyeri* (Edinger, 1938; Hopson, 1979); the goniopholid *Goniopholis pugnax* (Edinger, 1938); and the extant crocodylians *Alligator mississippiensis* (Witmer & Ridgely, 2008) and *Crocodylus johnstoni* (Witmer et al., 2008). Phytosaurs are included here as they either represent the earliest diverging pseudosuchians (Brusatte et al., 2010; Ezcurra, 2016) or are the sister-group to the Archosauria (Nesbitt, 2011); in either case, phytosaurs provide information on the plesiomorphic condition for Pseudosuchia. Further, we refrained from collecting morphometric data on the teleosauroid thalattosuchians *Teleosaurus eucephalus* (Seeley, 1880) and *Steneosaurus pictaviensis* (Wharton, 2000) as the endocasts are incomplete and not preserved with enough detail. These teleosauroid specimens are, however, used in a comparative context. For inter-taxon comparison, the raw morphometric data (Fig. 2; Table 1) were converted into ratios that highlight proportions of the olfactory tract, cerebrum, pituitary fossa, and endosseous labyrinth (see Table 2 for details).

DESCRIPTION

Narial cavity and associated structures

A number of major features are shared by *Pelagosaurus typus* and *Gavialis gangeticus*. Both have an elongate narial cavity (Figs. 3, 4; dark yellow) that extends posteriorly from the external naris at the tip of the snout to the retracted internal naris (=choana), ventral to the basicranium. Thus, a secondary palate is present in both taxa, and the narial passage spans almost the entire length of the skull. The external nares form a single, midline opening in both taxa, as seen in various crocodyliforms, including crocodylids, *Isisfordia* (Salisbury et al., 2006), pholidosaurids/dyrosaurids (e.g. Sereno et al., 2001; Jouve, 2005) and *Goniopholis* (Holland, 1905), as well as in other thalattosuchians (e.g. Fraas, 1901; Andrews, 1913; Gasparini et al., 2006). However, given the likely basal phylogenetic position of Thalattosuchia among crocodyliforms (e.g., Wilberg, 2015a), and the presence of paired external nares and unretracted choanae in many phylogenetically intermediate crocodyliforms (e.g. Ortega et al., 2000; Clark & Sues, 2002; Carvalho, Ribeiro & Avilla, 2004; Kley et al., 2010), these features shared by *Gavialis* and *Pelagosaurus* represent independent evolutionary acquisitions, probably reflecting adaptation to aquatic life.

The narial cavity of *Gavialis* exhibits three derived features that are absent in *Pelagosaurus*. (1) Anteriorly, the narial cavity of *Gavialis* is inflected abruptly dorsally (Fig. 4D; dark yellow), forming an expanded cylindrical recess that communicates externally via a dorsally-placed external naris; dorsal inflection of the external naris also characterizes other eusuchians such as *Alligator mississippiensis* (Witmer & Ridgely, 2008). In *Pelagosaurus*, the external naris faces anterodorsally (Fig. 3D; dark yellow), a morphology shared with other thalattosuchians (e.g. Andrews, 1913) and longirostrine crocodylomorphs, such as pholidosaurids/dyrosaurids (Serenio et al., 2001; Jouve, 2005). (2) The internal naris of *Gavialis* (Fig. 4D, E; dark yellow) is enclosed by the pterygoids, is located ventral to the labyrinth at the posterior end of the temporal fossa (as seen in other neosuchians; Salisbury et al., 2006; Turner & Buckley, 2008), and the cross-sectional area of the narial cavity here is expanded (perhaps incorporating part of the pterygoid sinus). This contrasts with the relatively unexpanded posterior region of the narial cavity of *Pelagosaurus*, and the more anterior location of the internal naris, enclosed by the palatines, and situated ventral to the cerebrum at the anterior end of the subtemporal fossa (Fig. 3D, E; dark yellow). The relatively anterior placement of the internal naris of *Pelagosaurus*, and its enclosure by the palatines, is widespread among thalattosuchians (e.g. Andrews, 1913) and other non-eusuchian crocodylomorphs (Salisbury et al., 2006; Turner & Buckley, 2008), although the 3D reconstruction of the narial cavity in the metriorhynchoid *Cricosaurus araucanensis* shows the internal naris ending far anterior to the cerebrum (Herrera, Gasparini & Fernández, 2013). (3) The pterygoid of *Gavialis* is pneumatized by a diverticulum of the nasal epithelium, forming an expanded bulla that is absent in *Pelagosaurus* (Fig. 4; light green). This bulla is only present in large individuals of *Gavialis*, and is proposed to have a function in vocalization (Martin & Bellairs, 1977).

Immediately anterior to the endocast, the narial cavity is expanded to form the olfactory region (used here in a loose sense) in both specimens (Fig. 3, 4; dark green). This is dorsal to, and distinct from, the posteroventral continuation of the narial passage, which is paired in this region in both taxa (Fig. 3E, 4E; dark yellow). In *Gavialis*, the central portion of the olfactory region bears a weak midline groove, and the central portion of the olfactory region is relatively smaller than in *Pelagosaurus*, being both anteroposteriorly shorter and mediolaterally narrower (Fig. 4A, C; dark green). Conversely, the central portion of the olfactory region of *Pelagosaurus* bears a deep midline dorsal groove, creating bilaterally symmetrical, bulbous expansions (Fig.

3A, C; dark green). A similar set of olfactory recesses to that seen in *Pelagosaurus* is present in the metriorhynchoid *Cricosaurus* (Fernández & Herrera, 2009; Herrera, Gasparini & Fernández, 2013). In *Cricosaurus*, the large, bulbous dorsal region is occupied by an apparent soft tissue structure comprised of ‘lobules’. This structure has been reported in multiple natural endocasts of metriorhynchoids (e.g. Fernández & Gasparini, 2000; Gandola et al., 2006; Fernández & Gasparini, 2008; Herrera, 2015), and has been interpreted as enlarged salt glands, which exit through the antorbital fenestra. Given their identical topology, we propose the enlarged bulbous recesses seen in *Pelagosaurus* to be osteological correlates of the same structures, suggesting the presence of antorbital salt glands in one of the earliest diverging thalattosuchians. This interpretation does not preclude the presence of other structures, such as olfactory and pneumatic epithelia, within the olfactory recess.

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 in extant crocodylians is closed, the internal paranasal sinus is still well developed (Witmer, 1997). The antorbital fenestra is small in *Pelagosaurus* (Pierce & Benton, 2006), more similar to early teleosauroids, such as *Teleosaurus* (Jourve, 2009; the fenestra is lost in *Machimosaurus*, Martin & Vincent, 2013) than to metriorhynchoid thalattosuchians (e.g. Andrews, 1913; Gasparini et al., 2006; Young & Andrade, 2009; Herrera, Gasparini & Fernández, 2013), and is located on the lateral surface of the bulbous, dorsal portion of the olfactory recess (Fig. 1A, B; star). In *Pelagosaurus* and *Gavialis*, there is a subconical, subsidiary outpocketing from the main portion of the olfactory region ventrolateral to the nasal passage (Figs. 3D, E, 4D, E; dark green). This suggests that the paranasal sinus contributes, at least in part, to the bulbous recess of the olfactory region, and that the outpocketing most likely represents part of the antorbital sinus (although see Fernández & Herrera, 2009 for a different interpretation of the antorbital fenestra). A similar feature was recently identified as the antorbital sinus in the metriorhynchoid *Cricosaurus* (Herrera, Gasparini & Fernández, 2013) and phytosaurs also have an enlarged antorbital sinus in this region (Lautenschlager & Butler, 2016). Also, in both *Pelagosaurus* and *Gavialis*, the antorbital sinus tapers anteriorly, giving rise to elongate internal canals that extend longitudinally along the length of the snout (Figs. 3, 4; dark pink). We identify these as neurovascular canals because small, subsidiary rami branch serially from them along their lengths, exiting via foramina on the lateral surface of the maxilla (not

