

The Braincase and Neurosensory Anatomy of an Early Jurassic Marine Crocodylomorph: Implications for Crocodylian Sinus Evolution and Sensory Transitions

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ABSTRACT

Modern crocodylians are a morphologically conservative group, but extinct relatives (crocodylomorphs) experimented with a wide range of diets, behaviors, and body sizes. Among the most unusual of these fossil groups is the thalattosuchians, an assemblage of marine-dwellers that transitioned from semiaquatic species (teleosaurids and kin) into purely open-ocean forms (metriorhynchids) during the Jurassic and Cretaceous Periods (ca 191–125 million years ago). Thalattosuchians can give insight into the origin of modern crocodylian morphologies and how anatomy and behavior change during a major evolutionary transition into a new habitat. Little is known, however, about their brains, sensory systems, cranial sinuses, and vasculature. We here describe the endocranial anatomy of a well-preserved specimen of the Jurassic semiaquatic teleosaurid *Steneosaurus* cf. *gracilirostris* using X-ray micro-CT. We find that this teleosaurid still had an ear well attuned to hear on land, but had developed large internal carotid and orbital arteries that likely supplied salt glands, previously thought to be present in only the fully pelagic metriorhynchids. There is no great gulf in endocranial anatomy between this teleosaurid and the metriorhynchids, and some of the features that later permitted metriorhynchids to invade the oceanic realm were apparently first developed in semiaquatic taxa. Compared to modern crocodylians, *Steneosaurus* cf. *gracilirostris* has a more limited set of pharyngotympanic sinuses, but it is unclear whether this relates to its aquatic habitat or represents the

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INTRODUCTION

Crocodylians are some of the most conspicuous animals in today's world, but they are not a particularly diverse group. There are approximately 25 species of modern crocodylians, all of which are semiaquatic predators that predominately lurk in tropical-to-subtropical shallow waters and use their powerful bites and conical teeth to subdue prey (e.g., Busbey, 1995; McHenry et al., 2006; Pierce et al., 2008). This morphological and ecological conservatism belies the long evolutionary history of crocodylians: survivors of about 250 million years of evolution, spanning from when the crocodylian lineage split from its sister group, which led to dinosaurs and birds, until the present day (Brusatte et al., 2010; Nesbitt, 2011). Fossil crocodylomorphs—members of the wider group that includes modern crocodiles and their closest extinct relatives—include numerous species of incredible morphological variety, ranging from the size of a dog to longer than a bus, among them plant-eating, fast-running, pug-nosed, and swimming taxa (Fig. 1). Studying these species can give insight into how the characteristic body plan, sensory abilities, and behaviors of modern crocodylians developed over evolutionary time.

One of the most intriguing groups of extinct crocodylomorphs is the thalattosuchians, a diverse assemblage of marine-dwellers that had a near global distribution during the Jurassic Period and survived into the Early Cretaceous, a total time span from ca 191–125 million years ago (e.g., Gasparini et al., 2000; Young et al., 2010; Chiarenza et al., 2015; Wilberg, 2015a). The thalattosuchians are divided into two main subgroups: Teleosauridae, a clade of long-snouted semi-aquatic forms that superficially resembled modern gharials, and Metriorhynchidae, a group of pelagic species that could swim fast and hunt in the open ocean, like living toothed whales (Young et al., 2012a, 2012b). The metriorhynchids are some of the most aberrant reptiles that ever existed. They evolved from land-living ancestors but became specialized for a fully aquatic existence by developing features such as large salt glands that allowed them to drink seawater and expel excess salt from their food, hydrofoil-like forelimbs and a hypocercal tail for increased swimming performance, and structural lightening of the skeleton and a loss of osteoderms that made them more buoyant and hydrodynamic in the water (Fraas, 1902; Andrews, 1913; Hua and Buffrénil, 1996; Fernández and Gasparini, 2000, 2008; Young et al., 2010; Herrera et al., 2013; Wilberg, 2015a).

Thalattosuchians are important for two main reasons. First, the transition from land-living or semi-aquatic species to the purely marine metriorhynchids was a major evolutionary transformation, akin to the origin of

whales from terrestrial mammals. It promises to give insight into how anatomy, behavior, and physiology change as vertebrates invade new habitats and are modified for new lifestyles. Second, because thalattosuchians are relatively basal members of Crocodylomorpha and are known from a wealth of fossil specimens, they can give insight into the primitive crocodylian bauplan and how the modern species developed their signature morphologies and behaviors from their fossil ancestors. Over the last decade, reexamination of long-known fossils, phylogenetic analyses, histological studies, and description of skull features relating to diet have helped to elucidate evolutionary patterns in thalattosuchians and cement their importance in untangling the early history of crocodylomorphs (e.g., Hua & Buffrénil, 1996; Fernández & Gasparini, 2008; Pierce et al., 2009; Young et al., 2010; Wilberg, 2015a).

One area that has been poorly explored, however, is thalattosuchian neuroanatomy and sensory capabilities. Only a limited number of specimens have been examined in the detail necessary to discuss these issues (e.g., Seeley, 1880; Wenz, 1968; Wharton, 2000; Holliday and Witmer, 2009; Fernández et al., 2011; Herrera et al., 2013; Herrera and Vennari, 2015). In particular, there has been very little study of the internal structure of the thalattosuchian brain, sinuses, sensory organs, nerves, and vessels, which are key to understanding the behaviors and senses of these animals, particularly with regard to their secondary adaptation to an aquatic environment. Recent papers have started to use computed tomography (CT) scanning to visualize the internal anatomy of some thalattosuchians (e.g., Fernández and Herrera, 2009; Fernández et al., 2011; Herrera et al., 2013), but only a few specimens have been studied this way, and much of the focus has been on the olfactory system and salt glands. The brain, sinuses, and inner ear of a thalattosuchian have yet to be described in detail using CT data.

We here describe the internal endocranial anatomy of a well-preserved specimen of a Jurassic teleosaurid thalattosuchian using X-ray micro-CT (μ CT). We make comparisons between the brain, air sinus, vascular, and ear anatomy of this specimen and other fossil and modern crocodylomorphs, and quantitatively compare the hearing capabilities of the fossil specimen (based on inner ear anatomical proxies) to that of modern crocodylians. We then discuss the importance of the fossil data for understanding how modern crocodylians evolved and how thalattosuchians transitioned from a terrestrial to an aquatic habitat.

Institutional abbreviations—**FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge,

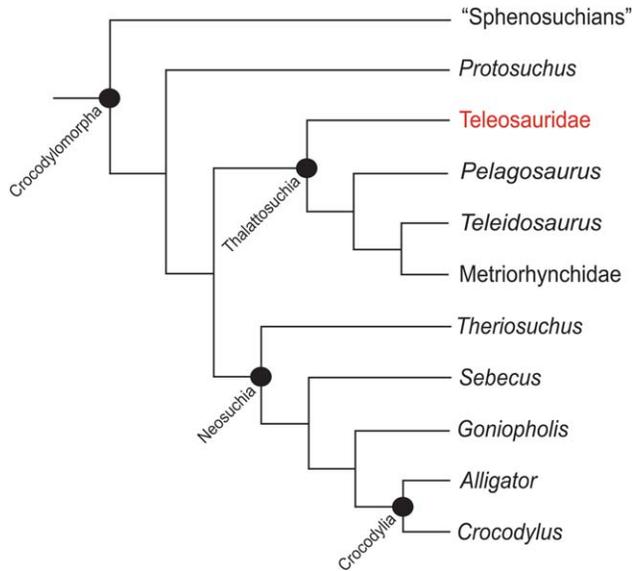


Fig. 1. Framework phylogeny showing the general relationships of crocodylomorphs, with teleosaurids (the group containing the specimen described here, NHMUK PV OR 33095) in red. Phylogeny based on Young et al. (2013).

Massachusetts; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; OUVC, Ohio University Vertebrate Collections, Athens, Ohio, USA; SMNS, Staatliches Museum für Naturkunde Stuttgart, Baden-Württemberg, Germany; TMM, Texas Memorial Museum, University of Texas, Austin, Texas, USA; USNM, United States National Museum of Natural History, Washington, DC, USA.

MATERIALS AND METHODS

Fossil Specimen

The braincase of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095) forms the basis for this study (Figs. 2 and 3). It is from the Whitby Mudstone Formation of Whitby, Yorkshire, UK (lower Toarcian, Early Jurassic, ca 183–178 million years ago). The specimen is relatively intact, comprising the neurocranium from the frontal posterior process posteriorward, and exhibits little dorsoventral distortion or mediolateral compression. The maximum preserved length is 115.26 mm and the maximum preserved width is 124 mm. As the skull is incomplete, we cannot be completely certain of its species identification. However, it shares numerous characteristics with the holotype (NHMUK PV OR 14792) and paratype (NHMUK PV OR 15500) of *Steneosaurus gracilirostris*, including a large, subtriangular parietal dorsal “table,” which in dorsal view has a pronounced convexity at the midline on its posterior margin; the anterior point of the parietal “table” is almost on the same plane as the raised ridges that delimit the two muscular fossae within each supratemporal (=dorsotemporal) fenestra; and the dorsal surfaces of the frontal and parietal have poorly defined

ornamentation composed of large, irregularly shaped ovals and elongate pits, which are irregularly spaced, with some being widely separated (note that much of the dorsal surfaces of these bones are in fact worn and damaged, so this texture is not uniformly visible).

Steneosaurus is taxonomically problematic, with recent phylogenetic analyses finding the genus to be either paraphyletic or polyphyletic (e.g., Young et al., 2012a; Wilberg, 2015a). Therefore, what species actually belong in *Steneosaurus* is a major issue in thalattosuchian taxonomy, one which is currently being investigated. As such, the description herein should not be considered as representative of the entire genus *Steneosaurus*.

Comparative Material

Three-dimensional virtual endocasts of the brain, inner ear, and sinuses reconstructed from CT data have been published for the extant crocodylians *Crocodylus johnstoni* (Witmer et al., 2008) and *Alligator mississippiensis* (Dufeu and Witmer, 2015). To add to the pool of comparative data for modern species, we also reconstructed the cranial endocast and inner ear of *Caiman crocodilus*, the spectacled caiman, based on a subadult specimen collected in Choco, Colombia, and accessioned into the collections of the Field Museum of Natural History (FMNH 73711). This is a well-preserved, three-dimensional specimen without any obvious distortion or breaks.

Computed Tomography and Visualization

The braincase of *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095) was μ CT scanned at the Natural History Museum (London) using their Nikon XT H 225ST CT system in 2014. It was scanned at 215 kV and 150 μ A, with the following parameters: 1.0 mm tin filter, projections were made with an angle of 0.115° between projections. Isotropic voxel size = 89 μ m. Distance from source to detector = 1170 mm. Distance from source to specimen = 523 mm. Mask radius = 89.33 mm.

The skull of *Caiman crocodilus* (FMNH 73711) was scanned at the High-Resolution Scanning Facility of the University of Texas, Austin in 2002. It was scanned along the coronal axis, and a total of 945 projections was made, each with a thickness of 0.142mm. The interslice spacing is also 0.142 mm, and the field of reconstruction is 67 mm. Voxel dimensions = 65 μ m (X) \times 65 μ m (Y) \times 142 μ m (Z). Further information on the specimen is available from the open source DigiMorph digital library of CT scan data: http://www.digimorph.org/specimens/Caiman_crocodilus/

For both specimens, three-dimensional models of the cranial endocast, inner ear, nerves and vessels, and sinuses were rendered by one of us (Muir) by digitally segmenting the CT slice data using Materialise Mimics 17.0 at the University of Edinburgh, School of GeoSciences. The 3D Livewire and Calculate 3D tools were used.

Standard linear measurements of the brain cavity endocast, associated nerve foramina, and vascular openings within the endocranium were made using the measuring tools in Materialise Mimics 17.0. All measurements were taken from 3D voxel model data rather than polygon mesh models or across the tomograph stack. Angular and distance measurements were also recorded for the inner ear labyrinth.

