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The braincase and inner ear of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* – implications for aquatic sensory adaptations in crocodylomorphs

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ABSTRACT—During their long evolutionary history crocodylomorphs achieved a great diversity of body sizes, ecomorphotypes and inferred feeding ecologies. One unique group of crocodylomorphs are the thalattosuchians, which lived during the Jurassic and Cretaceous (ca. 191 – 125 Ma). They transitioned from shallow marine species, like teleosauroids into fully pelagic forms with paddle shaped limbs and a vertically orientated tail fluke, the metriorhynchids. The osteological adaptations that allowed metriorhynchids to live in the water are generally well understood, but less is known about their neurosensory and endocranial systems, such as the brain, inner ears, sinuses and cranial nerves and how they were related to their aquatic lifestyle. Based on micro-computed tomography (μCT) data and three-dimensional models we here describe the braincase and endocranial anatomy of a fully marine metriorhynchid, '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617). We found several neuroanatomical features that likely helped this species function in its marine environment. This includes a unique flexure in the brain endocast not seen in other thalattosuchians. Other features that have previously been seen in thalattosuchians include enlarged cerebral hemispheres; a hypertrophied venous sinus system; enlarged internal carotid arteries and foramina; and closed/absent lateral pharyngotympanic foramina. The specimen also possesses a pelagic metriorhynchid bony labyrinth morphology, with a compact and dorsoventrally short shape, thick semicircular canals, an enlarged vestibule and potentially a short cochlear duct. A review of character distribution confirms that some of these features evolved at the base of Thalattosuchia in semiaquatic species, long before metriorhynchids became pelagic, suggesting that endocranial anatomy helped allow metriorhynchoids colonize the ocean realm.

INTRODUCTION

Mesozoic oceans were inhabited by various marine reptiles such as ichthyosaurs, mosasaurs, sauropterygians, and sea turtles. These groups achieved incredible morphofunctional diversity, often being at the top of their respective food chains. To successfully adapt to the marine environments, these reptile groups needed to fundamentally change their anatomy and physiology relative to their terrestrial ancestors, evolving a body plan well suited for life in the open ocean (e.g. Massare, 1988; Motani, 2009; Kelley and Pyenson, 2015; Foffa et al., 2018).

One of these marine reptile groups was Metriorhynchidae, a group of thalattosuchian crocodylomorphs that included the only known obligately aquatic archosaurs (Herrera, 2015; Herrera et al., 2017; Fig. 1). Metriorhynchidae evolved during the Middle Jurassic, and diversified throughout the Jurassic into highly successful marine predators, becoming extinct during the Early Cretaceous (Fraas, 1902; Andrews, 1913; Lepage et al., 2008; Pol and Gasparini, 2009; Young et al., 2010; Larsson et al., 2011; Chiarenza et al., 2015; Herrera and Vennari, 2015; Fernández et al., 2019; Sachs et al., 2020). As they transitioned from semiaquatic basal metriorhynchoids into open-ocean swimming metriorhynchids, their body plan underwent a radical change, evolving paddle-shaped limbs, a hypocercal tail fin, and hypertrophied nasal salt glands, while losing their osteoderms (Fraas, 1902; Andrews, 1913; Fernández and Gasparini, 2008; Young et al., 2010; Wilberg, 2015; Ősi et al., 2018). Osteological modifications in their pelvis suggest that metriorhynchids gave birth to live young (Herrera et al., 2017).

Besides their osteological changes, thalattosuchian sensory systems played an important role in their evolutionary transition, and these systems have only recently become a focus of research. Computed tomography (CT) scans and three-dimensional visualization of internal cranial anatomy has helped us better understand the land-to-sea transition in Thalattosuchia (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018; Schwab et al., 2020). Neuroanatomical and internal cranial features, such as the brain, sinuses, and sensory systems like the inner ear, provide unique insight into how thalattosuchians—and in particular metriorhynchids—adapted to their aquatic environment.