reconstructed, but distinguishable on the original μ CT images) and similar neurovascular canals were recently described in phytosaurs (Lautenschlager & Butler, 2016). In addition to the features above, *Gavialis* also has a sinus above the olfactory region, here identified as the prefrontal sinus (Fig. 4A, C, D; dark orange) as it occupies a similar position to the prefrontal sinus in *Alligator* (Witmer & Ridgely, 2008); this sinus is not present in *Pelagosaurus*. In overall morphology, the paranasal sinus system as seen in *Pelagosaurus* and *Gavialis* is simplified as compared to the condition in brevirostrine, broad-snouted crocodiles, such as *Alligator*, in which the sinus forms broad, mediolateral pockets along the snout, and in many non-crocodylomorph archosaurs with open antorbital fenestrae, in which the sinus also forms a large, broad recess (Witmer, 1997; Witmer & Ridgely, 2008).

Endocranial cast

In overall appearance, the endocast of *Pelagosaurus typus* is similar to *Gavialis gangeticus* and other crocodile-line archosaurs (Edinger, 1938; Colbert, 1946; Hopson, 1979; Witmer & Ridgely, 2008; Witmer et al., 2008; Kley et al., 2010; Herrera, Gasparini & Fernández, 2013), including phytosaurs (Holloway, Claeson & O’Keefe, 2013; Lautenschlager & Butler, 2016), being approximately ‘cylindrical’ in form (Fig. 5). In *Pelagosaurus*, the endocast appears proportionally larger than that of *Gavialis*, and is relatively more straight in outline. The angle of the cephalic and pontine flexure in *Pelagosaurus* is much greater (i.e. less acute) than most other psuedosuchians, indicating that the brain is relatively straight (Table 1). A straight brain is shared with the metriorhynchoid *Cricosaurus araucanensis* and the teleosauroid *Steneosaurus* cf. *gracilirostris* (Table 1), and the sectioned braincase of the teleosauroid *Teleosaurus eucephalus* also appears more straight in outline (Seeley, 1880). This may suggest that a straight brain is a derived feature of thalattosuchians. The degree of flexion in avian brain endocasts is determined by the position and morphology of the orbit (Kawabe, Ando & Endo, 2014), and it is possible that the more lateral position of the orbit in thalattosuchians (e.g. Andrews, 1913; Gasparini et al., 2006; Martin & Vincent, 2013) may explain the reduction of endocast flexion in these taxa.

Starting anteriorly in the forebrain, the fossa for the olfactory tract and bulbs in *Pelagosaurus* is straight and takes the form of a pair of tapering, anteriorly directed finger-like extensions that merge anteriorly with the olfactory region of the narial cavity (Fig. 5A-C). This is in contrast to *Gavialis*, which has an anteroventrally directed olfactory tract and does not have an

osteological division between the olfactory bulbs (Fig. 5D-F), a morphology similar to other extant crocodylians (Witmer & Ridgely, 2008; Witmer et al., 2008), phytosaurs (Holloway, Claeson & O'Keefe, 2013; Lautenschlager & Butler, 2016), and various crocodylomorphs (Edinger, 1938; Hopson, 1979); although, the fossa for the olfactory bulb is partially divided in *Sebecus* (Colbert, 1946; Hopson, 1979) and is proportionally larger in the notosuchian *Simosuchus clarki* (Kley et al., 2010). The aetosaur *Desmatosuchus* has a proportionally even larger pair of olfactory bulbs that likely represents an independently derived feature (Hopson, 1979). The olfactory bulb in the metriorhynchoid *Cricosaurus* is also undivided; however, the olfactory bulbs are reconstructed as attaching to a paired olfactory region in the snout (Herrera, Gasparini & Fernández, 2013). Such a paired structure may also be present in the olfactory region of *Pelagosaurus*, as the posterodorsal portion of this region sends off a pair of rami that connect with the olfactory bulbs posteriorly (Fig. 3). In terms of proportions, the olfactory tract (plus bulbs) 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).

Visually, the cerebrum of *Pelagosaurus* is laterally expanded and bulbous compared to that of *Gavialis* (Fig. 5). In fact, compared to other crocodile-line archosaurs, the cerebrum of *Pelagosaurus* is proportionally larger compared to skull width than in any taxon other than the notosuchian *Simosuchus* (Table 2). The outline of the cerebrum in *Pelagosaurus* in dorsal view is symmetrical along its length (Fig. 5A), whereas the cerebrum of *Gavialis*, phytosaurs (Holloway, Claeson & O'Keefe, 2013; Lautenschlager & Butler, 2016) and other crocodylomorphs (Edinger, 1938; Colbert, 1946; Hopson, 1979; Kley et al., 2010) is most strongly expanded posteriorly (Fig. 5D). 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 other pseudosuchians (Witmer & Ridgely, 2008; Witmer et al., 2008; Kley et al., 2010; Lautenschlager & Butler, 2016), including the metriorhynchoid *Cricosaurus* (Herrera, Gasparini & Fernández, 2013) and the teleosauroid *Steneosaurus pictaviensis* (Wharton 2000). However, Seeley (1880) alluded to the division of the cerebrum in *Teleosaurus*. The absence of this groove occurs because the anterior portion of the dorsal longitudinal sinus, which extends along the central portion of the brain, is covered by a thick dural envelope (Hopson,

1979). The appearance of the division between the cerebral hemispheres in the endocast of *Pelagosaurus* (and potentially *Teleosaurus*) is therefore unusual among pseudosuchians studied so far, and may suggest that the dural envelope was relatively thin in this taxon.

One of the most striking features in the endocast of *Pelagosaurus*, as compared to *Gavialis* and other crocodile-line archosaurs (Hopson, 1979; Kley et al., 2010; Lautenschlager & Butler, 2016), is the greatly enlarged pituitary fossa, which emerges posteroventrally from the cerebrum just anterior to the optic lobe region (Fig. 5). In *Pelagosaurus*, the pituitary fossa is anteroposteriorly long and is also proportionately wide as compared to its overall depth (Table 2). The fossa 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); the channels for the internal carotid artery curve dorsolaterally (and eventually posteroventrally) in *Gavialis* and other extant crocodylians (Hopson, 1979; Witmer et al., 2008; Dufeu & Witmer, 2015). The pituitary fossa described by Seeley (1880) for the teleosauroid *Teleosaurus* also appears to be anteroposteriorly expanded, at least in the sagittal view available, and that of the teleosauroid *Steneosaurus* is similar to *Pelagosaurus* (Table 2; the pituitary fossa of *Pholidosaurus* is also relatively large). Although Brusatte et al. (2016) described the pituitary fossa of *Steneosaurus* as being similar to that of extant crocodylians, our measurements indicate an anteroposteriorly enlarged pituitary fossa in *Steneosaurus* (Table 2). The endocast of *Steneosaurus* prepared by Wharton (2000) appears to have a pituitary fossa of similar dimensions to that of *Gavialis*; however, the morphology of this area is not well preserved in the silicone endocast. Unfortunately, the pituitary fossa of the metriorhynchoid *Cricosaurus* was not reported by Herrera, Gasparini & Fernández (2013), and visualizations of this structure in *Metriorhynchus* cf. *westermanni* by Fernández et al. (2011) are not sufficiently clear to determine the morphology. Therefore, a large and anteroposteriorly expanded pituitary fossa may be a synapomorphy of Thalattosuchia, but further data on metriorhynchoids is necessary to fully support this conclusion.