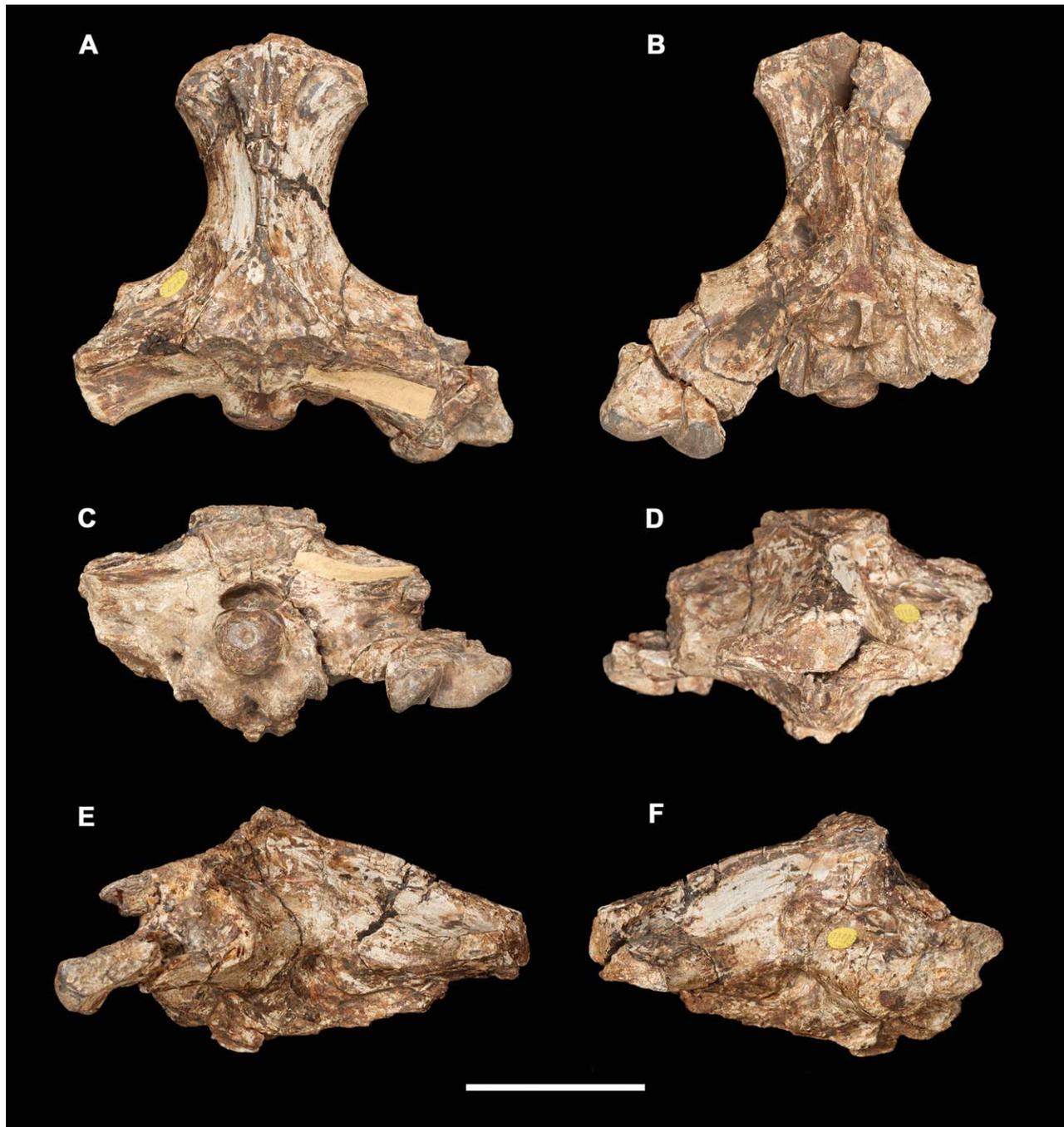


Fig. 2. Braincase of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095) in (A) dorsal, (B) ventral, (C) posterior, (D) anterior, (E) right lateral, (F) and left lateral views. Scale bar equals 5 cm.

We used the methods of Walsh et al. (2009) to estimate mean hearing frequency and hearing range of NHMUK PV OR 33095. This approach involves linear regression of measurements of the endosseous cochlear duct length that have been scaled to basicranial length and log transformed, against hearing sensitivity data derived from audiogram analysis of living crocodylian, avian,

squamate, and chelonian taxa. The same transformed values derived from NHMUK PV OR 33095 are then used to determine the position of this taxon on the audiogram regression line (for full methods, see Walsh et al., 2009). The calculation was made using measurements from the left labyrinth, as the right labyrinth could not be completely reconstructed.

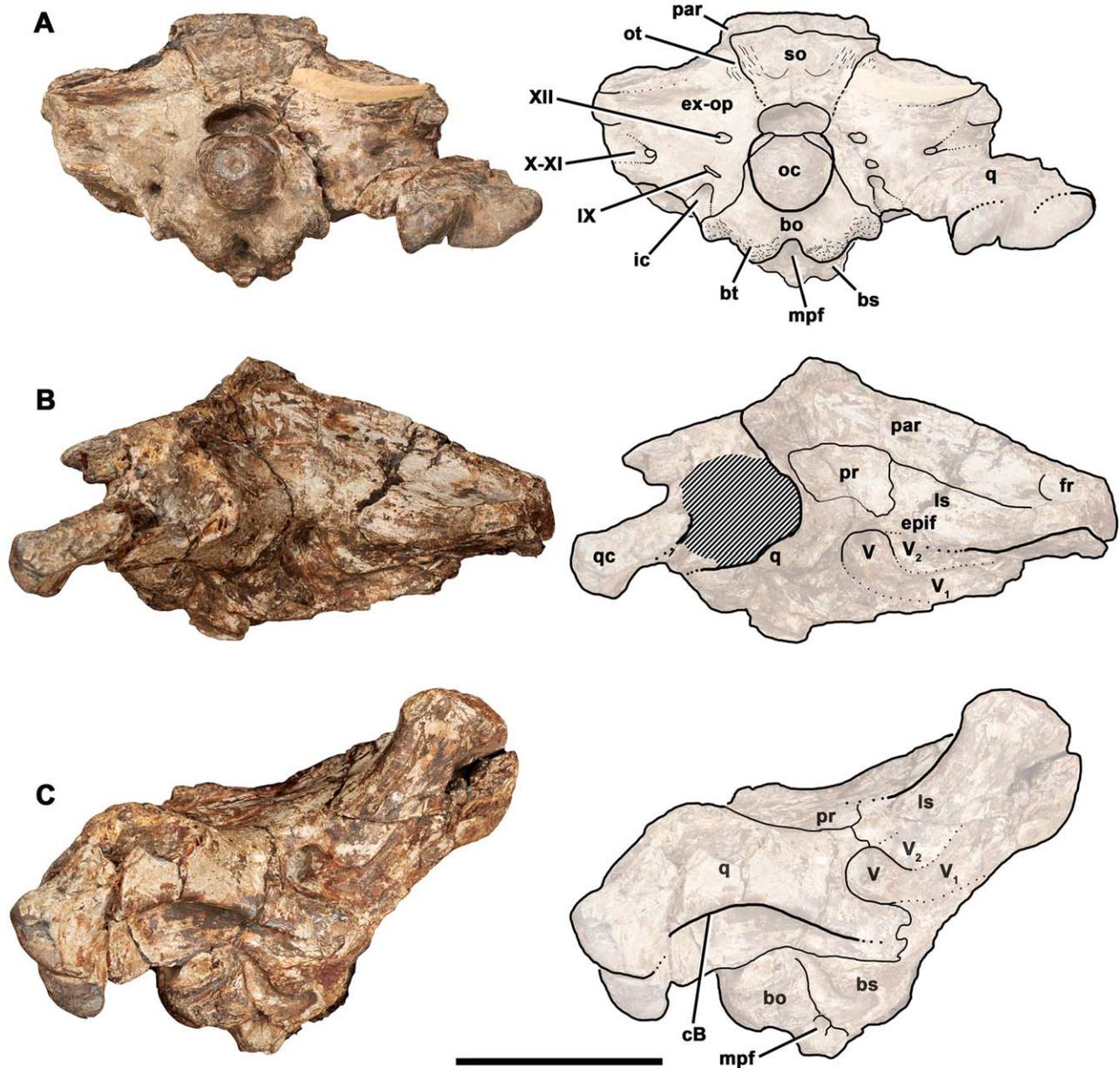


Fig. 3. Photos and line drawings of the braincase of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095) in (A) posterior, (B) right lateral, and (C) right ventrolateral oblique views. Scale bar equals 5 cm. Abbreviations: bo, basioccipital; bs, basisphenoid; bt, basal tubera; cB, crest B; epif, epipterygoid fossa; ex-op, exoccipital-opisthotic; fr, frontal; ic, internal carotid foramen; ls,

laterosphenoid; mpf, median pharyngeal foramen; oc, occipital condyle; ot, occipital tuberosity; par, parietal; pr, prootic; q, quadrate; qc, articular condyles of quadrate; so, supraoccipital. Roman numerals designate cranial nerves. Hatching indicates poorly preserved or damaged regions of the specimen.

RESULTS

External Cranial Anatomy of NHMUK PV OR 33095

Frontal. The frontal is poorly preserved and largely incomplete (Figs. 2 and 3). Only the frontal's contributions to the intertemporal bar and anteromedial corners of the supratemporal fenestrae are preserved. Unfortunately, the external frontal–parietal suture is difficult to discern, and thus we cannot be sure of the

sutural positions and the extent of the frontal. However, the visible morphology is very similar to that of other *Steneosaurus gracilirostris* skulls, and the morphology described by Jouve (2009) for *Teleosaurus cadomensis*. The external surface morphology of the frontal is worn and damaged, but poorly defined ornamentation consisting of large, irregularly shaped ovals and elongate pits can be seen.

There is a distinct “platform” in the anteromedial corner of the supratemporal fenestra. This also occurs in

other thalattosuchians (Fraas, 1902; Andrews, 1913; Lepage et al., 2008; Jouve, 2009; Young et al., 2010, 2012a, 2013, 2014a; Wilberg, 2015a), and is primarily composed by the frontal, with its outer edges contacting the parietal (and also the postorbitals in metriorhynchoids, in which this platform is proportionally larger). Thus, the “platform” likely is the maximal contribution of the frontal to the supratemporal fossa. This interpretation is supported by the position of the parietal–laterosphenoid suture, which is posteroventral to the “platform” (best seen in right lateral view: Fig. 3B). This would result in the parietal separating the frontal from the laterosphenoid, as in *Teleosaurus cadomensis* (MNHN.F AC 8746; Jouve, 2009).

Parietal. The parietal is relatively well preserved (Figs. 2 and 3). It appears as a single element, without any signs of the interparietal suture on the external surface. In dorsal view, the parietal should be “T”-shaped, with an elongate anterior process and two lateral processes. However, the two lateral processes are badly damaged, making their relationship with the medial processes of the squamosals impossible to trace. The parietal forms the posterior and medial margins of the supratemporal fenestrae and fossae. The anterior process forms most of the intertemporal bar and contacts the frontal anteriorly.

In dorsal view, the anterior process narrows dramatically as it extends posteriorly toward the occiput, forming a sagittal crest, until it broadens out again to form the “parietal table” (Fig. 2A). The “parietal table” is seen in all teleosaurids, being typically better developed in adult specimens (Andrews, 1913; Westphal, 1961, 1962; Lepage et al., 2008; Young et al., 2014a). It is a subtriangular, flat surface, which makes up the region where the anterior and lateral processes of the parietal meet. Its external surface has a similar ornamentation as that of the frontal. The “table” is particularly large, similar in size to those in the holotype and paratype of *Steneosaurus gracilirostris*, with its anterior point being almost on the same plane as the raised ridges at the laterosphenoid–prootic sutures on both sides of the skull, that delimit two muscular fossae within the supratemporal fenestra on each side (see below). In dorsal view, there is also a pronounced convexity at the midline of the posterior margin of the “table,” which overhangs the supraoccipital slightly.

Within the supratemporal fenestra, the parietal forms the dorsal half of the medial supratemporal wall. The prootic and the laterosphenoid can be seen ventral to the anterior process (Fig. 3), with the parietal separating the frontal from the laterosphenoid (see above). The laterosphenoid contacts the ventral margin of the anterior process along the anterior and middle regions of the anterior process, whereas the prootic contacts the ventral margin of the anterior process immediately posterior to the laterosphenoid. The parietal is devoid of ornamentation within the supratemporal fenestrae.