Here we describe the braincase and endocranial anatomy of the Middle Jurassic metriorhynchid '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* from the Vaches Noires cliffs of Normandy (France), based on an isolated but well preserved and, rare for thalattosuchian fossils, uncrushed specimen. CT scanning allows analysis of the brain endocast, inner ear, vasculature, and pneumatic sinuses of this metriorhynchid, which we compare with other extant and extinct crocodylomorphs. This allows us to better understand the morphological and physiological features that allowed these unique crocodylomorphs to adapt to their ocean realm.

Institutional Abbreviations—**FMNH,** Field Museum of Natural History, Chicago, Illinois, USA; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, Beijing, China; **MLP,** Museo de La Plata, La Plata, Argentina; **NHMUK**, Natural History Museum, London, England, United Kingdom.

MATERIALS AND METHODS

Fossil Specimen

The braincase of the basal geosaurine thalattosuchian '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617; Fig. 2) was purchased in 1857 by the British Museum, and now forms part of the Tesson Collection in the Natural History Museum London. The specimen was discovered from the Vaches Noires cliffs of Normandy, France, where late Callovian/early Oxfordian formations are exposed (Brignon, 2016). Although fragmentary, the braincase is relatively well preserved with no evidence of shearing or dorsoventral compression.

While Lydekker (1888:96) initially referred NHMUK PV OR 32617 to *Metriorhynchus superciliosus* (now referred to the genus *Thalattosuchus*; Young et al., 2020), we refer it to '*M.*' cf. '*M.*' *brachyrhynchus*. This is due to (1) the strongly concave supraoccipital that is noticeably inset relative to the occipital surface of the cranium, (2) the pronounced nuchal crest along the midline of the supraoccipital, (3) the basioccipital tuberosities not being proportionally enlarged, (4) and the occipital condyle being as wide mediolaterally as it is high dorsoventrally. These characters match those seen in the English '*M.*' *brachyrhynchus* specimens (NHMUK PV R 3699, NHMUK PV R 3700, NHMUK PV R 3804; Andrews, 1913). The distinctly concave supraoccipital is a readily identifiable character, and it is not seen in the Vaches Noires specimens of *Thalattosuchus superciliosus* or *Suchodus durobrivensis* (see Lepage et al., 2008). Nor is this feature seen in *Maledictosuchus riclaensis* (Parrilla-Bel et al., 2013), *Dakosaurus andiniensis* (Pol and Gasparini, 2009), *D.* cf. *andiniensis* (Herrera and Vennari 2015), *Plesiosuchus manselii* (Young et al., 2012), or *Torvoneustes coryphaeus* (Young et al., 2013). *Purranisaurus potens* also has a concave supraoccipital (Herrera et al., 2015). However, there the concavity is 'open' laterally, being contiguous with the concave dorsal-half of the otoccipital.

Computed Tomography and Visualisation

The braincase of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617) was imaged by means of microfocus Computed Tomography (μCT) at the μ-VIS X-ray Imaging Centre at the University of Southampton, using the custom designed Nikon/Metris dual source high energy microfocus walk-in enclosure system. A 450 kVp source was used, coupled with a 1621 PerkinElmer caesium-iodide detector. Peak voltage was set at 430 kVp and the current at 120 μA. A total of 3142 projections (4 frames per projection) were collected during a 360° rotation, with each projection occurring over an exposure time of 250 ms.

Source to detector and source to object distances were set to 684.0 mm and 186.8 mm respectively, resulting in a radiograph pixel-size of 54.6 μm and a field of view of c. 90 mm x 90 mm. Imaging of the whole specimen (W ≈ 65 mm, D ≈ 85 mm, H ≈ 128 mm) was achieved in two halves as shown in (Fig. S1) allowing for an overlap of approximately 20%. The raw projection data for each scan were reconstructed into 3D volumes (32-bit raw) using an isotropic voxel-size (with an edge length) of 54.6 μm by means of Nikon's reconstruction software (CT Pro 3D, v. XT 2.2 SP10), which uses a filtered back projection algorithm.