As is typical of crocodile-line archosaurs, the optic lobes (or midbrain) are not well delimited due to the thick dural envelope in this region. However, the hindbrain, composed of the cerebellum and medulla oblongata (and embracing the vestibular system), is distinguishable. In keeping with the forebrain, the cerebellum is expanded in *Pelagosaurus* compared to that of *Gavialis* (Fig. 5A, D); in fact, the cerebellum of *Gavialis* seems to be smaller than that of other

extant crocodylians, including *Alligator* (Witmer & Ridgely, 2008), *Crocodylus johnstoni* (Witmer et al., 2008), and *Caiman crocodilus* (Hopson, 1979). In contrast to *Gavialis*, the cerebellum in *Pelagosaurus* is characterized by two large, dorsally projecting rami, which are identified as branches of the dorsal longitudinal sinus (Figs. 5A, B). These branches connect posteriorly with a tube-like cavity that forms the dorsolateral portion of the paratympanic sinus (Fig. 3B, D). Branches of the dorsal longitudinal sinus do not connect via the paratympanic sinus in other crocodile-line archosaurs, including phytosaurs, but were recently described in the braincase of the metriorhynchoid *Metriorhynchus* cf. *westermanni* (Fernández et al., 2011), and similar dorsally directed branches extending from the cerebellum have been described for the teleosauroid *Steneosaurus* (Wharton, 2000; Brusatte et al., 2016), suggesting this is a thalattosuchian synapomorphy. Furthermore, the medulla oblongata is foreshortened posterior to the vestibular depression in *Pelagosaurus* as compared to *Gavialis* (Fig. 5) and other pseudosuchians (e.g. Hopson, 1979), although it is relatively broad in cross-section. There is also a ventral swelling on the medulla in *Pelagosaurus*, just at the posterior limit of the vestibular depression, which is here identified as part of the basal artery (Fig. 5B, C). Such a swelling was also described as the basal artery in the endocast of the extant *Caiman* (Hopson, 1979).

Due to the preservation of *Pelagosaurus* and low resolution of the scan in *Gavialis*, delicate features like the cranial nerves were not easily delineated during segmentation. Most of the cranial nerves in the two taxa appear to be originating from similar areas on the endocast (Fig. 5). However, there are two features of note. Firstly, large, paired channels emerge anterodorsally from the pituitary fossa of *Pelagosaurus* (Fig. 5B, C; green). This morphology is absent from *Gavialis* and the endocasts of most archosaurs, both crocodile-line and bird-line (Hopson, 1979; Witmer et al., 2008). But similar large channels have been described extending anteriorly from the pituitary fossa 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. Seeley (1880) identified these channels as housing the optic nerve (CN II), although this is likely an error, as the optic nerve is visible anteriorly and was mistakenly labeled as the olfactory nerve (CN I) in his figure (Seeley, 1880:pl. 24). Wharton (2000) labeled this feature as the oculomotor nerve (CN III) in her silicon mould, a more-likely identification as CN III is closely associated with the anterior region of the

pituitary fossa (Hopson, 1979; Witmer et al., 2008). Most recently, Brusatte et al. (2016) suggested instead that these channels housed the orbital arteries (a branch of the cerebral carotid arteries). We do not make further judgment on the identity of these channels here, other than noting that they may represent either CN III or the orbital artery (or a combination of both). The second feature of note is the trigeminal nerve fossa (CN V). Compared to *Gavialis* and other extant crocodylians (Hopson, 1979; Witmer & Ridgely, 2008; Witmer et al., 2008) and pseudosuchians (Edinger, 1939; Hopson, 1979, Kley et al., 2010; Lautenschlager & Butler, 2016; Brusatte et al., 2016), CN V fossa is relatively small in *Pelagosaurus* (Fig. 5A-C), with limited lateral projection and a small cross-section, which may indicate that the trigeminal ganglion is situated outside the braincase wall in this taxon.

Endosseous labyrinth

Several differences distinguish the endosseous labyrinth of *Pelagosaurus typus* from that of *Gavialis gangeticus* (Fig. 6; Table 2). The aspect ratio (anteroposterior width:dorsoventral height) of vestibular region is high in *Gavialis* (Figure 6; Table 2), and the anterior and posterior semicircular canals arc dorsally from the common crus in a smooth curve, such that any given segment of either canal is curved along its length, and resulting overall in an ‘m’-shape to the anterior and posterior canals when seen in lateral view (Fig. 6F). This is similar to the morphology seen in other crocodylians (e.g. Georgi & Sipla, 2008; Witmer et al., 2008; Dufeu & Witmer, 2015; Brusatte et al., 2016), crocodylomorphs (Kley et al., 2010), and phytosaurs (Lautenschlager & Butler, 2016) (Fig. 7). By contrast, in *Pelagosaurus* the anterior and posterior canals extend dorsally from the common crus, but are then strongly inflected near their apices, and then are approximately straight for most of their length (Fig. 6B). This confers a ‘pyramidal’ appearance to the labyrinth of *Pelagosaurus*, which is also present in the teleosauroid *Steneosaurus* (Brusatte et al., 2016), and may ultimately be found to be a synapomorphy of Thalattosuchia as it is absent in *Euparkeria*, phytosaurs, *Simosuchus*, and many extant crocodylians (Fig. 7). 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.

The path of the anterior semicircular canal is substantially longer than that of the posterior semicircular canal in *Gavialis* (Fig. 6F, H), and extends far anteriorly. This morphology is also widespread among extant and extinct crocodylians (Georgi & Sipla, 2008; Witmer & Ridgely, 2008; Witmer et al., 2008; Bona, Degrange & Fernández, 2013; Dufeu & Witmer, 2015; Brusatte et al., 2016), but differs from the more equal proportions of the anterior and posterior canals seen in *Pelagosaurus* (Fig. 6B, D; Table 2), *Steneosaurus* (Brusatte et al., 2016), the notosuchian *Simosuchus* (Kley et al., 2010), phytosaurs (Lautenschlager & Butler, 2016), and the crownward stem-group archosaur *Euparkeria* (Sobral et al., 2016) (Fig. 7; Table 2). Therefore, the larger size of the anterior canal in extant crocodylians is probably a derived feature of eusuchians or crocodylians, and future work will determine its functional significance and when it evolved on the crocodylian stem lineage. The size of the semicircular canals is considered proportional to their sensitivity (Sipla & Spoor, 2008) and the presence of a larger anterior canal in mammals (Spoor et al., 2007), including most cetaceans (Ekdale & Racicot, 2015), has been suggested to increase the sensitivity to pitch motions of the head (reviewed by Ekdale, 2015), but this seems unlikely to be true in crocodylians which have laterally undulating locomotion.

The length of the cochlear duct (=lagenar recess) 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 (Serenio et al., 2007; Knoll et al., 2012). An elongated cochlear duct is also present in the teleosauroid *Steneosaurus* (Brusatte et al., 2016), and it is likely that this feature may be a synapomorphy of Thalattosuchia (Fig. 7). Elongation of the cochlear duct may indicate enhanced auditory capabilities given that dorsoventral length of the cochlea is correlated with acoustic capabilities in extant birds and reptiles (Wever, 1978; Gleich & Manley 2000; Witmer et al., 2008; Walsh et al., 2009).