In occipital view, the supraoccipital is ventral to the “parietal table,” which terminates laterally approximately level with the occipital tuberosities. The contacts between the parietal and the exoccipital–opisthotic complex cannot be seen in occipital view because of the damage to the lateral processes of the parietal.

Squamosal. The squamosals appear to be missing. However, because of damage along the postorbital–squamosal ridges (sensu Young et al., 2013) it is not possible to discern externally whether or not the medial processes of the left and right squamosals might be present.

Prootic. Both prootics are fairly well preserved (Figs. 2 and 3). When observed within the supratemporal fenestra, the prootic is a subtriangular bone that forms the posteromedial corner of the supratemporal wall. Dorsally it contacts the parietal, posteroventrally the quadrate, and anteriorly the laterosphenoid. The suture between the prootic and laterosphenoid is expressed as a pronounced, raised, dorsoventrally trending ridge that begins slightly dorsal to the midpoint of the dorsal margin of the trigeminal foramen (cranial nerve V). This ridge is seen in other thalattosuchians, including both teleosaurids and metriorhynchids (Holliday and Witmer, 2009; Jouve, 2009; Fernández et al., 2011). In NHMUK PV OR 33095, the ridge extends far dorsally, dividing the supratemporal fossa into attachments for two muscles, as described by Holliday and Witmer (2009) in *Pelagosaurus typus*. The more posterior fossa, located mostly on the prootic, is interpreted as an attachment site for the *M. adductor mandibulae externus profundus*, whereas the more anterior fossa, located on the laterosphenoid and the parietal, housed the *M. pseudotemporalis superficialis* (Holliday and Witmer, 2009). Unfortunately, the dorsolateral corners of both prootics are damaged, and thus we cannot determine the nature of the contact with the squamosals. CT data show that the prootic and opisthotic house the inner ear cavity.

Laterosphenoid. The left and right laterosphenoids are well preserved (Figs. 2 and 3). This bone has a ventral contact with the basisphenoid, and forms the ventral half of the medial supratemporal wall and anteromedial corner of the supratemporal fenestra (Fig. 3). Where the laterosphenoid forms the medial supratemporal wall, it contacts the anterior process of the parietal dorsally. As the laterosphenoid curves and forms the anteromedial supratemporal corner, it closely approaches the frontal (the anteromedial fossa “platform”), but is separated by the parietal. Ventral to the contact with the prootic, the laterosphenoid has a posterior suture with the quadrate in the region of the trigeminal foramen.

The trigeminal opening is a deep, funnel-like structure (Fig. 3, V). The surrounding fossa would have housed the trigeminal ganglion, and thus the various branches of the trigeminal nerve would have diverged from each other outside the endocranial cavity. This is also the case in other modern and extinct crocodylomorphs, along with close outgroup taxa (Holliday and Witmer, 2009; George and Holliday, 2013), although some other archosaurs evolved conditions in which the trigeminal branches exit the endocranial cavity separately and emerge through the bony braincase walls via individual foramina (e.g., Brusatte and Sereno, 2007; Witmer and Ridgely, 2009). In NHMUK PV OR 33095, the fossa extends only slightly posterior to the foramen to excavate a portion of the external surface of the quadrate, which differs from the expansive posterior extent of the fossa in metriorhynchids (Fernández et al., 2011). There is a deep groove extending anteroventrally from the trigeminal foramen on the external surface of the

laterosphenoid, which transmitted the ophthalmic branch of the trigeminal nerve (CN V₁). The groove extends far anteriorly before fanning out on the ventral surface of the frontal. A smaller, shallower triangular fossa borders the anterodorsal corner of the trigeminal foramen, which transmitted the maxillary branch of the trigeminal nerve (CN V₂). These two nerve grooves are also seen in *Pelagosaurus typus* and metriorhynchids (Holliday and Witmer, 2009; Fernández et al., 2011), and the nerves exit the trigeminal foramen in a similar pattern in modern crocodylians (Holliday and Witmer, 2009).

Anterodorsal to the trigeminal foramen and ventral to the pseudotemporalis fossa of the supratemporal region, there is a shallow and elongate concavity, which we interpret as the epipterygoid fossa (Fig. 3B, epif). It is in the same location in *Pelagosaurus typus* and metriorhynchids (Holliday and Witmer, 2009; Fernández et al., 2011). Although the epipterygoid itself is not preserved in NHMUK PV OR 33095, the fossa indicates that it would have been present. Epipterygoids are present in most archosaurs, including many extinct crocodylomorphs, but are lost in some eusuchians, including the modern species (Holliday and Witmer, 2009).

Supraoccipital. The supraoccipital forms the dorso-medial part of the occipital region of the skull (Figs. 2 and 3). In posterior view, the supraoccipital is trapezoid-shaped, broader dorsally than ventrally. It has a pronounced concavity on its posterior surface, with a raised rim along its lateral and dorsal margins. The lateral rims form part of the occipital tuberosities (along with a raised region on the exoccipital–opisthotic complex) (Fig. 3, ot). The occipital tuberosities are paired processes also seen in other teleosaurids, such as *Teleosaurus cadomensis* (MNHN.F AC 8746; Jouve, 2009), *Steneosaurus heberti* (MNHN.F 1890-13), *Steneosaurus obtusidens* (NHMUK PV R 3168; Andrews, 1913), and *Machimosaurus buffetauti* (SMNS 91415; Martin and Vincent, 2013; Young et al., 2014a). They are somewhat similar to the tuberosities seen in dyrosaurid crocodyliforms (e.g. MNHN.F ALG 1; Jouve, 2005), albeit less pronounced. Based on external examination, the supraoccipital of NHMUK PV OR 33095 appears to lack a nuchal crest running along the midline of the element, which would be unusual as the previously listed teleosaurids species all have this crest. However, there is still some matrix adhering to the bone, and CT data show that the matrix is obscuring a low nuchal crest.

The supraoccipital contacts the parietal along its dorsal margin and the exoccipital–opisthotic complex along its lateral margins, and also has a slight ventral contact with the exoccipital–opisthotic. In occipital view, the ventral margin of the supraoccipital forms the medial portion of the dorsal margin of the foramen magnum (we note that the preservational state of the specimen hinders confidence in this interpretation and supraoccipital contribution to the foramen magnum may be less than that appears on the specimen). However, within the foramen magnum, there is a suture between the supraoccipital and the exoccipital–opisthotic, demonstrating that the supraoccipital overlies the exoccipital–opisthotic in this region. This overlapping morphology might explain why participation of the supraoccipital in the dorsal margin of the foramen magnum is so variable

within Thalattosuchia, as independent regressions of this overlap in different lineages could explain how the exoccipital–opisthotic complex sometimes separates the supraoccipital from the foramen magnum.

In dorsal view, the posterior surface of the supraoccipital is broadly exposed. This is the result of a “step”-like arrangement of the posterior skull, with the parietal terminating anterior to the supraoccipital, followed posteriorly by the exposure of the supraoccipital posterior face, followed by the thickened dorsal rim of the foramen magnum, and finally the occipital condyle. This arrangement is seen in other teleosaurids, such as *Teleosaurus cadomensis* (MNHN.F AC 8746; Jouve, 2009), *S. heberti* (MNHN.F 1890-13), and *Steneosaurus obtusidens* (NHMUK PV R 3168; Andrews, 1913), and is present in the basal metriorhynchoid *Pelagosaurus typus* (NHMUK PV OR 32599; Pierce and Benton, 2006). This differs markedly from the condition in metriorhynchids, which have verticalized the occipital surface, such that the supraoccipital is rarely visible in dorsal view, or if it is, it is not as broadly exposed as in teleosaurids (e.g., Andrews, 1913; Young et al., 2010, 2012a, 2013; Fernández et al., 2011; Foffa and Young, 2014).

Exoccipital–opisthotic. The exoccipital–opisthotic complex (Figs. 2 and 3) contacts the supraoccipital along its medial margin dorsally, and the parietal and squamosal along its dorsal margin lateral to the supraoccipital. Ventral to its contact with the supraoccipital, the exoccipital–opisthotic forms most of the foramen magnum, including the lateral walls, the dorsal wall (with the exception of the supraoccipital overlap at the occipital surface), and the ventrolateral corners. These paired ventrolateral projections form part of the occipital condyle, contacting the basioccipital. The suture between the exoccipital–opisthotic and the basioccipital continues ventrolaterally until it reaches the ventral margin of the skull. The exoccipital–opisthotic contacts the quadrate along its ventrolateral margin. This can only be seen on the right side, as the left quadrate is incomplete. However, this suture is difficult to discern because of numerous cracks in the vicinity. Overall, the exoccipital–opisthotic is devoid of ornamentation, covers the majority of the occipital surface, and has a slightly convex external surface medial to the paroccipital processes.

Both paroccipital processes are preserved, although they are missing their distal ends. They are large, pronounced, and oriented horizontally in posterior view. The dorsal surface is slightly concave, with this concavity extending from the exoccipital–opisthotic contribution to the occipital tuberosities medially along the dorsal surface of the exoccipital–opisthotic complex. The ventral margin of this concave surface is sharply delimited by a ridge, which is contiguous with the thickened ventral rim of the supraoccipital.

There are several foramina for nerves and vessels on the posterior surface of the exoccipital–opisthotic. These are better preserved on the left side. The foramen magnum is the largest opening on the occipital surface, situated at the skull midline between the supraoccipital, the exoccipital–opisthotic, and the basioccipital. It is oval-shaped, at least twice as wide mediolaterally than tall dorsoventrally (although this may be exaggerated by slight dorsoventral crushing). Lateral to the foramen magnum,

and level with the dorsal margin of the occipital condyle, is a subcircular foramen that transmitted the hypoglossal nerve (CN XII).

Further lateral to the hypoglossal opening is a large foramen situated ventral to the proximal paroccipital process. We interpret this as transmitting either the vagus nerve (CN X) or a combination of the vagus, accessory (CN XI), and possibly glossopharyngeal (CN IX) nerves and associated vessels (this is labeled as transmitting X-XI in Fig. 3A). Different workers have considered varying combinations of these nerves as passing through this foramen in other thalattosuchians (e.g., Wenz, 1968; Jouve, 2009; Fernández et al., 2011; Young et al., 2012a, 2013; Herrera and Vennari, 2015). Unfortunately, in NHMUK PV OR 33095, the μ CT data are not helpful in tracing this opening far internally into the endocranium because the canal extending from the foramen enters the otoccipital sinus, disappears into this pneumatic chamber, and does not clearly reconnect with the endocast. This indicates that the neurovascular bundle would have been surrounded by the sinus, as is also the case in *Alligator mississippiensis* (Dufeu and Witmer, 2015). The lack of other large foramina on the occipital surface (except for a small one above the carotid opening, see below) suggests that the large foramen underneath the paroccipital process was most likely a multipurpose opening that transmitted more than just the vagus nerve.

Ventrally and slightly laterally to the hypoglossal foramen, at the level of the ventral base of the paroccipital process, is a smaller, slit-like foramen. We suggest that if this small opening did transmit a cranial nerve, it most likely was for the glossopharyngeal nerve (as labeled in Fig. 3A), or possibly for a second branch of the hypoglossal nerve. However, this is not clear because the slit can only be traced a few millimeters internally before disappearing in the CT slices. A much larger foramen opens immediately below the slit. This is for the internal carotid artery and it takes the form of a large, funnel-like structure that opens posteroventrally (Fig. 3, ic). It is located immediately along the ventral margin of the braincase and lateral to the suture between the exoccipital–opisthotic and basioccipital. The internal carotid foramen is larger than the aforementioned openings for the cranial nerves. Unfortunately, the braincase is broken laterally on each side, so the cranioquadrate opening, which can often be large in thalattosuchians and is connected to the tympanic sinuses (e.g., Fernández et al., 2011), is not preserved.

There is some potentially phylogenetically useful variation in the orientation of the nerve foramina in thalattosuchians. The presence of a large vagus (or multipurpose) foramen near the base of the paroccipital processes in NHMUK PV OR 33095 is shared with the teleosaurid *Teleosaurus cadomensis* (MNHN.F AC 8746; Jouve, 2009) and the basal metriorhynchoid *Pelagosaurus typus* (NHMUK PV OR 32599). In metriorhynchids, the large vagus foramen is located in a different position: dorsolateral to the internal carotid artery foramen (see Fernández et al., 2011; Young et al., 2013; Herrera and Vennari, 2015). It therefore appears that the position of the foramen shifts from a dorsolateral position (near the paroccipital process) in basal thalattosuchians to a ventromedial one (closer to the internal carotid artery foramen) in metriorhynchids.