The two raw reconstructed volumes were then concatenated using Fiji/ImageJ (Schindelin et al., 2012) matching one of the overlapped slices of bottom and top volumes, to generate a single volume that contained the whole specimen which assured anatomy continuity (Supplementary Video SV1).

To allow for further analysis and segmentation the CT volumes were contrast-enhanced using a custom-made algorithm, which was developed and optimised for this specimen. The script was written in ImageJ macro language (IJ1 Macro), to generate and apply a contrast and edge enhancement filter on a slice-by-slice basis. The macro 1. duplicated the scan volume and run a bandpass filter (parameters: filter_large =15; filter_small=5; source: https://imagej.nih.gov/ij/docs/menus/process.html#fft) on it. It then ran a 3D median filter (2 x 2 x 2 pixel) to improve on signal to noise ratio, followed by an unsharp mask (blur radius = 1 pixel; filter weighting = 0.7). The resulted "filter" volume was then multiplied with the original in 32-bit domain to generate the enhanced "filtered" volume, which was then sampled down to 16-bit to reduce size while maintaining a wide dynamic range (Fig. S2).

The filtered volumes were then further analysed using the software Materialise Mimics 20.0. The lasso tool was used for manual image segmentation of anatomical structures. For structures with minimal shape changes we interpolated between slides. Three dimensional models of the brain cavity, endosseous labyrinth, pneumatic sinuses, cranial nerves, veins, and arteries were created based on those segmentations.

Three dimensional models have been uploaded to Morphosource (https://www.morphosource.org/) and can be accessed here: https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/1209.

RESULTS

External Cranial Anatomy

In our description of the braincase of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617) we do not include the quadrate and squamosal, as they are largely incomplete and not well preserved (Fig. 2, 3).

Frontal—The frontal is largely incomplete, with only the frontal participation to the intertemporal bar, supratemporal fossae and part of the lateral processes present (Fig. 2A, 3A). The left and right elements are fused, with no evidence internally or externally for a midline suture. The frontal contacts the parietal along its posterior margin and the laterosphenoids ventrolaterally. The frontal forms the majority of the anteromedially expanded supratemporal fossae, as in other metriorhynchids (e.g. Andrews, 1913; Young et al., 2013). The preserved part of the frontal is higher on the lateral edge than in the medial part (Fig. 2A, 3A).

Parietal—The parietal is relatively well preserved and is a single fused element with no evidence of an interparietal suture internally or externally. It forms part of the dorsal and posterolateral wall of the braincase, also contributing to the posterior and medial margins of the supratemporal fenestrae. It is a single Y-shaped element, with the anterior process forming the posterior half of the intertemporal bar and the two lateral processes diverge posteriorly, where the supraoccipital fits between them (Fig. 2A, 3A). The parietal bears a sagittal crest, as in most other thalattosuchians (e.g. Andrews, 1913; Young et al., 2013; Brusatte et al., 2016; Herrera et al., 2018). The parietal contacts the frontal along its anterior margin, and within the supratemporal fenestrae along its ventral margin, it contacts laterosphenoid anteroventrally and the prootic posteroventrally (Fig. 2B, 3B). In occipital view, the parietal contacts the otoccipital and the supraoccipital ventrally (Fig. 2C, 3F).

Prootics—The prootics are located on the lateral wall of the braincase and form the posteromedial region of the supratemporal fenestra, as in other thalattosuchians (e.g. Andrews, 1913; Young et al., 2013; Herrera et al., 2018; Fig. 2B, E, 3B, E). Each prootic dorsally contacts the parietal, posteroventrally the quadrate, and anteriorly the laterosphenoid. This subtriangular bone forms part of the dorsal margin of the trigeminal fossa and is broadly visible in dorsal view (Fig. 2A, 3A). The prootic and otoccipital house the cavity of the inner ear internally.