Paratympanic sinuses

The otic region in archosaurs is pneumatised by diverticula of the middle ear, forming paratympanic sinuses that function to enhance acoustic capabilities of the middle ear in extant crocodylians (Witmer & Ridgely, 2008; Dufeu & Witmer, 2015). The 3D morphology of the paratympanic sinuses has been described in *Alligator mississippiensis* (Witmer & Ridgely, 2008; Dufeu & Witmer, 2015) and *Crocodylus johnstoni* (Witmer et al., 2008); however, little is

known about the system outside extant crocodylians. There are a number of differences between the paratympanic sinuses of *Pelgaosaurus typus* (Fig. 3; dark purple) and extant crocodylians (see further below), but the morphology is very similar to that recently described for the metriorhynchoid *Metriorhynchus cf. westermanni* (Fernández et al., 2011). In *Pelagosaurus*, the paratympanic sinus is separated into three cavities or sinus channels (Fig. 3A, B). A dorsal sinus (sinus 1; cavity 1 of Fernández et al., 2011) connects with the dorsal longitudinal sinus on the endocast (Fig. 3B, D) and extends ventrolaterally to join with the middle ear cavity, close to the tympanum. Moving medially from the tympanum in *Pelgaosaurus*, there are two sinus channels that run parallel with each other (cavity 2 of Fernández et al., 2011), and communicate with each other (Fig. 3A, B). The more medially placed or central sinus (sinus 2) runs medially towards and anteroventrally underneath the vestibular system where it becomes confluent with the ventral sinus (sinus 3); at this point it wraps around the endocast ventrally presumably forming the anterior branch of the pharyngeal (=Eustachian) sinus (Colbert, 1946; Dufeu & Witmer, 2015) (Fig. 3D, E). The ventral sinus (sinus 3) runs medially towards the vestibular system and then branches; with an anterior portion merging with sinus 2 and a posterior portion which dives ventrally and wraps around the endocast posteriorly forming the posterior branch of the pharyngeal sinus (Colbert, 1946) (Fig. 3 B, D, E). Ventrally, there is an anteroposterior directed median pharyngeal sinus that connects the anterior and posterior pharyngeal sinuses (Colbert, 1946) (Fig. 3 D, E).

The morphology of the paratympanic sinus system in *Pelagosaurus* contrasts strongly with that in *Gavialis* (Fig. 4; dark purple) and other extant crocodylians (Witmer & Ridgely, 2008; Witmer et al., 2008; Dufeu & Witmer, 2015). Although *Gavialis* has a dorsal branch of the paratympanic sinus (Fig. 4A, B), it connects to the parietal sinus dorsally (Dufeu & Witmer, 2015) and runs ventrolaterally to join with the middle ear cavity; there is no direct connection with the endocast via the dorsal longitudinal sinus. Moving medially from the tympanum (which is relatively large as compared to *Pelagosaurus*), there is a large intertympanic sinus (composed of various diverticula; see Dufeu & Witmer, 2015) that connects the right and left middle ear cavities and runs dorsally around the endocast (Fig. 4B). Branching ventrally from the intertympanic sinus is the pharyngeal (=Eustachian) sinus system (Colbert, 1946; Dufeu & Witmer, 2015) (Fig. 4B, D). Unlike *Pelgaosaurus*, the medial pharyngeal sinus in *Gavialis*, and other extant crocodylians, extends ventrally into the basisphenoid sinus/diverticulum causing the

sinus to become vertically oriented (Dueau & Witmer, 2015). In addition, there is a pair of lateral pharyngeal sinuses that extend ventrally and parallel to the medial sinus; these eventually merge at their ventral extents (Colbert, 1946). Finally, in *Gavilais* the intertympanic sinus sends a channel posteriorly down the medial aspect of the quadrate forming a quadrate sinus (Fig. 4B), which is not present in *Pelagosaurus*.

DISCUSSION

The detailed anatomical observations presented here expand our knowledge of endocranial anatomy in early thalattosuchians, building on landmark studies of Late Jurassic members of the group (Fernández & Gasparini, 2000; Gondola et al., 2006; Fernández & Gasparini, 2008; Herrera, Gasparini & Fernández, 2013; Herrera & Vennari, 2015) and less complete data provided so far for some Early Jurassic teleosauroids (Seeley, 1880; Wharton, 2000; Brusatte et al., 2016). Based on our 3D endocranial reconstructions of the thalattosuchian *Pelagosaurus typus*, and of the extant crocodylian *Gavialis gangeticus*, we are able to clarify the phylogenetic status of key soft-tissue features observed in thalattosuchians, including features of the paranasal and paratympanic sinus systems, the neuroanatomy of the brain and vestibular organ, and potential physiological adaptations. Below, we propose functional interpretations relevant to the construction of the snout in longirostrine pseudosuchians, the evolutionary origins of thalattosuchian salt excretion and regulation, as well as neuroanatomical and sensory adaptations in some of the earliest diverging members of the Crocodylomorpha.

Simplified sinuses: Our reconstructions show that the paranasal sinus system in *Pelagosaurus* and *Gavialis* (Figs. 3, 4; dark green) is simplified as compared to other extant crocodylians such as *Alligator* or bird-line archosaurs (Witmer & Ridgely, 2008), being restricted to the posterior region of the snout (or olfactory region). This simplification is presumably correlated with a longirostrine snout morphology, as longirostrine phytosaurs also have less elaborate paranasal sinuses (Lautenschlager & Butler, 2016). The difference in the extent of the paranasal sinus system in longirostrine versus brevirostrine archosaurs suggests that archosaurian snout development may be influenced by outpocketing of the nasal epithelium (Witmer, 1997) or that the morphology of the skull bones themselves may impose limits on the outpocketing of the nasal epithelium. Irrespective of the underlying developmental mechanism, the simplified paranasal sinuses in longirostrine forms, as demonstrated here in *Pelagosaurus*

and *Gavialis*, appear to allow the snout to maintain a long, tubular morphology – a construction mechanically beneficial for feeding on fast moving prey (Pierce, Angielczyk & Rayfield, 2008; 2009b). As a longirostrine snout morphology typifies the Thalattosuchia, a simplified paranasal sinus system may characterize the clade, with some exceptions. For instance, the derived metriorhynchoid *Dakosaurus andiniensis* has a relatively short and tall snout (Gasparini et al., 2006), meaning this taxon may have had more elaborate paranasal sinuses. Such a hypothesis should be tested by future work.

Before this study, little was known about the paratympanic sinuses outside of *Alligator* and bird-line archosaurs (e.g. Witmer & Ridgely, 2008; Dufeu & Witmer, 2015). It is clear from our reconstructions that the system in *Gavialis* (Fig. 4; dark purple) is similar to *Alligator*, but that *Pelagosaurus* (Fig. 3; dark purple) shows a number of differences, some of which are shared with the metriorhynchoid *Metriorhynchus* cf. *westermanni* (Fernández et al., 2011). The most conspicuous feature of the paratympanic sinuses in *Pelagosaurus* and *Metriorhynchus* is that the dorsal cavity (sinus 1) is confluent with branches of the dorsal longitudinal sinus which project posterodorsally from the cerebellum (Fig. 3B, D). As the dorsal longitudinal sinus typically drains venous blood from the brain into the internal jugular, it is unclear what the functional implications of this morphology may be (e.g. why venous blood would drain through the paratympanic sinus). Another key difference is that *Pelagosaurus* lacks an intertympanic sinus connecting the left and right middle ear cavities above the endocast, as seen *Gavialis* (Fig. 4; dark purple). In modern crocodylians, the tympanic air spaces enhance low-frequency hearing (Witmer & Ridgely, 2009; Dufeu & Witmer, 2015) and the intertympanic space, in particular, helps to conduct vibrations through the head allowing for sound localization (see Dufeu & Witmer, 2015). Thus, the lack of an intertympanic sinus in *Pelagosaurus* may indicate it was less capable of detecting the direction and distance of sound; although the large cochlea may have compensated for this (see below). A final difference between *Pelagosaurus* and extant crocodylians is that the pharyngeal sinus (=Eustachian tube) is not ‘verticalized’ in *Pelagosaurus* (Fig. 3 B, D). ‘Verticalization’ of the pharyngeal sinus is possible in modern crocodiles and other eusuchians (Fig. 4B, D) due to the ventral displacement of the basicranium, especially the basioccipital and basisphenoid, due in part to the development of a complete secondary palate and reorganization of the jaw musculature (Tarsitano, Frey & Riess, 1989; Gold, Brochu & Norell, 2014).