Furthermore, it has been suggested that the large external opening for the carotids on the posterior braincase is a synapomorphy of metriorhynchids (Pol and Gasparini 2009; Fernández et al., 2011). However, the opening is also enlarged in NHMUK PV OR 33095, as well as other teleosaurids (e.g., *Teleosaurus cadomensis*: Jouve, 2009: fig. 3) and basal metriorhynchoids (e.g., *Pelagosaurus typus*: Pierce and Benton, 2006), suggesting it is a wider thalattosuchian feature. The large size and position of the foramina at the ventral edge of the braincase in thalattosuchians does differ from the much smaller, more dorsally positioned openings in early crocodylomorphs such as *Junggarsuchus sloani* (Clark et al., 2004: fig. 2), *Dibothrosuchus elaphros* (Wu and Chatterjee, 1993: fig. 3), and *Almadasuchus figarii* (Pol et al., 2013: fig. 1).

Occipital condyle. The occipital condyle is subcircular in posterior view, slightly mediolaterally wider at its dorsal margin than ventrally (Figs. 2 and 3). There is a deep depression at the center of the posterior surface. The condyle is mostly formed by the basioccipital, with the exoccipital–opisthotics contributing only to the dorsolateral corners. The gap between the corners, filled by the basioccipital, comprises most of the dorsal margin of the condyle and the ventral margin of the foramen magnum. This is the normal condition within Thalattosuchia, and is seen in other teleosaurids, basal metriorhynchoids, metriorhynchine metriorhynchids, and basal geosaurine metriorhynchids (Andrews, 1913; Pierce and Benton, 2006; Lepage et al., 2008; Jouve, 2009; Foffa and Young, 2014). In derived geosaurine metriorhynchids, however, the exoccipital–opisthotic forms the entire dorsal margin of the occipital condyle (*Plesiosuchus manselii*, Young et al., 2012a; *Torvoneustes coryphaeus*, Young et al., 2013).

Basioccipital. In addition to constituting the majority of the occipital condyle, the basioccipital forms the ventromedial part of the occipital region of the skull (Figs. 2 and 3). The suture between the exoccipital–opisthotic and the basioccipital is clearly seen on the occipital condyle, and is also visibly laterally and ventrally to the condyle. Here, the lateral contact between the exoccipital–opisthotic and basioccipital is expressed as a subtle suture that projects ventrolaterally from the occipital condyle to the lateral margin of the basal tuber (=basioccipital tuberosity) (Fig. 3, bt). The left and right tubera extend ventrolaterally from the ventral edge of the braincase in posterior view. Between the tubera is a deep fossa, which houses a foramen that transmitted the median pharyngeal tube and leads into a recess underneath the occipital condyle that is part of the median pharyngeal sinus system (Fig. 3, mpf). This opening has various names in the literature, including the median Eustachian foramen (e.g., Jouve, 2009) and foramen intertympanicum (e.g., Pol et al., 2013). We prefer the simple term median pharyngeal foramen (e.g., Fernández et al., 2011). In ventral view, the tuber contacts the quadrate along much of its lateral margin. Also in ventral view, what remains of the basisphenoid can be seen contacting the ventral margins of both tubera.

Basisphenoid. The basisphenoid is poorly preserved, but in ventral view, it clearly contacts the basioccipital

along its dorsal margin and the orbital process of the quadrate along its anterolateral margin (Figs. 2 and 3). Posteriorly, the basisphenoid broadens laterally and develops a “trident” shape on its exposed ventral surface, consisting of three distinct prongs with notches between them. These house the median pharyngeal canal and lateral (true) Eustachian tubes. A portion of the basisphenoid is also visible in occipital view, as the bone immediately ventral to the basal tubera of the basioccipital. The basisphenoid continues anteriorly as an elongate and narrow structure along the skull midline, which is broadly visible in ventral view. It is unclear if there is a separate parasphenoid or not in this region, so we are referring to this portion of the braincase as the basisphenoid for simplicity. Dorsally, this region of the basisphenoid contacts the laterosphenoid. Anteriorly, the basisphenoid is damaged and reveals a hollow passage that housed the orbital arteries after they emerged from the pituitary fossa (see below).

Quadrate. The quadrates are incompletely preserved (Figs. 2 and 3), with the right one much more complete than the left. The condylar region is oriented posteroventrally. The medial hemicondyle is noticeably smaller than the lateral hemicondyle, with a deep sulcus separating them. The articular surfaces of both hemicondyles are almost parallel and are oriented dorsolaterally. In ventral view, the quadrate contacts the basal tubera along its medial margin. The orbital process of the quadrate overlaps the basisphenoid, and as with other thalattosuchians, this process remains free of bony attachment at its anteromedial surface (Holliday and Witmer, 2009; Jouve, 2009; Fernández et al., 2011). There is also a prominent crest (“crest B” of Iordansky, 1973) on the ventral surface of the bone, running from the lateral hemicondyle distally toward the orbital process. Within the supratemporal fenestra, the quadrate forms the ventral half of the posterior supratemporal wall (Fig. 3). Dorsally, the quadrate contacts the squamosals (although the squamosals are apparently missing, so details of this contact are not clear), medially the prootic, and anteriorly and anteromedially the laterosphenoid. Because of damage, we cannot describe how the quadrate participates in the external otic aperture, cranioquadrate canal, or infratemporal (= laterotemporal) fenestra, nor can we describe the sutural contacts with the jugal, quadratojugal, or pterygoid. CT data show that the quadrate forms much of the middle ear cavity.

Internal Cranial Anatomy of *Caiman crocodilus*

A three-dimensional model of the cranial endocast, inner ear, and associated nerves and vessels is shown in Figure 4. As the primary purpose of this reconstruction is to provide data from an extant taxon to which we can compare the *Steneosaurus* fossil braincase, we do not present a detailed verbal description of it here, but rather rely on our images to present the morphology.

Internal Cranial Anatomy of NHMUK PV OR 33095

Our CT-based reconstruction of the cranial endocast, inner ear endocast (endosseous labyrinth and columella), associated nerves and vessels, and pneumatic cavities in NHMUK PV OR 33095 is shown in Figures 5 and 6.

Because the brain of extant crocodiles and other nonavian reptiles does not entirely fill the endocranial cavity, the resulting cranial endocast is more accurately considered a cast of the dural envelope (including many dural venous sinuses) rather than the brain itself (e.g., Jerison, 1973; Hopson, 1979; Rogers, 1999; Witmer et al., 2008). However, although the exact size and shape of the brain are unclear, many portions of the brain (such as the cerebral hemispheres and pituitary fossa) are identifiable, as are some of the cranial nerves and vessels that emanate from the brain. For ease of description, we refer to these structures using Anglicized terms for the neuroanatomy under discussion, although it should be noted that these terms actually refer to endocranial osteological correlates of the neural structures.

Cranial endocast. The endocast of NHMUK PV OR 33095 is incomplete, due to the breakage of the specimen anteriorly (Figs. 5 and 6). The break is located somewhere near the forebrain–midbrain juncture, meaning that the midbrain and hindbrain are present but the olfactory tracts and bulbs and other features of the forebrain are not preserved. The preserved portion of the endocast is long and narrow, similar to the shape in another teleosaurid specimen from which a latex endocast was constructed (Wharton, 2000), a teleosaurid specimen in which the endocranial cavity is visible in cross-section (Owen, 1842: 83; Seeley, 1880:pl. XXIV; Wilberg, 2015a: fig. 7), and the metriorhynchids “*Metriorhynchus*” cf. *westermanni* (Fernández et al., 2011), *Dakosaurus* cf. *andiniensis* (Herrera and Vennari, 2015), and *Cricosaurus araucanensis* (Herrera et al., 2013). Modern crocodylians have a similar shape, although with greater flexures between the midbrain and hindbrain (cephalic flexure) and within the hindbrain (pontine flexure) (Colbert, 1946a; Witmer et al., 2008; Dufeu and Witmer, 2015; Fig. 4). Because they have very subtle flexures, thalattosuchian endocasts appear tubular in shape, compared to the more kinked, sigmoidal endocasts of extant species.

The cerebral hemispheres can be clearly located on the endocast (Fig. 6, cer). They are large, bulbous structures that project laterally, although not to the same extent as in modern crocodylians (Witmer et al., 2008; Fig. 4). The optic lobes are visible as subtle swellings directly posterior to the cerebral region. In most modern adult crocodylians, the optic lobes typically do not appear as discrete swellings on the endocast (e.g., *Crocodylus johnstoni*; Witmer et al., 2008), but in young specimens, the optic lobes protrude further laterally (e.g., *Caiman crocodilus*: Fig. 4; *Alligator mississippiensis*: Dufeu and Witmer, 2015). Ventral to the cerebrum is the pituitary fossa (Figs. 5 and 6, pf), which is anteroposteriorly elongate and dorsoventrally low, as in modern crocodylians (e.g., Witmer et al., 2008) and other thalattosuchians (e.g., Seeley, 1880; Fernández et al., 2011). The fossa is larger relative to the rest of the endocast than in extant taxa. In NHMUK PV OR 33095 and other thalattosuchians, the pituitary fossa is oriented roughly parallel to the main axis of the endocast (with the lateral semicircular canal of the ear oriented horizontally for reference), whereas in modern crocodylians, the fossa is often angled obliquely, in a posteroventral–anterodorsal direction (Fig. 4; Witmer et al., 2008; Dufeu and Witmer, 2015). This may be related to the more flexed endocasts of these species, or a geometric consequence of the pituitary fossa

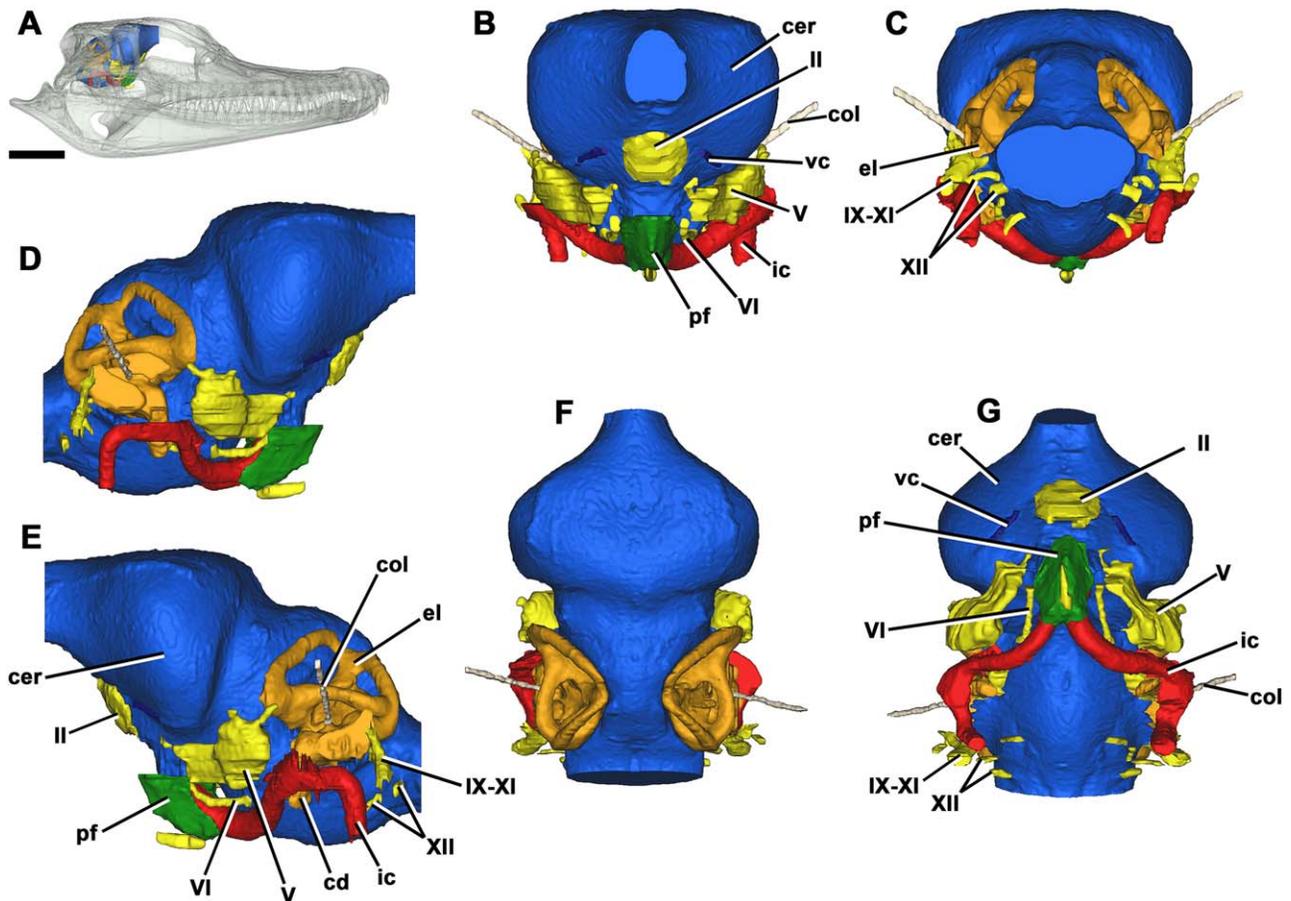


Fig. 4. Internal endocranial anatomy of the extant spectacled caiman, *Caiman crocodilus* (FMNH 73711). Endocranial features illustrated (A) inside transparent skull, with scale bar equaling 2 cm. Endocranial features illustrated in (B) anterior, (C) posterior, (D) right

lateral, (E) left lateral, (F) dorsal, and (G) ventral views. Abbreviations: cd, cochlear duct; cer, cerebrum; col, columella (=stapes); el, endosseous labyrinth; ic, internal carotid artery; pf, pituitary fossa; vc, venous canal. Roman numerals designate cranial nerves.