Laterosphenoids—The laterosphenoids form the lateral walls of the braincase (Fig. 2B, E, 3B, E). Internally, they house the cerebral hemispheres. The laterosphenoid forms the anteromedial margin of the supratemporal fenestra. Ventrally, each laterosphenoid contacts the basisphenoid, anterodorsally the frontal, posterodorsally the parietal, and posteriorly the prootic. The laterosphenoid forms the anterior and anteroventral margins of the trigeminal foramen (Fig. 2B, 3B). The trigeminal foramen is bilobate, or hour-glass-shaped, as is the case in metriorhynchids generally (Herrera et al., 2018), differing from the more commonly found circular foramen of other crocodylomorphs. Of the two lobes, the posterodorsal one is smaller than the anteroventral one.

Supraoccipital—The supraoccipital forms the dorsal part of the occipital region of the braincase in posterior view, where it is a singular median bone dorsal to the foramen magnum but does not participate in its margins (Fig. 2C, 3F). It is lateromedially broader than dorsoventrally tall and exhibits two dorsoventrally long grooves, separated by a pronounced nuchal rest running along the midline of the bone. This has been noted previously in the teleosauroid *Plagiophthalmosuchus* cf. *gracilirostris* ('*Steneosaurus'* cf. *gracilirostris* in Brusatte et al., 2016), but in *Cricosaurus araucanensis* the supraoccipital is flat in this region (Herrera et al., 2018). Dorsally the supraoccipital contacts the parietal and ventrolaterally articulates with the otoccipital, with the latter bones excluding the supraoccipital from the foramen magnum. Participation of the supraoccipital in the dorsal margin of the foramen magnum is variable in Thalattosuchia, and most thalattosuchians have a midline otoccipital contact dorsal to the foramen magnum that excludes the supraoccipital. However, Brusatte et al., (2016) suggested that the supraoccipital overlays the otoccipital and this could explain why in some specimens the supraoccipital forms the dorsomedial margin of the foramen magnum.

Otoccipital—The otoccipital is a single element, comprised of the fused exoccipital and opisthotic on either side of the braincase. It contacts the supraoccipital dorsomedially and the parietal along the dorsal margin, lateral to the supraoccipital (Fig. 2C, 3F). Ventromedially it contacts the basioccipital and ventrolaterally the quadrate, but in this specimen the quadrate is largely missing. The otoccipital forms the dorsal and lateral margins of the foramen magnum, which is oval with the major axis mediolaterally oriented. The otoccipital contacts the basioccipital at the dorsolateral corners of the occipital condyle. The paroccipital processes are not preserved in this specimen. The foramen for the cranial nerve XII (hypoglossal foramen) is located on the occipital surface of the braincase ventrolateral to the foramen magnum. It appears to be a single opening as in most other thalattosuchians

(Jouve, 2009; Fernández et al., 2011; Brusatte et al., 2016; Herrera et al., 2018) although the foramen for the second hypoglossal canal might not be preserved in this specimen. The foramina for cranial nerves IX-XI are not preserved in this specimen. The carotid foramen is located ventrolateral to the occipital condyle. It is enlarged as in other thalattosuchians (e.g. Jouve, 2009; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018).

Occipital Condyle—The occipital condyle is round and mediolaterally as wide as dorsolaterally tall (Fig. 2C, 3F). It is mostly formed by the basioccipital centrally and the otoccipital, which forms the left and the right dorsolateral corners. The dorsal margin forms the ventral floor of the foramen magnum. In essence, there is a gap between the two otoccipital corners, which is filled by the basioccipital. This is the case in most other thalattosuchians (Andrews, 1913; Pierce and Benton, 2006; Lepage et al., 2008; Jouve, 2009; Foffa and Young, 2014). In derived geosaurine metriorhynchids such as *Plesiosuchus manselii* (Young et al., 2012) and *Torvoneustes coryphaeus* (Young et al., 2013), however, the otoccipital covers the entire dorsal margin of the occipital condyle, the left and right otoccipitals meet to exclude the basioccipital from the dorsal margin of the condyle, and thus the floor of the foramen magnum.