Advanced osmoregulation: There is a major difference between the olfactory region of *Pelagosaurus* and that of *Gavialis* (Figs. 3, 4; dark green), with the region in *Pelagosaurus* showing bilaterally symmetrical bulbous expansions of the olfactory recess anterior to the orbits (Fig. 3A, C, D). We interpret these expanded recesses as osteological correlates of enlarged nasal glands. Such glands have been reported in a similar anatomical position in natural endocasts of various metriorhynchoids (Fernández & Gasparini, 2000, 2008; Gandola et al., 2006; Herrera, Gasparini & Fernández, 2013; Herrera, 2015) and are proposed to represent hypertrophied salt-secretion glands due to their ‘lobular’ surface texture. Previous workers have suggested that nasal salt glands are a derived feature of the highly-specialized metriorhynchoids, enabling them to maintain constant plasma osmolality (Fernández & Gasparini, 2000, 2008). However, Brusatte et al. (2016) recently hypothesized the presence of a metriorhynchoid-like salt gland in the Toarcian teleosauroid *Steneosaurus* and we document this structure in *Pelagosaurus*, suggesting that advanced salt-excretion capabilities were present amongst some of the earliest thalattosuchians. In addition to nasal salt glands, the endocast of *Pelagosaurus* shows a greatly expanded pituitary fossa (=sella turcica) (Fig. 5B, C), which may have housed an enlarged pituitary gland (=hypophysis); a similar expansion is also seen in *Steneosaurus* (Brusatte et al., 2016). In reptiles, the posterior pituitary is thought to have an antidiuretic effect by constricting glomerular capillaries thereby decreasing blood flow and water loss, a mechanism known as “glomerular antidiuresis” (Heller, 1942, 1950). This raises the possibility that secretion of an increased volume of antidiuretic hormone (e.g. vasopressin) in thalattosuchians may have aided in preventing dehydration in a marine environment.

Neuroanatomic adaptations: The endocast of *Pelagosaurus* shows several characteristics that distinguish it from *Gavialis* and other crocodile-line archosaurs (Fig. 5). For instance, the cerebrum in *Pelagosaurus* is relative large, and is elongated along its anteroposterior length, being symmetrical in form with a deep longitudinal fissure (Fig. 5A-C). This contrasts with the smaller cerebral regions of phytosaurs and other crocodylomorphs (with the exception of the notosuchian *Simosuchus clarki*; Table 2), which are asymmetrical and expanded posteriorly (Fig. 5D-E); Hopson, 1979; Witmer et al., 2008). A large, symmetrically expanded cerebrum may also be present in the teleosauroids *Teleosaurus eucephalus* (Seeley, 1880) and *Steneosaurus* (Wharton, 2000; Brusatte et al., 2016), but the cerebral region in the metriorhynchoid *Cricosaurus araucanensis* is comparatively small (Table 2; Herrera, Gasparini & Fernández,

2013). In birds (and mammals), larger cerebral regions are associated with refined interpretation of sensory inputs and greater neuronal area to execute increasingly complex behaviors (Roger 1999). Although we cannot directly assess behavioral complexity in *Pelagosaurus*, various other features documented here suggest that *Pelagosaurus*, and perhaps other thalattosuchians, received greater sensory input from the eyes and labyrinth (see below) than most other pseudosuchians, which is consistent with an enhanced capacity to process sensory information.

The most conspicuous feature in the endocast of *Pelagosaurus* is a pair of greatly enlarged channels extending anterodorsally from the expanded pituitary fossa (Fig. 5B, C). A similar channel extending from the pituitary fossa was identified as the optic nerve or CN II in the teleosauroid *Teleosaurus eucephalus* by Seeley (1880), although CN II is clearly visible further anteriorly, and Wharton (2000) described anteriorly projecting channels from the pituitary region of *Steneosaurus* as the oculomotor nerve or CN III. If these channels housed nerves, they most-likely represent the bony signature of enlarged oculomotor nerves, as CN III is located ventral to CN II and is in close association with the anterior margin of the pituitary fossa in modern crocodylians (Hopson, 1979; Witmer et al., 2008). Large oculomotor nerves would allow for controlled movements of the large, laterally placed eyes in thalattosuchians, and particularly *Pelagosaurus*, supporting the interpretation that these animals were highly visual predators (Pierce & Benton, 2006); it may also indicate they were able to focus under water, which is absent in extant crocodylians (Fleishman et al., 1988). Large, laterally placed eyes may also be correlated with the relatively straight brain seen in *Pelagosaurus* and other thalattosuchians (Table 1). However, similar channels were recently described by Brüssatte et al. (2016) in a second specimen of *Steneosaurus* as enlarged orbital arteries. Their interpretation proposes that the enlarged internal carotid (also seen in *Pelagosaurus* and metriorhynchoids; Herrera, 2015) and orbital arteries were supplying the salt glands with a large volume of blood for osmoregulation. An alternative interpretation may be that large orbital arteries increased blood supply to the large orbits and their associated muscles. Whether these channels housed nerves, arteries, or both, requires further investigation of endocasts in other thalattosuchians and crocodylomorphs, but either way, this structure is very distinct among all crocodile-line and bird-line archosaurs studied thus far and may represent a thalattosuchian synapomorphy.

Hearing and balance: The morphology of the endosseous labyrinth points towards enhanced sensory capabilities in *Pelagosaurus*. Compared to *Gavialis* and other crocodile-line

archosaurs, *Pelagosaurus* has a long cochlear duct (Figs. 6, 7; Table 2). Cochlear length has been used as a rough proxy for hearing capabilities in crocodylians and birds (Wever, 1978; Gleich & Manley, 2000; Witmer et al., 2008; Walsh et al., 2009), as it directly relates to the length of the sensory epithelium (or basilar membrane) that stimulates the organ of Corti to transduce mechanical sound vibrations into nerve impulses (Witmer et al., 2008). Thus, the long cochlea in *Pelagosaurus* suggests an enhanced ability to discriminate auditory stimuli. Brusatte et al. (2016) observed a long cochlear duct in the thalattosuchian *Steneosaurus*, similar to that of *Pelagosaurus*. They interpreted this as a plesiomorphic retention of terrestrial-type hearing in a derived marine archosaur lineage. However, short cochlear ducts are not only widespread among pseudosuchians (including Triassic taxa such as phytosaurs; Fig. 7; Table 2) they are also present in early members of the avian stem lineage (the sister taxon of Pseudosuchia) such as *Herrerasaurus* and *Massospondylus* (Serenio et al., 2007; Knoll et al., 2012). This suggests that a short, not long, cochlea represents the primitive condition for Pseudosuchia, indicating that the long cochlea seen in *Pelagosaurus* and *Steneosaurus* is a derived morphology (Fig. 7). Furthermore, there is no evidence that adaptation to aquatic life in tetrapods involves reduction of the cochlea. For example, the relationship between cochlea length and body mass in cetaceans is similar to that in terrestrial mammals (Spoor et al., 2002). Marine tetrapod lineages that evolved from terrestrial ancestors with impedance-matching middle ears, including mosasauroids, sea turtles, cetaceans, pinnipeds and other taxa have retained use of the tympanic route in underwater sound perception, which may result in improved ability to localize the direction of the sound sources (Hetherington, 2008). The key modifications to auditory anatomy seen in secondarily aquatic taxa involve features of the middle ear, especially the stiffness and size of the tympanum (Hetherington, 2008). No information on these characteristics is yet available for thalattosuchians, so the question of whether they had ‘terrestrially adapted’ hearing remains open.