being somewhat larger in thalattosuchians than in extant crocodyles.

The internal carotid arteries are the most salient arterial vessels associated with the endocast (Figs. 5 and 6, ic). The carotid canals extend from the large foramina on the posterior surface of the braincase, one on each side ventrolateral to the foramen magnum, and then continue anteriorly into the braincase, where their internal tracts are temporarily lost in the CT data as they pass through the pharyngotympanic sinus, as in extant crocodylians (Dufeu and Witmer, 2015). The carotid tracts reemerge ventral to the endosseous labyrinth, where each carotid sharply deflects medially. The left and right carotid canals converge at the posterior end of the pituitary fossa (in the region of the hypophyseal recess) and continue into the fossa as a single large midline vessel. This architecture is similar to that known in other thalattosuchians (e.g., Fernández et al., 2011) and modern crocodylians (Fig. 4; e.g., Colbert, 1946a; Witmer et al., 2008; Dufeu and Witmer, 2015).

All the cranial nerves are at least partially visible in the CT data, although these are usually most discernable either near the external braincase surface (where they traverse the braincase through foramina) or near

the endocast (where they emerge from the brain). The largest and most distinctive nerve is the trigeminal (cranial nerve V), the large ganglion of which would have been located outside of the endocranial cavity, within the huge fossa on the lateral surface of the braincase (see above) (Figs. 5 and 6). A large external trigeminal ganglion was also present in other thalattosuchians (e.g., Holliday and Witmer, 2009; Fernández et al., 2011), other early crocodylomorphs (e.g., *Sphenosuchus acutus*: Walker 1990), close crocodylomorph outgroups (e.g., *Gracilisuchus stipanicorum*: Holliday and Witmer, 2009), and the extant crocodylians (e.g., Colbert, 1946a; Witmer et al., 2008; Dufeu and Witmer, 2015). This is therefore a plesiomorphic feature of crocodylomorphs that they retained from their distant archosaurian ancestors.

The major nerves extending from the ventrolateral portion of the midbrain and passing near the pituitary fossa are difficult to trace. There is a set of narrow, paired nerves emerging from the ventral surface of the endocast anterior to the endosseous labyrinth, which extend anteriorly and are partially covered in ventral view by the large pituitary fossa (Fig. 6). The oculomotor (CN III), trochlear (CN IV), and abducens (CN VI) nerves emerge from this region in *Crocodylus johnstoni* (Witmer et al., 2008).

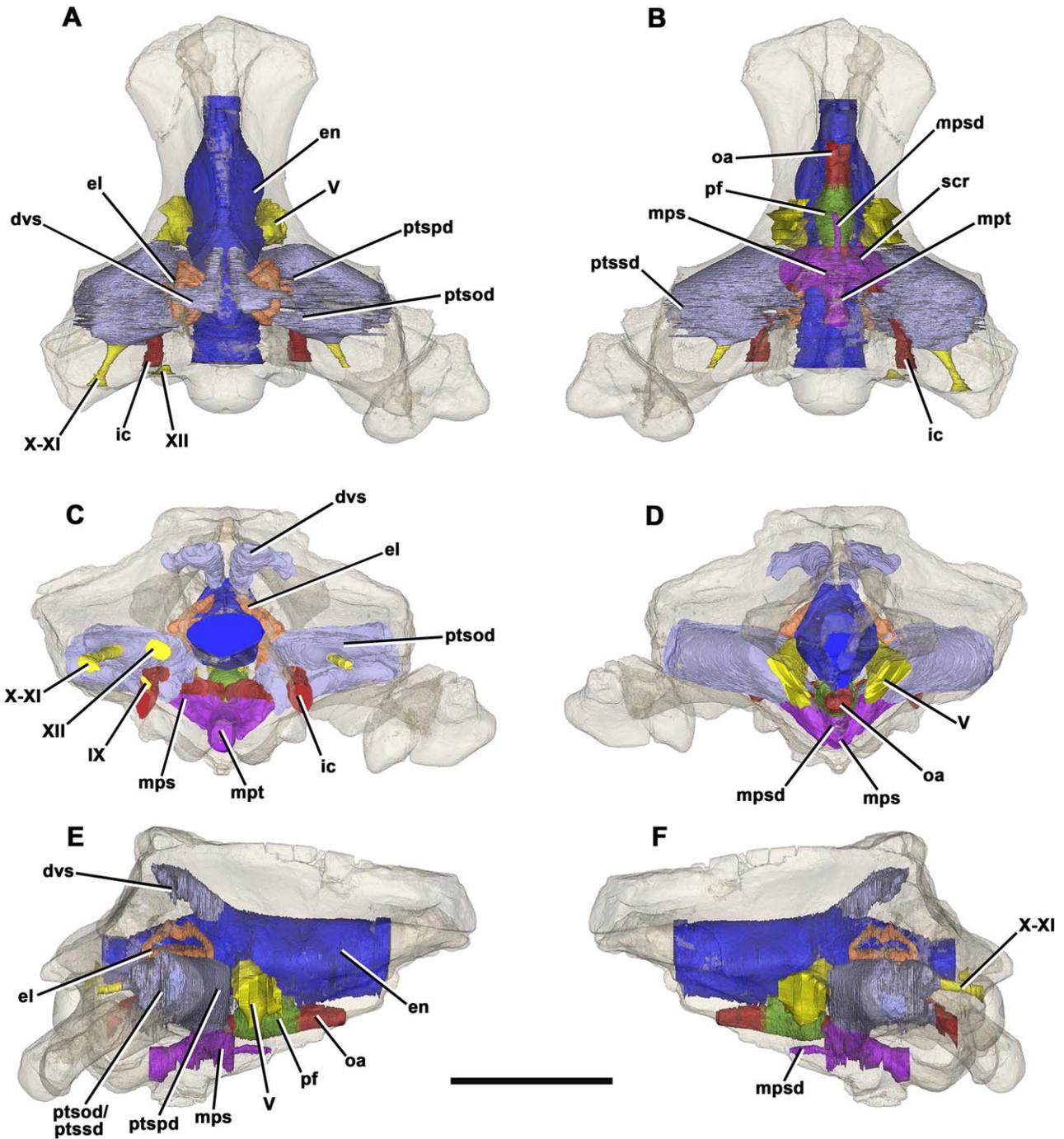


Fig. 5. Internal endocranial anatomy of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095), derived from CT scan data. The specimen is illustrated in (A) dorsal, (B) ventral, (C) posterior, (D) anterior, (E) right lateral, and (F) left lateral views. Scale bar equals 5 cm. Abbreviations: dvs, dorsal dural venous sinus; el, endosseous labyrinth; en, cranial endocast; ic, internal carotid artery; mps, median pharyngeal sinus; mpsd, median pharyngeal sinus

diverticulum; mpt, median pharyngeal tube; oa, orbital artery; pf, pituitary fossa; ptsod, pharyngotympanic sinus otoccipital diverticulum; ptspd, pharyngotympanic sinus prootic diverticulum; ptsod, pharyngotympanic sinus suspensorium diverticulum; scr, subcarotid recess extension of the median pharyngeal sinus. Roman numerals designate cranial nerves.

These structures in NHMUK PV OR 33095 could potentially be the oculomotor nerves, as large oculomotor nerves have been identified in this area in "*Metriorhynchus*" cf. *westermanni* (Fernández et al., 2011). However, they are

located in a similar position to the abducens nerves in *Pelagosaurus typus* (Dufeu, 2011), and therefore, we consider this to be the most likely identification. The nerves exiting the posterior surface of the braincase—CN IX to

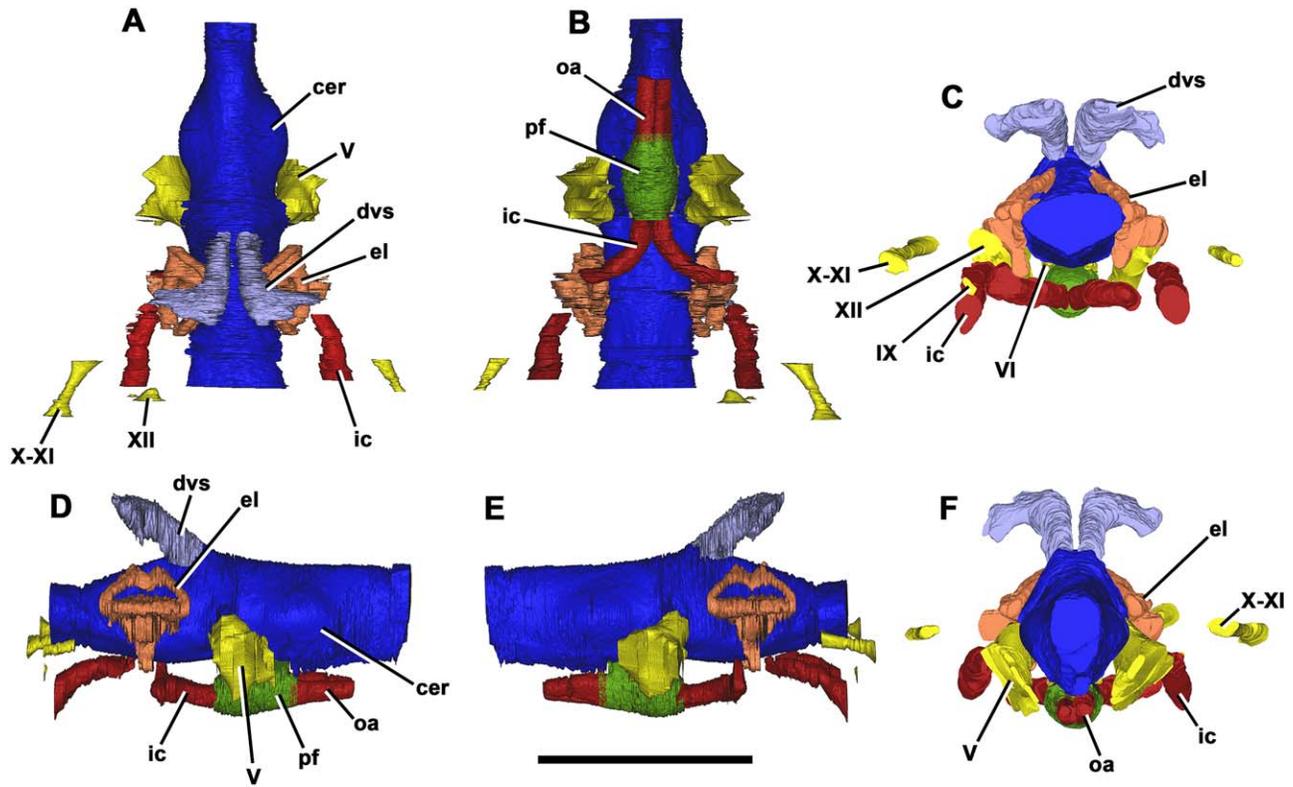


Fig. 6. Cranial endocast, endosseous labyrinth, and endocranial nerve and vascular structures of the teleosauroid thalattosuchian *Steneosaurus* cf. *gracillirostris* (NHMUK PV OR 33095), derived from CT scan data. Figures are in (A) dorsal, (B) ventral, (C) posterior, (D) right

lateral, (E) left lateral, and (F) anterior views. Scale bar equals 5 cm. Abbreviations: cer, cerebrum; dvs, dorsal dural venous sinus; el, endosseous labyrinth; ic, internal carotid artery; oa, orbital artery; pf, pituitary fossa. Roman numerals designate cranial nerves.