Basioccipital—The basioccipital, a midline bone, forms the ventromedial portion of occipital region of the braincase, including most of the occipital condyle. In occipital view, it contacts the otoccipital dorsolaterally (Fig. 2C, 3F), and in ventral view, it contacts the basisphenoid anteriorly (Fig. 2D, 3D). It forms the left and right basal tubera, located ventrolateral to the occipital condyle, which extend in the posteroventral direction. Medial to tuberosities is the median pharyngeal foramen (Fig. 2D, 3D).

Basisphenoid—The basisphenoid is partially preserved. In ventral view, the basisphenoid contacts the basioccipital along its posterior margin. The basisphenoid forms the anterior margin of the median pharyngeal foramen (Fig. 2D, 3D). Here the lateral pharyngeal foramina (pharyngotympanic or Eustachian tube) are absent, as in *Cricosaurus araucanensis* and other metriorhynchids (e.g. *Purranisaurus potens*, *Thalattosuchus superciliosus*, supporting the hypothesis that metriorhynchids lacked these foramina, at least in morphologically mature individuals, see Herrera et al., 2018). The basisphenoid is partially visible in occipital view, ventral to basal tubera of the basioccipital (Fig. 2C, 3F). The basisphenoid continues anteriorly as a narrow structure along the midline. The basisphenoid is expected to house the orbital arteries, but the braincase is broken in this region.

Internal Cranial Anatomy

Three-dimensional models of the brain endocast, pneumatic sinuses, bony labyrinth, cranial nerves and vasculature are described in detail below (Figs. 4–7, S3).

Cranial Endocast—The cranial endocast is incomplete due to a break in the anterior part. The break is located in the forebrain region and hence the olfactory tract and bulbs are missing. NHMUK PV OR 32617 shows a concave dorsal curvature in lateral view in the forebrain/midbrain region and it seems that the dorsal surface of the cerebellum forms a dural peak, which might be part of the venous sinus (Fig. 5). Other thalattosuchian brain endocasts have been generally described as elongated, straight and narrow, however *Cricosaurus araucanensis* shows a slight curvature in its forebrain region as well (Wharton, 2000; Fernández et al., 2011; Herrera, 2015; Herrera and Vennari, 2015; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018).Extant crocodylians, in contrast, have greater flexure between the midbrain and hindbrain (cephalic flexure) and between the midbrain and hindbrain (pontine flexure) (Colbert, 1946; Witmer et al., 2008; Dufeau and Witmer, 2015). Outside of Crocodylomorpha, cephalic and pontine flexure has also been found in ornithosuchids, aetosaurs, erpetosuchids and phytosaurs (Baczko and Desojo, 2016; Lautenschlager and Butler, 2016; Baczko et al., 2018; Nesbitt et al., 2018). The cerebrum is enlarged laterally, symmetrical, positioned behind the olfactory tract and is more laterally expanded than in other thalattosuchians (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018). Metriorhynchids generally have larger cerebral hemispheres than teleosauroids and basal metriorhynchoids such as *Pelagosaurus typus* (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018). The optic lobes are positioned posterior to the cerebral region. They are not discrete in modern adult crocodylians but are more defined in juveniles (Dufeau and Witmer, 2015; Brusatte et al., 2016). The cerebellum starts at the level of cranial nerve V and extends to the anterior semicircular canal of the bony labyrinth (Fig. 5B, E). The pituitary fossa is ventral to the midbrain and posteroventral to the cerebrum, and the anterior part is connected to the brain cavity in the region of the cerebrum (Fig. 5B, E). In most other thalattosuchians it is elongated anteroposteriorly and dorsoventrally low (Brusatte et al., 2016; Pierce et al., 2017). In NHMUK PV OR 32617 it appears more bulbous and rounded than in other thalattosuchians. It is positioned parallel to the brain endocast, but in extant crocodylians it is oriented anterodorsally, such that the internal carotid vessels are noticeably ventral to where the orbital vessels would exit anteriorly. The brain endocast is ventrally more bulbous than in other thalattosuchians (Fig. 5D), but this shape also characterises modern crocodylians. The rostral middle cerebral vein forms a ridge at the dorsal region of the brain endocast, in the midbrain region (Fig. 5A–C, D–E). It exits the braincase through the trigeminal foramen, contributing to its hour-glass shape.