In addition to hearing, the morphology of the vestibular system – the sensory organ of balance – is unlike that seen in *Gavialis* and other pseudosuchians, with a few exceptions among crocodylians (e.g. *Crocodylus johnstoni*; Fig. 7). In *Pelagosaurus*, the anterior and posterior canals form a ‘pyramidal’ shape and the posterior canal is relatively large, especially compared to modern crocodylians (Fig. 6). A similar vestibular shape can be seen in the teleosauroid *Steneosaurus* (Brusatte et al., 2016), indicating that this morphology may be more widespread

among thalattosuchians. Semicircular canals sense angular rotations of the head and increases in their size have been linked to enhanced agility and aerobatic ability (Witmer et al., 2003; Alonso et al., 2004; Spoor et al., 2007; Ekdale, 2015). Distinct labyrinth morphologies are present in the most aquatic members of many extant tetrapods (Georgi & Sipla, 2008; Spoor & Thewissen, 2008), including cetaceans (Spoor et al., 2002) and carnivoran mammals (Gröhe et al., 2016), although they do not seem to be present in diving birds (Smith & Clarke, 2012). Furthermore, distinct morphological adaptations to aquatic life are seen in the labyrinths of different groups among reptiles and mammals (Georgi & Sipla, 2008; Spoor & Thewissen, 2008; Yi & Norell, 2015), so general patterns of change in labyrinth morphology in response to the evolution of aquatic life seem to be absent. Nevertheless, the distinct labyrinth morphology of *Pelagosaurus* (and *Steneosaurus*) is most likely explained by its distinct locomotor ecology — representing an early member of the most aquatically-adapted clade of pseudosuchians. This hypothesis will be tested as additional data on pseudosuchian, and particularly thalattosuchian, labyrinths become available, and potentially also by comparative studies of crocodylomorph labyrinth evolution.

CONCLUSIONS

Based on our analysis of the endocranial anatomy of *Pelagosaurus typus* and *Gavialis gangeticus*, in comparison to other thalattosuchians and pseudosuchian taxa, we propose the following thalattosuchian synapomorphies: (1) a pyramidal morphology of the semicircular canals; (2) an elongate cochlear duct (indicating greater sensitivity to hearing); (3) large, paired channels extending anteriorly from an enlarged pituitary fossa (that may have housed either an enlarged oculomotor (III) cranial nerve, orbital artery, or both); (4) a relatively straight brain (possibly due to the presence of large, laterally placed orbits); and (5) an enlarged dorsal longitudinal sinus which is confluent with the paranasal sinus system. Further to this, we found that *Pelagosaurus* possessed a large bulbous expansion of the nasal cavity anterior to the orbits, homologous in structure to that which houses a hypothesized salt gland in Late Jurassic metriorhynchoids, providing evidence that this physiological adaptation evolved early in thalattosuchian evolution. Finally, the pyramidal semicircular canals of thalattosuchians, long cochlear duct, enlarged pituitary fossa and early evolution of a hypothesized salt gland may reflect a high level of sensory and physiological adaptation to aquatic life in this clade, occurring well in advance of postcranial adaptations to marine open water swimming.

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658

659 ADDITIONAL INFORMATION

660 Competing interest

661 The authors declare there are no competing interests.

662 Author contributions

- 663 • Stephanie E. Pierce conceived and designed the project, performed the CT scanning,
664 reconstructed and analyzed the data, prepared the figures/tables, and wrote the paper.
- 665 • Megan Williams reconstructed and analyzed the *Pelagosaurus* scan data and wrote the paper.
- 666 • Roger B.J. Benson analyzed the data, prepared figures, and wrote the paper.

667 Data availability

668 The following information was supplied regarding data availability:

669 Interactive 3D PDFs of the anatomical reconstructions are provided as supplementary
670 figures to this paper. In addition, the CT data for *Gavialis gangeticus* has been repositied in the
671 University Museum of Zoology, Cambridge, and the CT data for *Pelagosaurus typus* is stored on
672 DigiMorph (http://digimorph.org/specimens/Pelagosaurus_typus/whole/).

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Table 1 (on next page)

Table 1: Raw morphometric data.

Measurements were collected on pseudosuchian (phytosaur and crocodile-line archosaurs) endocast and labyrinth reconstructions currently available in the literature (see table for sources), in addition to *Pelagosaurus typus* and *Gavialis gangeticus* (this study). All data are reported in mm or degrees and were measured in ImageJ (<http://imagej.nih.gov/ij>). Question marks denote missing data. The measurement protocol can be found in Figure 1.

(rounded to nearest mm)	<i>Ebrachosaurus</i> (phytosaur)	<i>Parasuchus</i> (phytosaur)	<i>Pseudopalatus</i> (phytosaur)	<i>Desmatosuchus</i> (aetosaur)	<i>Pelagosaurus</i> (thalattosuchian)	<i>Steneosaurus</i> (teleosauroid)	<i>Cricosaurus</i> (metriorhynchoid)
Skull width at cerebrum (b/w postorbitals)	101	78	150	?	52	?	136
cephalic flexure angle (CF)	147	137	133	132	160	175	155
pontine flexure angle (PF)	146	136	141	131	160	170	155
Endocast length (EL)	100	95	138	117	57	?	138
Olfactory tract length (OL)	53	47	71	30	21	?	72
Brain length (EL-OL)	47	48	67	82	36	75	66
Cerebrum width (CW)	18	19	20	34	15	28	26
Pituitary fossa width (PW)	?	?	?	?	6	14	?
Pituitary fossa height (PH)	12	11	?	11	7	12	?
Pituitary fossa length (PL)	7	8	?	12	10	17	?
Labyrinth height (LH)	14	14	?	?	14	26	?
Labyrinth width (LW)	18	18	?	?	11	26	?
Cochlear duct length (CL)	5	6	?	?	8	13	?
Anterior semicircular canal area (AA)	23	16	?	?	9	38	?
Posterior semicircular canal area (PA)	18	9	?	?	6	19	?
Lateral semicircular canal area (LA)	8	11	?	?	4	14	?
Source	Lautenschlager & Butler 2016	Lautenschlager & Butler 2016	Holloway et al. 2013	Hopson 1979	This study	Brusatte et al. 2016	Herrera et al. 2013

1

(rounded to nearest mm)	<i>Simosuchus</i> (notosuchian)	<i>Sebecus</i> (sebecid)	<i>Pholidosaurus</i> (pholidosaur)	<i>Goniopholis</i> (goniopholid)	<i>Gavialis</i> (crocodylan)	<i>Alligator</i> (crocodylan)	<i>Crocodylus</i> (crocodylan)
Skull width at cerebrum (b/w postorbitals)	58	147	?	?	168	73	?
cephalic flexure angle (CF)	142	150	143	140	150	135	145
pontine flexure angle (PF)	165	160	150	161	154	145	153
Endocast length (EL)	79	120	138	117	146	98	103
Olfactory tract length	25	46	51	42	55	48	46

(OL)							
Brain length (EL-OL)	54	74	87	75	91	50	57
Cerebrum width (CW)	25	30	28	31	32	21	29
Pituitary fossa width (PW)	5	?	12	15	6	5	5
Pituitary fossa height (PH)	9	9	9	?	9	8	8
Pituitary fossa length (PL)	10	8	20	?	11	10	11
Labyrinth height (LH)	?	?	?	?	21	18	13
Labyrinth width (LW)	?	?	?	?	21	14	14
Cochlear duct length (CL)	?	?	?	?	9	8	6
Anterior semicircular canal area (AA)	?	?	?	?	36	35	18
Posterior semicircular canal area (PA)	?	?	?	?	15	12	5
Lateral semicircular canal area (LA)	?	?	?	?	22	13	8
Source	Kley et al. 2010	Colbert 1946; Hopson 1979	Edinger 1938; Hopson 1979	Edinger 1938	This study	Witmer & Ridgely 2008	Witmer et al. 2008

Table 2 (on next page)

Table 2: Comparison of endocast and labyrinth proportions in pseudosuchians (phytosaurus and crocodile-line archosaurs).