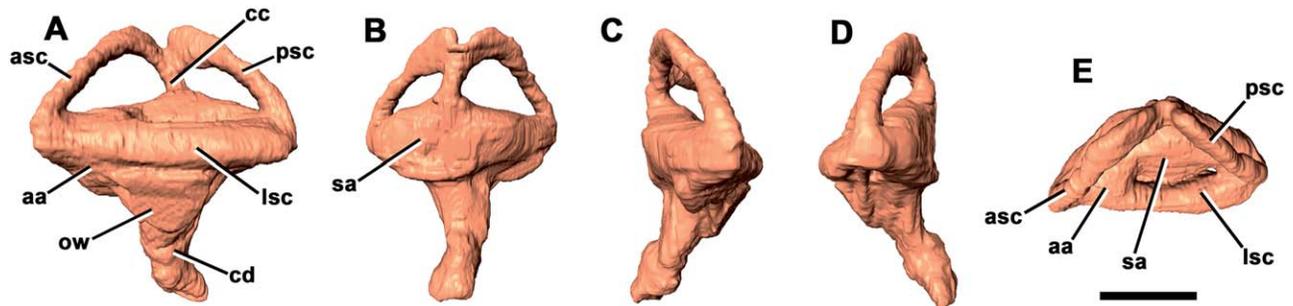


Fig. 7. Endosseous labyrinth of the teleosauroid thalattosuchian *Steneosaurus* cf. *gracillirostris* (NHMUK PV OR 33095), derived from CT scan data. Left labyrinth in (A) lateral, (B) medial oblique, (C) anterior, (D) posterior, and (E) dorsal views. Scale bar equals 1 cm. Abbreviations: aa, anterior ampula; asc, anterior semicircular canal; cc, common crus; cd, cochlear duct; lsc, lateral semicircular canal; ow, oval window; psc, posterior semicircular canal; sa, sacculus.

CN XII—can be traced in the CT data. We illustrate the best-preserved regions, where small portions of their tracts are seen to extend internally from the external foramina before becoming less distinct further internally (Figs. 5 and 6). As explained above, the neurovascular bundle leading internally from the vagus (or multipurpose) opening can be traced in the CT data, but disappears into the otoccipital diverticulum of the pharyngotympanic sinus and is not seen to reemerge to meet the endocast.

There is a single midline hollow structure extending anteriorly from the basisphenoid diverticulum of the median pharyngeal sinus, in the region where the carotids meet the pituitary fossa (Figs. 5 and 6, mpsd). It would have continued further anteriorly, as its internal tract is exposed at the broken anterior surface of the braincase. The identity of this structure is somewhat uncertain, as it is not present in *Alligator mississippiensis*, whose internal sinus system has been the subject of

detailed description (Dufeau and Witmer, 2015), but is likely an anterior pneumatic diverticulum of this sinus (which is part of the median pharyngeal sinus system and pneumatized by the median pharyngeal tube between the basioccipital and basisphenoid posteriorly) or vasculature leading into the sinus. A similar sinus diverticulum has been noted in the thalattosuchian *Pelagosaurus typus* (Dufeau, 2011).

Furthermore, there are large, thick, paired vessels extending anteriorly from the pituitary fossa (Figs. 5 and 6, oa). These continue to the broken anterior surface of the specimen, so they would have extended further anteriorly in life. These vessels are not present (or at least not as large) in modern crocodylians (Colbert, 1946a; Witmer et al., 2008; Dufeau and Witmer, 2015). They are not visible in recently studied thalattosuchians whose braincases are either not well preserved or are broken too far posteriorly to contain these vessels (e.g., Wharton, 2000; Fernández et al., 2011; Herrera and Vennari, 2015). They were, however, noticed by Seeley (1880:pl. XXIV) in his study of a teleosaurid skull in which the endocranial cavity was visible in cross section. He identified them as the optic nerves (CN II), but recent work on modern crocodylians shows that the optic nerves actually project from the endocast much further anterodorsally, in front of the cerebrum and far anterior to the pituitary fossa (e.g., Witmer et al., 2008; Dufeau and Witmer, 2015). Instead, we interpret these structures as the orbital arteries, because these vessels extend anteriorly out of the pituitary fossa in extant diapsids (Porter, 2015). These large vessels extending anteriorly from the pituitary fossa are approximately the same size as the internal carotids from which they branch posteriorly within the fossa.

There is a large paired venous sinus above the hind-brain that is continuous with the dural space (Figs. 5 and 6, dvs). This represents a portion of the dural venous sinus system that was described in a teleosaurid by Wharton (2000) and subsequently noted in metriorhynchid thalattosuchians (Fernández et al., 2011; Herrera and Vennari, 2015), but is not present in such a hypertrophied form in modern crocodylians (Witmer et al., 2008; Dufeau and Witmer, 2015).

In NHMUK PV OR 33095, the venous sinus on each side connects to the dorsal portion of the endocast in the region between the endosseous labyrinth and trigeminal foramen. This venous structure is the posterior portion of the transverse sinus (middle cerebral vein) system that is a very consistent element of the encephalic venous drainage system in archosaurs, albeit reduced in extant crocodylians (Wharton, 2000; Sampson and Witmer, 2007; Witmer et al., 2008; Witmer and Ridgely, 2009; Porter and Witmer, 2015). In thalattosuchian specimens in which this area is observable, this posterior branch (the posterior middle cerebral vein) is hypertrophied. In *Pelagosaurus typus* (LMW, pers. obs.), the vein has a branch that reaches the occiput, which is very common in archosaurs, including such non-crocodylomorph suchians as *Gracilisuchus* (MCZ 4117; LMW, pers. obs.); this is probably also the case in NHMUK PV OR 33095, although the CT data are not entirely clear on this point.

However, thalattosuchians apparently diverge from other archosaurs in that the posterior middle cerebral vein (Figs. 5 and 6, part of the structure labeled dvs) is

large and turns laterally toward the middle ear region, passing through the bone behind the supratemporal fenestra. In “*Metriorhynchus*” cf. *westermanni*, Fernández et al. (2011, p 370) referred to this laterally directed vein as the “tube-like cavity communicating the cranio-quadrate passage with the dorsal longitudinal venous sinus” (labeled as “1” in their fig. 4). *Pelagosaurus typus* (LMW, pers. obs.) has the same venous feature, and in both taxa, it is directed laterally to open into the supratemporal fossa via a large aperture and then continues on to open into the middle-ear region. The branch leading to the supratemporal opening would correspond to the dorsal head vein of other diapsids (Sampson and Witmer, 2007; Witmer et al. 2008) or the temporoorbital vein of extant crocodylians (Porter, 2015). Although not fully illustrated here, the CT data for NHMUK PV OR 33095 do indeed show that this lateral extension of the posterior middle cerebral vein does open via a large dorsal head vein aperture in the posterior portion of the supratemporal fossa. However, unlike in “*Metriorhynchus*” cf. *westermanni* (Fernández et al., 2011) and *Pelagosaurus typus* (LMW, pers. obs.), there is no evidence in NHMUK PV OR 33095 that that vein reaches the middle-ear space or any of its pneumatic diverticula.

Pneumatic sinuses. The braincase of NHMUK PV OR 33095 is pneumatic, with internal sinuses filling many of the bones surrounding the endocast. Most of these sinuses are in the same positions as those identified in modern crocodylians by Dufeau and Witmer (2015), and therefore, we use their terminology here. As in the extant taxa, the braincase sinuses of NHMUK PV OR 33095 can be divided into two systems: a median pharyngeal sinus system underneath the endocast that communicates with the pharynx via a midline median pharyngeal tube (sometimes called the “median Eustachian tube”), and a pharyngotympanic sinus system on each side of the endocast, which communicates with the pharynx via a lateral (true) Eustachian tube and is intimately associated with the middle ear (Witmer et al. 2008; Dufeau and Witmer 2015).

The median pharyngeal sinus excavates the interior of the basisphenoid (Fig. 5, mps). The median pharyngeal tube (Fig. 5, mpt) enters the recess by passing through the median pharyngeal foramen, the large opening on the ventral surface of the braincase between the basioccipital and basisphenoid (Fig. 3, mpf). The sinus fills nearly the entire posterior portion of the basisphenoid, terminating anteriorly where the internal carotids meet the endocast. Extensions of the sinus, the subcarotid recesses, extend laterally to underlie the carotids in the region where they curve medially to enter the pituitary fossa (Fig. 5, scr). The subcarotid recesses are large in NHMUK PV OR 33095. These recesses become larger during ontogeny in *Alligator* (Dufeau and Witmer, 2015). A median pharyngeal sinus system is also present in “*Metriorhynchus*” cf. *westermanni* (Fernández et al., 2011) and *Dakosaurus* cf. *andiniensis* (Herrera and Vennari, 2015), and the large median pharyngeal foramen seen in many other early crocodylomorphs, visible externally without the aid of CT, indicates that this sinus system is a common feature of crocodylomorphs (e.g., Nesbitt, 2011; Pol et al., 2013).

The pharyngotympanic sinus system is much more extensive and complex than the relatively simple midline

median pharyngeal sinus. Dufeu and Witmer (2015) have shown that the pharyngotympanic system consists of eight main diverticula in modern *Alligator*, which throughout ontogeny generally become larger, begin to coalesce, and ultimately merge together into an expansive sinus. Some, but not all, of these diverticula are present in NHMUK PV OR 33095. These recesses are discussed individually below.

(1) The basioccipital diverticulum that fills the basal tubera and part of the surrounding bone is absent, as the basioccipital is solid internally. (2) The recessus epitubericus, a finger-like cavity that fits between the trigeminal ganglion (above) and internal carotid (below) and extends anterior to the internal carotids in ventral view, is also absent. (3) Because the pterygoid is unknown in NHMUK PV OR 33095, it is not clear if there was a pterygoid diverticulum. However, as this extends from the recessus epitubericus into the pterygoid in *Alligator*, the lack of the recessus epitubericus in NHMUK PV OR 33095 suggests that, if present, a pterygoid diverticulum must have emerged from another source. (4) The intertympanic diverticulum, which pervades the prootic and supraoccipital above the foramen magnum and occasionally extends into the parietal in *Alligator*, is absent. This is also the case in other thalattosuchians in which this area is visible (Wilberg, 2015a). The enlarged dorsal dural venous sinus occupies a similar position (although it has a different source), so this may be precluding the development of an intertympanic sinus. (5) There is no sign of a parietal diverticulum.

(6) There is a large prootic diverticulum filling much of the prootic posterior to trigeminal ganglion and immediately anterior to the inner ear canals (Fig. 5, ptspd). This appears to be equivalent to what Fernández et al. (2011) refer to as the “middle-ear cavity” in “*Metriorhynchus*” cf. *westermanni*, as it occupies the same part of the prootic surrounding the inner ear and posterior to the ganglion. Unlike the case in *Alligator*, there is no external fossa on the prootic leading into this recess (Dufeu and Witmer, 2015: fig. 9).