Dorsal Dural Venous Sinus—Above the hindbrain, there is a pair of large venous sinuses. They merge with the brain endocast dorsally, between the where cranial nerve V emerges and the anterior semicircular canal of the bony labyrinth (Fig. 5). The sinuses are positioned dorsal to the crus commune of the bony labyrinth, then bend ventrolaterally to exit the braincase through the temporo-orbital foramen. The parietal forms the dorsal, the prootic the ventral and the squamosal the lateral margins of the temporo-orbital foramen, which leads into the supratemporal fenestra. Based on comparisons with extant crocodylians (Porter et al., 2016), this canal would have housed the caudal middle cerebral vein. The hypertrophy of this venous sinus system is present in all other digitally segmented and natural endocasts of thalattosuchians (Fernández et al., 2011; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018), and is never seen in this hypertrophied form in modern crocodylians (Witmer et al., 2008; Dufeau and Witmer, 2015).

Pneumatic Sinuses—The braincase of NHMUK PV OR 32617 is pneumatized, with internal air sinuses surrounding the brain endocast (Fig. 4, S3). Those sinuses can be divided into two main systems (following Dufeau and Witmer, 2015): (1) the median pharyngeal sinus system ventral to the brain endocast and (2) the pharyngotympanic sinus system lateral to the endocast.

The median pharyngeal sinus is located within the basisphenoid. It enters the braincase at the posteroventral external surface at the median pharyngeal foramen, which is located ventral to the foramen magnum, between the basioccipital and the basisphenoid (Fig. 4B, E). The median pharyngeal sinus tube then extends anteriorly and connects to the pharyngotympanic sinus system via two laterally diverging canals. The median pharyngeal sinus diverticulum is a midline structure extending anteroventrally from the basisphenoid of the median pharyngeal sinus in the anteroventral direction, as in *Plagiophthalmosuchus* cf. *gracilirostris* (Brusatte et al., 2016).

The pharyngotympanic sinus is the more extensive system, being located lateral to the brain endocast and connected to the median pharyngeal sinus. It is less extensive compared to teleosauroids (Brusatte et al., 2016; Herrera et al., 2018) and the basal metriorhynchoid *Pelagosaurus typus* (Pierce et al., 2017). This sinus system has been divided into eight main diverticula in the modern crocodylian species *Alligator mississippiensis* (Dufeau and Witmer, 2015). The basioccipital diverticulum is absent in NHMUK PV OR 32617 but has been reported in the teleosauroid *Macrospondylus bollensis* and the basal metriorhynchoid *Pelagosaurus typus* (Pierce et al., 2017; *Steneosaurus bollensis* in Herrera et al., 2018). The recessus epitubaricum is absent in the specimen described here, as in most other thalattosuchians. Ventral to the brain endocast, at the base of the pharyngotympanic sinus, the pterygoid diverticulum is located anteriorly (Fig. 4B). This diverticulum seems to be absent, or at least highly reduced, in most other thalattosuchians but might be present in *Macrospondylus bollensis* (Herrera et al., 2018), however it is worth noting that due to its small size this might be a segmentation error or a resolution issue. The intertympanic diverticulum and the parietal diverticulum are absent here, as in all other thalattosuchians. It has been debated, whether the prootic diverticulum is present in thalattosuchians. It has been reported in *Plagiophthalmosuchus* cf. *gracilirostris* and *Pelagosaurus typus* (Brusatte et al., 2016; Pierce et al., 2017), but suggested to be absent in thalattosuchians by Herrera et al. (2018) due to its position and forming an isolated recess in modern crocodylians (Dufeau and Witmer, 2015). Laterally the pharyngotympanic sinus system is incomplete due to the absence of the squamosal and quadrate, and hence a potential suspensorium diverticulum is not preserved, as it is in more complete specimens like those of *Cricosaurus araucanensis* and *Pelagosaurus typus* (Pierce et al., 2017; Herrera et al., 2018). The pharyngotympanic sinus is divided at its posterior end into two diverticula, the otoccipital diverticulum dorsally and the pharyngotympanic (Eustachian) tubes ventrally (Fig. 4B, E).