Ratios highlight proportions of the olfactory tract, cerebrum, pituitary fossa, and endosseous labyrinth, and are calculated from Table 1. Question marks denote missing data.

1

	<i>Ebrachosaurus</i> (phytosaur)	<i>Parasuchus</i> (phytosaur)	<i>Pseudopalatus</i> (phytosaur)	<i>Desmotosuchus</i> (aetosaur)	<i>Pelagosaurus</i> (thalattosuchian)	<i>Steneosaurus</i> (teleosauroid)	<i>Cricosaurus</i> (metriorhynchoid)
cerebrum width: skull width	0.18	0.24	0.13	?	0.29	?	0.19
cerebrum width: endocast length	0.18	0.20	0.14	0.29	0.26	?	0.18
olfactory tract length: endocast length	0.53	0.50	0.51	0.26	0.37	?	0.52
pituitary fossa width: height	?	?	?	?	0.86	1.16	?
pituitary fossa width: length	?	?	?	?	0.60	0.82	?
pituitary fossa length: brain length	0.15	0.17	?	0.18	0.28	0.23	?
labyrinth width: height	1.29	1.29	?	?	0.79	1.00	?
cochlear duct length: labyrinth length	0.39	0.43	?	?	0.55	0.50	?
anterior canal area: posterior canal area	1.25	1.80	?	?	1.50	2.00	?
anterior canal area: lateral canal area	2.84	1.44	?	?	2.25	2.71	?
posterior canal area: lateral canal area	2.27	0.80	?	?	1.50	1.36	?

2

	<i>Simosuchus</i> (notosuchian)	<i>Sebecus</i> (sebecid)	<i>Pholidosaurus</i> (pholidosaur)	<i>Goniopholis</i> (goniopholid)	<i>Gavialis</i> (crocodylean)	<i>Alligator</i> (crocodylean)	<i>Crocodylus</i> (crocodylean)
cerebrum width: skull width	0.43	0.20	?	?	0.19	0.13	?
cerebrum width: endocast length	0.32	0.25	0.20	0.26	0.22	0.22	0.28
olfactory tract length: endocast length	0.32	0.38	0.37	0.36	0.38	0.49	0.45
pituitary fossa width: height	0.56	?	1.33	?	0.67	0.63	0.63
pituitary fossa width: length	0.50	?	0.6	?	0.55	0.50	0.45
pituitary fossa length: brain length	0.19		0.23	?	0.12	0.20	0.19
labyrinth width: height	?	?	?	?	1.00	0.78	1.05
cochlear duct length: labyrinth length	?	?	?	?	0.43	0.44	0.45
anterior canal area: posterior canal area	?	?	?	?	2.39	2.88	3.68
anterior canal area: lateral canal area	?	?	?	?	1.63	2.82	2.16
posterior canal area: lateral canal area	?	?	?	?	0.68	0.98	0.59

3

Figure 1(on next page)

Figure 1: Three-dimensional reconstruction of the skull and underlying endocranial morphology.

A-B, *Pelagosaurus typus* (BRLSI M1413); and C-D, *Gavialis gangeticus* (UMZC R 5792). The star indicates the position of the antorbital fenestra in *Pelagosaurus*.

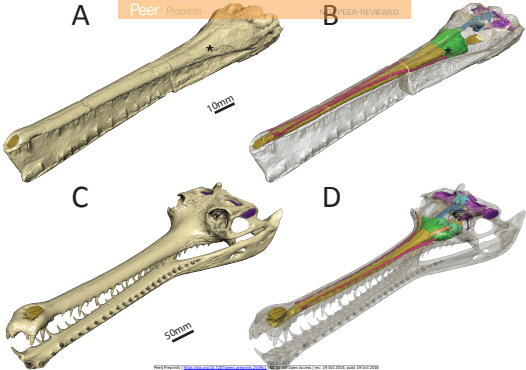


Figure 2(on next page)

Figure 2: Morphometric measurements shown on illustrations of the endocast and labyrinth of *Pelagosaurus*.

A-D, endocast shown in: A – lateral view; B – ventral view; C – dorsal view. D-E, left labyrinth shown in: D – lateral view; E – dorsal view. Abbreviations: AA, anterior semicircular canal area; CL, cochlea length; CW, maximum width of cerebrum; EL, total length of endocast; LA, lateral semicircular canal area; LH, maximum height of labyrinth; LW, maximum width of labyrinths; OL; length of olfactory tract; PA, posterior semicircular canal area; PH; pituitary height; PL; pituitary length; PW, pituitary width. Anterior is towards the left, except in E, where it is pointing down. See more detailed figures for anatomical identifications and size.

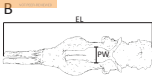
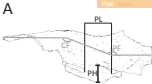


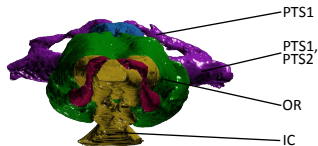
Figure 3(on next page)

Figure 3: Reconstruction of the brain and associated sinuses in *Pelagosaurus typus*.

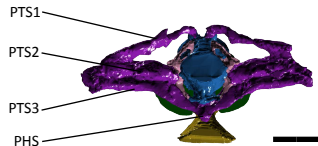
A - anterior view; B - posterior view; C - dorsal view; D - lateral view; E - ventral view.

Abbreviations: DLS, posterodorsal branch of the dorsal longitudinal sinus; EC, external choana; END, endocast; EL, endosseous labyrinth; IC, internal choana; NC, narial canal; OR, olfactory region; PNS, paranasal sinus; PHS, pharyngeal sinus; PTS, paratympanic sinus; PTS1, paratympanic sinus 1 (dorsal); PTS2, paratympanic sinus 2 (medial); PTS3, paratympanic sinus 3 (ventral); VC, neurovascular canal. Scale bars equal 1cm.

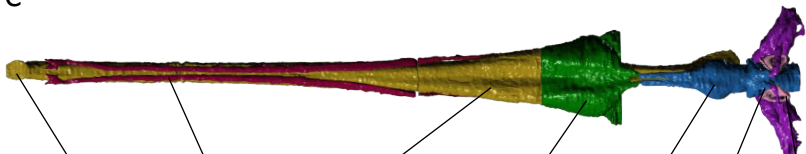
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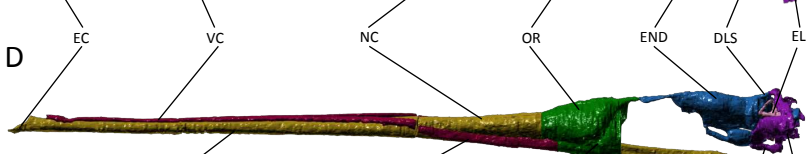
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C



D



E

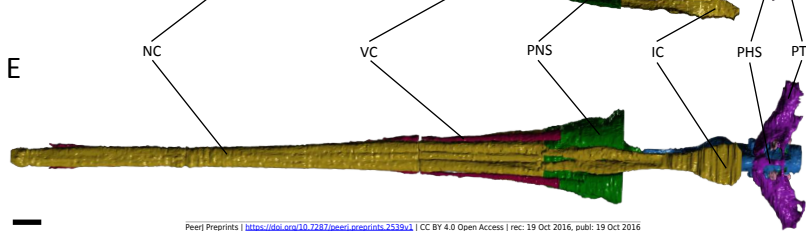


Figure 4(on next page)

Figure 4: Reconstruction of the brain and associated sinuses in *Gavialis gangeticus*.