(7) There is limited pneumaticity in the quadrate, the result of a suspensorium diverticulum (Fig. 5, ptssd). Dufeu and Witmer (2015) described how this diverticulum consists of two separate but convergent diverticula in *Alligator*: an infundibular diverticulum filling much of the main body of the quadrate and a quadrate diverticulum that hollows out the quadrate condyles and sends a thin extension, the siphonium, out through an external foramen on the condyles and into the articular bone. The infundibular diverticulum is clearly present in NHMUK PV OR 33095. It pervades most of the ventral portion of the quadrate body, and communicates with the prootic diverticulum anteriorly and dorsally, otoccipital diverticulum posteriorly and medially, and median pharyngeal sinus ventrally. This is equivalent to “cavity 2” of Fernández et al. (2011), which they identified in “*Metriorhynchus*” cf. *westermanni*. However, there is no sign of a quadrate diverticulum in NHMUK PV OR 33095. The quadrate condyles are solid internally and there is no external foramen for transmitting the siphonium.

(8) There is a large otoccipital diverticulum that fills the otoccipital lateral and ventral to the foramen magnum, completely surrounding the neurovascular bundle for nerves IX–XI (Fig. 5, ptsod). This recess occupies only

the ventral half of the paroccipital process, making it much less extensive than the condition in all stages of *Alligator* ontogeny, in which the recess fills the entire depth of the otoccipital (Dufeu and Witmer, 2015). “*Metriorhynchus*” cf. *westermanni* also has an otoccipital diverticulum limited to the ventral half of the paroccipital process, which may indicate that this is a common feature of thalattosuchians (Fernández et al., 2011). In NHMUK PV OR 33095, the otoccipital recess is divided into dorsal and ventral partitions, which are separate from each other posteriorly but merge anteriorly. The bundle for the vagus nerve and associated structures leads into the dorsal partition. Based on the condition in “*Metriorhynchus*” cf. *westermanni*, it is likely this dorsal partition communicated with the expansive dorsal dural venous sinus above the endocast (Fernández et al., 2011).

Inner ear. The endosseous labyrinth is similar in shape to that of modern crocodylians, with a triangular vestibular apparatus dorsally (consisting of the semicircular canals and sacculus) and an elongate cochlear (lagena) duct ventrally, which is dorsoventrally deeper than the vestibular apparatus (Figs. 5 and 7; Owen, 1850; Colbert, 1946b; Witmer et al., 2008; Dufeu and Witmer, 2015). As in most living species, the cochlear duct is directed medially, with a slight curvature along the posterior margin. The three semicircular canals are approximately orthogonal to each other, and the anterior and posterior canals meet at the common crus, which is approximately the same diameter as the canals themselves (Table 1). The anterior semicircular canal is expanded very slightly further anteriorly than the posterior canal is posteriorly. As a result, there is a slightly larger gap between the anterior canal and the common crus than there is between the posterior canal and the crus. Unlike in modern crocodylians (Fig. 8) and most other archosaurs, however, the anterior and posterior semicircular canals extend to the same level dorsally when seen in lateral view (e.g., Witmer et al., 2008: fig. 6.5). It should be noted that modern crocodylians are unusual among fossil and extant archosaurs in having an anterior canal that is only marginally expanded dorsally relative to the posterior canal.

Using the methods of Walsh et al. (2009), we estimate that NHMUK PV OR 33095 had a mean hearing sensitivity (MHS) of 1500 Hz, and a hearing range (HR) of 2400 Hz (Fig. 9). These values are toward the upper end of the spectrum of hearing sensitivity known in living crocodylian species (*Crocodylus acutus*: MHS 1650 Hz, HR 2700 Hz [Wever, 1978]; *Alligator mississippiensis*: MHS 550 Hz, HR 900 Hz [Wever, 1978]; *Caiman crocodylus*: MHS 1150 Hz, HR 1700 Hz [Manley, 1990]).

DISCUSSION

The CT data for *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095) provide important new information on the ears, cranial sinuses, and cranial vascularization of extinct crocodylomorphs. This, in turn, provides insight into the origin of modern crocodylian morphologies and helps reveal how the peculiar extinct thalattosuchians were modifying their senses and cranial systems as they transitioned into an aquatic habitat.

TABLE 1. Dimensions and angular measurements of the brain cavity endocast and endosseus inner ear

	Length (mm)	Width (mm)	Depth (mm)	Diameter (mm)	Deg.	Volume (mm ³)
BCE	76.5	22.8	22.8	—	—	8612.7
ASSC	18.1	—	—	2.0	—	—
LSSC	20.4	—	—	3.8	—	—
PSSC	16.0	—	—	2.0	—	—
ASSC/PSSC	—	—	—	—	94	—
ASSC/BA*	—	—	—	—	51	—
PSSC/BA*	—	—	—	—	70	—
ECD	13.8	—	—	—	—	—
OW*	—	—	—	5.9	—	—
LAB	—	—	—	—	—	885.7

Abbreviations: ASSC, anterior semicircular canal; ASSC/PSSC, intersection angle between the canals; ASSC/BA, intersect angle between ASSC and BA; BA, main (sagittal) brain axis; BCE, brain cavity endocast; ECD, endosseous cochlear duct; LAB, whole labyrinth; LSSC, lateral semicircular canal; OW, oval window; PSSC, posterior semicircular canal; PSSC/BA, intersect angle between PSSC and BA.

All linear measurements are in millimeters, rounded to tenths of a millimeter, and collected using Materialise Mimics 17.0. Measurements marked with an asterisk are averages of left and right labyrinth values; where the right labyrinth was too incomplete to measure, values were taken from the left labyrinth alone.

Hearing and Balance

Some of the most striking evidence comes from the endosseous labyrinth, which would have housed the membranous inner ear in life. Relative to the overall proportions of the inner ear labyrinth, NHMUK PV OR 33095 has an elongate cochlear duct, the part of the inner ear related to hearing. An elongate cochlear duct is known to have been present in the Permian basal diapsid reptile *Youngina capensis*, pointing to an early origin for enhanced hearing frequency sensitivity in at least some terrestrially adapted diapsids (Walsh et al., 2014), the larger group of reptiles to which lizards, crocodylomorphs, and birds belong. However, extant diapsid clades (e.g., squamates, rhynchocephalians and, if included within Diapsida, turtles) possess relatively short cochlear ducts (Walsh et al., 2009), and the trend toward duct elongation appears to be largely confined to Archosauromorpha (the diapsid subclade including crocodylomorphs, dinosaurs, pterosaurs, and birds). This elongation was presumably present in fully terrestrial stem archosauromorphs, and the relatively elongate cochlear duct in *Steneosaurus* cf. *gracilirostris* must therefore be retained from a fully terrestrial crocodylomorph ancestor. This fits with our current understanding of crocodylomorph phylogenetics as the oldest and most primitive members of the group are terrestrial species such as *Sphenosuchus* and *Terrestriuchus* (e.g., Nesbitt, 2011). Determining the most parsimonious explanation of cochlear duct evolution is clearly important, but will only become possible when the spectrum of cochlear duct development in fossil and living diapsids is better known and can be mapped onto robust phylogenies.

When scaled by body mass estimates, the length of the cochlear duct is strongly correlated with, and thus predictive of, best hearing range and mean hearing frequency in extant birds and reptiles (Gleich et al., 2005; Walsh et al., 2009). When we add NHMUK PV OR 33095 to a dataset of recorded audiogram activation values from a variety of modern taxa, we estimate its hearing sensitivity to be towards the known upper range of living crocodylian auditory sensitivity values (Fig. 9). Furthermore, the cochlear duct length of NHMUK PV OR 33095 is located within a point cloud of many other taxa (mostly vocalizing squamates such as geckos and

anole lizards), meaning that it is not an outlier and not greatly different in relative length to the cochleae of modern reptiles and birds. This strongly suggests that hearing in air remained important to *Steneosaurus* cf. *gracilirostris* (at least as important as in modern crocodylians), and that only limited, if any, adaptation to sound transmission in water had occurred in this thalattosuchian. Further information from the middle-ear ossicle would be useful for determining whether there are differences in impedance matching between terrestrial (fossil) and aquatic/semiaquatic crocodylians, but to our knowledge, this has yet to be tested quantitatively.

As with the auditory region of the labyrinth, the vestibular apparatus of NHMUK PV OR 33095 is not greatly different to that seen in living crocodylians. The vestibular system in extinct archosaurs has received a great deal of attention in recent years thanks to the advent of μ CT approaches, but much of this has centered on birds and dinosaurs, with far fewer studies of fossil crocodylians and stem archosaurs (Walsh et al., 2014). Although variation in vestibular system morphology over archosaur evolution is presently incompletely known, a strong trend toward anterior semicircular canal expansion is clearly apparent in bipedal archosaurs (Georgi et al., 2013), and also in pterosaurs (Witmer et al., 2003). This has been attributed to sensitivity to the pitching motion of the head (Sipla, 2007), but some expansion of the anterior canal is also apparent in quadrupedal dinosaurs and crocodylians (Witmer et al., 2008). The reason for this is unclear, but anterior canal expansion may also be positively correlated with head mass (Georgi et al., 2013).

In NHMUK PV OR 33095, the anterior semicircular canal is only slightly longer than the posterior canal (Table 1), suggesting sensitivity to pitching was less important for this taxon. This may be consistent with a more aquatic lifestyle involving reduced head rotation along the sagittal plane. However, although the lateral (horizontal) semicircular canal is slightly longer than the anterior canal; its larger cross-sectional diameter (Table 1) and relatively straight and uncurved morphology around the sacculus seem poorly optimized for sensitivity. By comparison, the lateral semicircular canals of extant crocodylian taxa shown in Figure 8 are all notably more curved than in NHMUK PV OR 33095 (Fig. 7), although

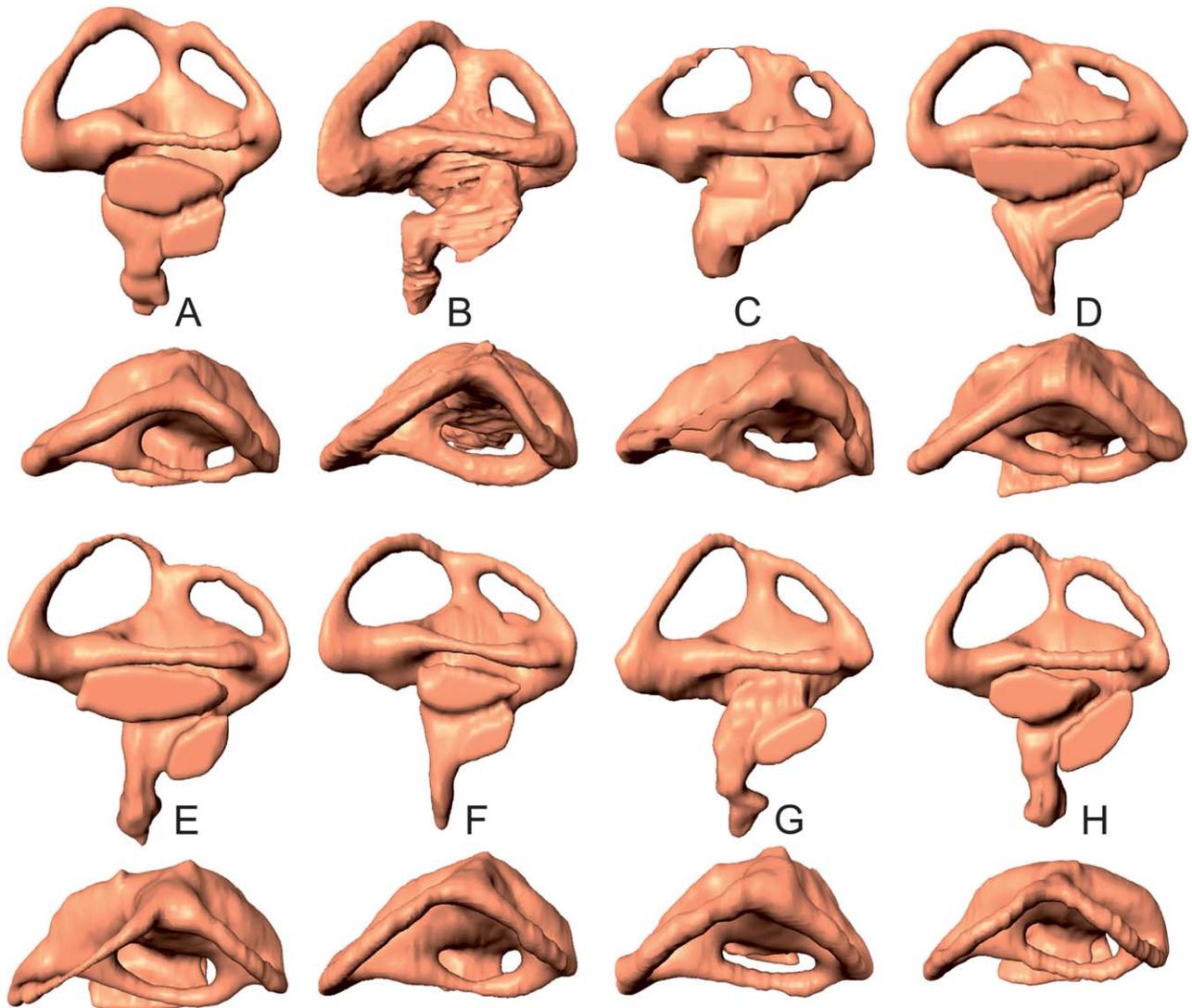


Fig. 8. Comparative selection of left endosseous labyrinths in lateral (upper rows) and dorsal (lower rows) views, from extant crocodylian taxa (LMW unpublished CT data). (A) *Alligator mississippiensis* (USNM 211233); (B) *Caiman crocodilus* (FMNH 73711); (C) *Gavialis gangeticus* (TMM M-5490); (D) *Tomistoma schlegelii* (USNM 211322); (E) *Crocodylus acutus* (FMNH 59071); (F) *C. intermedius* (FMNH 75662); (G) *C. johnstoni* (OUVC 10425); (H) *C. moreletii* (TMM M-4980).

the cross-sectional diameter of the canals of *Gavialis*, *Tomistoma*, and *Caiman* are similar to those of the fossil.