Endosseous Labyrinth—The endosseous labyrinth resembles those of other metriorhynchids, as it has a dorsoventrally short and compact appearance with thick canal cross-sectional diameters, which has been associated with their pelagic lifestyle (Schwab et al., 2020; Fig. 6). This differs from the dorsoventrally taller labyrinths, with thinner canals, that are present in semiaquatic and terrestrial crocodylomorphs. The right labyrinth is completely preserved, including all three semicircular canals, the vestibule and the cochlear duct. The left labyrinth, however, is difficult to trace in the CT scan and hence we did not include it here. The endosseous labyrinth of NHMUK PV OR 32617 has an overall triangular appearance and the canal region takes the form of an ‘M’ shape from the anterior to the posterior canal, as seen in most crocodylians (Brusatte et al., 2016). The anterior canal extends slightly higher dorsally than the posterior one and is oval shaped, whereas the posterior canal is more triangular. The lateral semicircular canal is the smallest. All three semicircular canals are more or less perpendicular to each other, and the crus commune is slightly bent anteriorly and short. The anterior ampulla appears to be larger than in most other crocodylomorphs (Schwab et al., 2020). The vestibule does not dorsally expand beyond the lateral canal. No columellae or endolymphatic ducts are preserved. The cochlear duct (lagena) projects straight ventrally in lateral view and is relatively short. Metriorhynchids generally have shorter cochlear ducts than other crocodylomorphs (Schwab et al., 2020), but, due to the fact that the end of the lagena is not fully enclosed by bone, as in most archosaur clades (Evers et al., 2019), this is just the minimum cochlear duct length.

Cranial Nerves—Canals for cranial nerves (CN) V (trigeminal), VI (abducens), and XII (hypoglossal) were recognized and reconstructed (Fig. 5). Usually they are most discernible close to the brain endocast or external braincase surface. Due to the missing anterior part of the braincase, CN I (olfactory), CN II (optic), and CN III (oculomotor) are missing, and the CN IV (trochlear), CN VII (facial) and CN VIII (vestibulocochlear) cannot be traced in the scan but could have potentially shared a canal with other cranial nerves. The largest of the nerves is the CN V. It is positioned at the lateral surface of the midbrain, posterior to cerebrum/optic lobes. Other crocodylomorphs also exhibit a large trigeminal ganglion in this position (e.g., Dufeau and Witmer, 2015; Brusatte et al., 2016). The trigeminal fossa is generally very large in metriorhynchids, but due to the lack of the quadrate it is difficult to interpret its exact size and shape in the specimen described here (e.g.

Fernández et al., 2011; Herrera et al., 2018). The canals of CN VI are positioned lateral to the pituitary fossa, ventral to CN V, and pass in an anteroventral direction. CN XII is paired and exits the posterior surface of the braincase, laterally to the foramen magnum. Following anteriorly from its external foramen, it meets the endocast posteroventrally to the ampulla of the posterior semicircular canal of the bony labyrinth. A left second hypoglossal canal is present (with the right one not being preserved in this specimen) and can easily be seen at the posterior surface of the braincase, ventrolateral to the foramen magnum in the anterior direction.