A - anterior view; B - posterior view; C - dorsal view; D - lateral view; E - ventral view.

Abbreviations: BL, bulla; EC, external choana; END, endocast; IC, internal choana; ITS, intertympanic sinus; NC, narial canal; OR, olfactory region; PAS, parietal sinus; PFS, prefrontal sinus; PHS, pharyngeal sinus; PNS, paranasal sinus; PTS, paratympanic sinus; PTSd, dorsal branch of paratympanic sinus; QS, quadrate sinus; SC, semi-circular canal; VC, neurovascular canal. Scale bars equals 1cm.

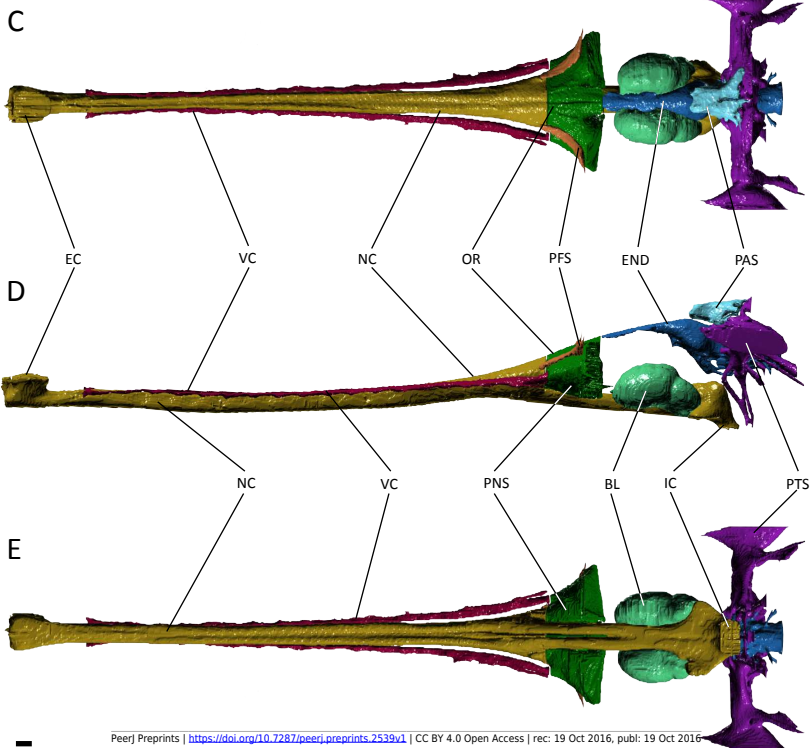
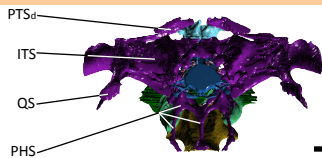
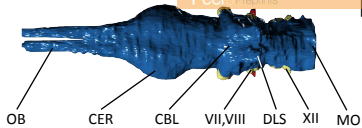


Figure 5(on next page)

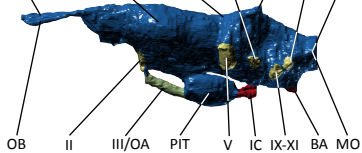
Figure 5: Endocast morphology.

A-C endocast of *Pelgaosaurus typus* and D-F endocast of *Gavialis gangeticus*. A-D, dorsal view; B-E, lateral view; C-F, ventral view. Abbreviations: BA, basilar artery; CBL, cerebellum; CER, cerebrum; DLS, dorsal branch of longitudinal sinus; IC, internal carotid; MO, medulla oblongata; OB, olfactory bulb; PIT, pituitary fossa; II, optic nerve region; III, oculomotor nerve region; V, trigeminal nerve region; VII, facial nerve region; VIII, vestibulocochlear nerve; IX-XI, glossopharyngeal, vagus, and accessory nerve region; XII, hypoglossal nerve region . For visualization, the endocast of *Gavialis* has been scaled to the same anteroposterior length as *Pelagosaurus*. Scale bars equal 1 cm.

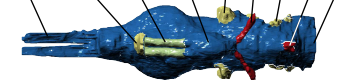
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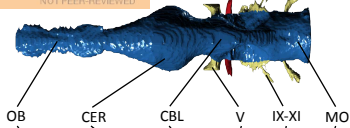
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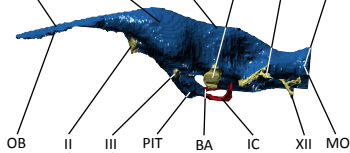
C



D



E



F

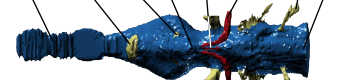


Figure 6(on next page)

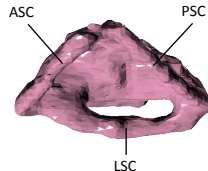
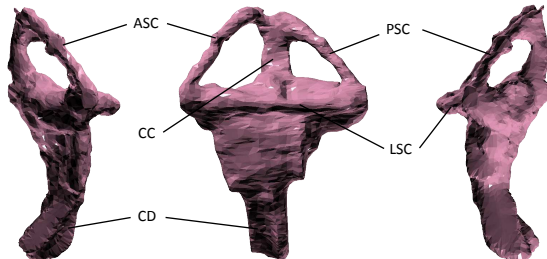
Figure 6: Endosseous labyrinth.

A-D left semicircular canal and vestibular system of *Pelagosaurus typus* and E-H left semicircular canal and vestibular system of *Gavialis gangeticus*. A,E - anterior view; B,F - lateral view; C,G - posterior view; D,H - dorsal view. Abbreviations: ASC, anterior semicircular canal; CC, common crus; CD, cochlear duct; LSC, lateral semicircular canal; PSC, posterior semicircular canal. For visualization, the labyrinth of *Gavialis* has been scaled to the same anteroposterior width as *Pelagosaurus*. Scale bars equal 1 cm.

A

C

D



E

F

G

H

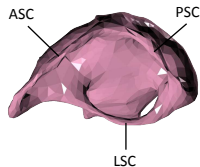
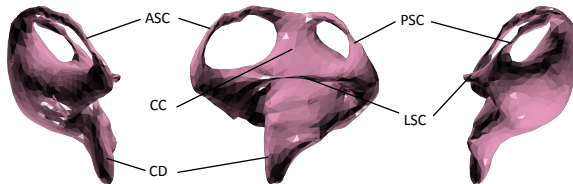


Figure 7 (on next page)

Figure 7: Evolution of the labyrinth in pseudosuchians and proximate stem-group archosaurs.

Labyrinths in lateral view are redrawn from Sobral et al. (2016: *Euparkeria*, left labyrinth), Lautenschlager & Butler (2016: the phytosaur *Parasuchus*, left labyrinth), Brusatte et al. (2016: *Steneosaurus* and *Crocodylus johnstoni*, left labyrinths), Kley et al. (2010: the notosuchian *Simosuchus*, reversed right labyrinth). Abbreviations: asc, anterior semicircular canal; cd, cochlea duct; lsc, lateral semicircular canal; psc, posterior semicircular canal.