Another possibility is that the neck of *Steneosaurus* cf. *gracilirostris* was less flexible than the neck of most living crocodyles, removing some of the requirement for sensitivity to pitch and yaw through increased coupling with the trunk (but see Spoor et al., 2002 for an alternative view of this situation in cetaceans). However, the cervical flexibility of teleosaurids appears to have been comparable with that of living crocodylians, and reduction in flexibility would have had important implications for feeding behavior in this longirostrine taxon. We suspect that this canal circumference reduction instead relates to lower head mass relative to other crocodylomorphs (sensu Georgi et al., 2013), due to a more gracile and lighter rostrum. This possibility is supported by the

slightly less pronounced anterior canal expansion in the longirostrine *Tomistoma* and *Gavialis*, relative to broad-snouted living crocodylians (Fig. 8).

It should be noted that some of the anterior and posterior semicircular canal height is a result of thickening of the canals at their most dorsal point, and this unusual feature is unambiguous in the CT dataset. While the dimensions of the bony labyrinth must constrain the maximum size of the sensory membranous labyrinth, the actual interrelationship between the morphology of the two structures is presently not well known across vertebrates as a whole. Because the diameter and path of the membranous labyrinth in life may not have exactly conformed to the shape of the endosseous canals in NHMUK PV OR 33095, our inferences of functional significance of the endosseous labyrinth in this fossil are cautious.

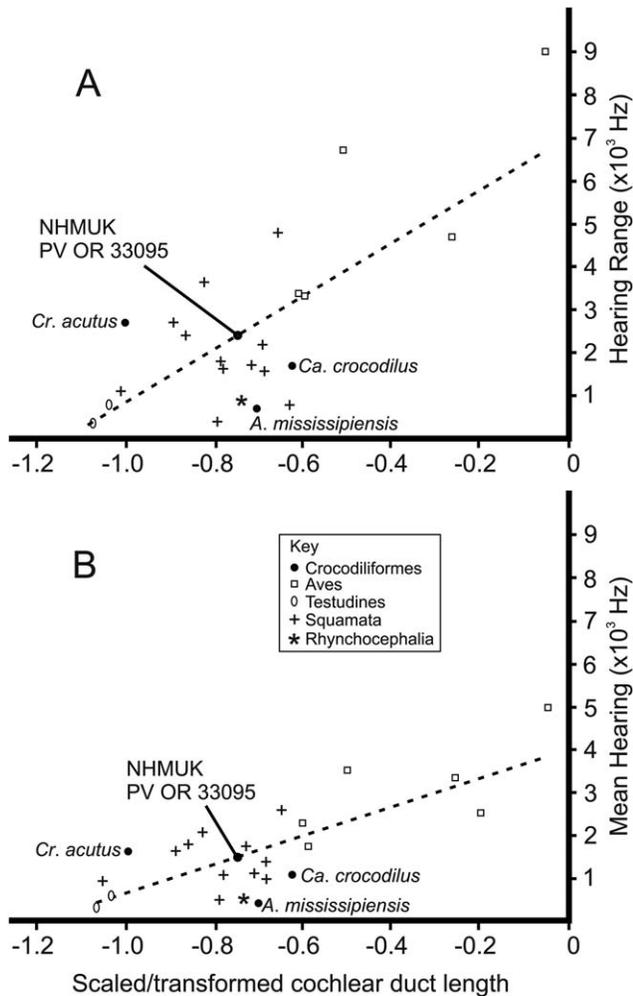


Fig. 9. Hearing sensitivity estimates for *Steneosaurus cf. gracilirostris* using the methods of Walsh et al. (2009; see text for further details). Although extant crocodylian taxa have more elongate cochlear ducts than squamates and turtles relative to the overall proportions of the labyrinth, squamate, and crocodylian taxa are mixed in this analysis because raw cochlear duct length measurements have been scaled to basicranial length.

Cranial Pneumaticity

NHMUK PV OR 33095 possesses some, but not all, of the standard pharyngotympanic sinuses of modern crocodylians (Dufeau and Witmer, 2015). The basioccipital diverticulum, recessus epitubericus, and intertympanic diverticulum are absent. Furthermore, the suspensorium diverticulum is greatly reduced compared to modern species, such that it only occupies a portion of the quadrate and does not extensively hollow out the bone and extend posteriorly from the braincase, out through the siphoneal opening on the quadrate condyle and into the articular, as in the extant taxa. Only the prootic and otoccipital diverticula are similar in their position and large sizes to the same recesses in the living species. What is particularly interesting is that all the recesses lacking in NHMUK PV OR 33095 appear very early in the ontogeny of *Alligator* and are uniformly present in all studied specimens (Dufeau and Witmer, 2015),

meaning that their absence in the teleosaurid specimen is not likely due to ontogeny or individual variation.

It is difficult to explain why NHMUK PV OR 33095 had limited pneumaticity compared to modern crocodylians, but there are several possibilities. First, it may be that a more limited set of pharyngotympanic sinuses is the ancestral condition for Crocodylomorpha, and thus *Steneosaurus cf. gracilirostris* is exhibiting this morphology because of its relatively basal position in the family tree. Perhaps extensive sinuses evolved in concert with a quadrate that is more firmly sutured to the remainder of the braincase (see discussion in Dufeau and Witmer [2015]), which occurred later in crocodylomorph evolutionary history. Second, it is possible that NHMUK PV OR 33095 evolved from ancestors with a more extensive array of pharyngotympanic sinuses similar to modern crocodylians, but it (and possibly other thalattosuchians) apomorphically lost some of the diverticula. If so, this could potentially be related to lifestyle, perhaps due to changes resulting from the transition to a more aquatic habitat such as increased reliance on diving to catch prey, changes in buoyancy, or alterations to the hearing system. Third, there may be a link with diet, as Dufeau and Witmer (2015) observed that feeding specialists with long snouts and enlarged adductor chambers, like modern gharials, exhibit a reduction in the number and extent of diverticula, whereas feeding generalists, like the extinct *Hamadasuchus*, have more expansive sinuses. Although the functional link between sinus morphology and diet is unclear, it is noteworthy that teleosaurids are gharial-like in morphology, and probably had a similar diet, so this could explain the moderate sinuses. Finally, it may be that NHMUK PV OR 33095 is simply an unusual individual in a species or clade that is rife with variation. This may be unlikely, but we note that modern *Alligator* exhibits more extensive pneumaticity than *Crocodylus* (Witmer et al., 2008; Dufeau and Witmer, 2015). Testing these hypotheses will require CT-based sinus reconstructions for other thalattosuchians and, critically, other basal crocodylomorphs such as “sphenosuchians” that will give insight into the primitive conditions of the clade and variability among closely related taxa.

Vasculature and Salt Glands

Among the most noticeable internal features of NHMUK PV OR 33095 are the enlarged internal carotid and orbital arteries. These two vessels are anatomically linked, as the carotids enter the pituitary fossa posteriorly, and then the orbital arteries emerge from the fossa and continue anteriorly towards the snout. Therefore, the large size of one is probably linked to the enlargement of the other.

Previously, it has been suggested that enlarged internal carotids (as indicated by large foramina on the posterior surface of the braincase) are diagnostic of metriorhynchids, but here we show that they are also present in teleosaurids. Thus, large internal carotids appear to be a thalattosuchian feature. Why are these arteries so large in thalattosuchians? Branches of the internal carotids supply the salt glands in some modern vertebrates, and the large size of the carotids in metriorhynchids has been explained as a mechanism for increasing blood flow to the glands, which are known to

have been present based on CT data (e.g., Herrera et al., 2013) and natural endocasts (Fernández and Gasparini, 2000, 2008). We therefore suggest that these large vessels in NHMUK PV OR 33095 also supplied large salt glands. This can be tested further by CT scanning teleosaurid specimens with more complete snouts, to determine whether the osteological correlates of metriorhynchid salt glands are also present.

Previous studies have considered large salt glands to be a unique adaptation of metriorhynchids among basal crocodylomorphs, an integral component of their transition to a fully marine existence (e.g., Fernández and Gasparini, 2000, 2008; Gandola et al., 2006; Fernández and Herrera, 2009; Herrera et al., 2013). If teleosaurids like *Steneosaurus* cf. *gracilirostris* also possessed large salt glands, this would indicate that the glands evolved first in semiaquatic thalattosuchians that were still well adapted for hearing sounds on land (see above), not just in the fully marine species. Or, perhaps the salt glands evolved even earlier in crocodylomorph phylogeny, in terrestrial taxa, and thus were a “preadaptation” that helped thalattosuchians become so successful in semiaquatic and pelagic niches (see discussion in Wilberg, 2015b). This can be tested by CT scanning a wider range of basal crocodylomorphs to determine if osteological correlates of salt glands are present.

Transition from Semiaquatic to Aquatic Habitats

Teleosaurid thalattosuchians such as *Steneosaurus* cf. *gracilirostris* were semiaquatic animals, closely related to the pelagic metriorhynchids and proxies for the ancestral morphologies and behaviors that were modified as metriorhynchids transitioned into a fully aquatic niche. CT data for NHMUK PV OR 33095 indicate that teleosaurids had already developed several signature cranial features of metriorhynchids, such as a large dorsal dural venous sinus (see also Wharton, 2000), enlarged internal carotids, and potentially a salt gland. Furthermore, in overall morphology, the braincase of *Steneosaurus* cf. *gracilirostris* is remarkably similar to those of metriorhynchids (e.g., Pol and Gasparini, 2009; Fernández et al., 2011). This indicates that there was no great morphological gulf in endocranial anatomy between these two groups of thalattosuchians, and some of the features that later permitted metriorhynchids to successfully invade the aquatic realm were first developed in the semiaquatic teleosaurids and other basal thalattosuchians.

Future work should focus on detailed internal endocranial descriptions of metriorhynchid braincases, using CT data. This will hold the key to determining how other features of the skull and sensory systems were modified as metriorhynchids moved into the open water. Most problematically, little is currently known about the inner ears and pharyngotympanic sinuses of metriorhynchids, so it is unclear whether they shared with NHMUK PV OR 33095 an ear that was still well attuned to hear on land, and if not, when an ear better equipped to function in the water evolved. Similarly, changes in semicircular canal circumference may be expected in metriorhynchids as their heads became increasingly coupled with their bodies as cervical flexibility was lost (reduction to five cervical vertebrae: Andrews, 1913; Wilkinson et al., 2008). It is also uncertain whether metriorhynchids shared with NHMUK

PV OR 33095 the same limited array of pharyngotympanic sinuses relative to modern crocodylians, and if there were detailed differences between the sinus systems of teleosaurids and metriorhynchids that could be explained by the latter’s unusual habitat. As more CT data become available for teleosaurids and metriorhynchids, these thalattosuchians may emerge as something of a model system for understanding how anatomy changes during major evolutionary transitions in deep time.

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