Vasculature—The internal carotid canals were completely visible and reconstructed in the scan (Fig. 5). These hypertrophied canals enter at the posterior surface of the braincase, ventrolateral to the foramen magnum in occipital view. Anteriorly from their exit foramina, the internal carotid canals are visible through the entire scan and contacting the pharyngotympanic sinus. Having the internal carotids pass through the pharyngotympanic sinus has only been reported previously for metriorhynchids in *Cricosaurus araucanensis* previously (Herrera et al., 2018), but modern crocodylians (Dufeau and Witmer, 2015) and non-metriorhynchoid thalattosuchians (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018) also have the medial portion of these canals pass through the pharyngotympanic sinus. The internal carotid canals run parallel to the brain until the cochlear duct where they turn in a ventromedial direction. The canals then pass over into the upper posterior end of the pituitary fossa, with the left and right canals entering the fossa through a single midline foramen. However, in most other thalattosuchians (Fernández et al., 2011; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018) and modern crocodylians (Dufeau and Witmer, 2015) the carotid canals enter the pituitary fossa through two separate foramina anteriorly. The orbital vessels are not preserved due to the break in the braincase but, it seems that the orbital canals exit the pituitary fossa through two separate foramina (Fig. 5B, D). This is the case for other thalattosuchians, which like NHMUK PV OR 32617, have hypertrophied orbital arteries, similar in dimension to the internal carotid canals (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018).

DISCUSSION

Braincase

One of the most notable features of the braincase of NHMUK PV OR 32617 is the unique shape of the brain endocast (Fig. 5). Thalattosuchians are generally characterised by a straight endocast (Herrera, 2015; Herrera and Vennari, 2015; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018). Most extinct and extant crocodylomorphs have a flexure in their mid/hindbrain region (Colbert, 1946; Witmer et al., 2008; Kley et al., 2010; Leardi et al., 2017). NHMUK PV OR 32617, however, is unique in having a pronounced brain flexure in the forebrain/midbrain region and a curved dorsal margin. This flexure may be present in *C. araucanensis*, albeit in a less pronounced manner, and therefore could be a unique characteristic of metriorhynchids. Previously there have been two ideas proposed for why thalattosuchians lack the brain flexures (Herrera et al., 2018). First, most thalattosuchians are characterised by a long tubular snout, with a very flat transition between the skull roof and the snout. Another proposed explanation is that the extended dorsal venous sinus hides the midbrain/hindbrain flexure. However, this does not explain the unusual kinked brain morphology of NHMUK PV OR 32617, where there is no evidence for particularly large sinuses dorsal to the forebrain/midbrain region, yet it is still obviously flexed. One other interesting feature of the NHMUK PV OR 32617 brain endocast is that the pituitary fossa is more bulbous and round compared to other thalattosuchians (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018). Reptilian pituitary glands are correlated with water metabolism (Heller, 1942, 1950) and hence an enlarged pituitary fossa in thalattosuchians might be correlated with their water regulation to prevent dehydration (Pierce et al., 2017). An alternative hypothesis is that the pituitary fossa was enlarged due to hypertrophy of the cavernous sinus, as the cavernous sinus is located within the pituitary fossa in extant crocodylians (see Porter et al., 2016). Given the hypertrophy of the transverse sinus and stapedial canals in thalattosuchians (Fernández et al., 2011; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018), hypertrophy of the cavernous sinus would not be unexpected.

The cerebral hemispheres appear enlarged, as in other metriorhynchids (Herrera et al., 2018). In birds, enlarged cerebral hemispheres have been interpreted as an adaptation to process increased sensory inputs, and to coordinate increasingly complex behaviours (Rogers, 1999; Walsh and Milner, 2011; Balanoff et al., 2013). The enlarged cerebral hemispheres in NHMUK PV OR 32617 and other metriorhynchids could be linked to the pelagic lifestyle, as these animals had to deal with more complex body movements and a greater sensory input than terrestrial and semiaquatic relatives, because they lived and moved in a three-dimensional environment.

It should also be noted that the brain endocast does not accurately represent the actual brain morphology. The brain does not fill the entire endocranial cavity in crocodylomorphs, as parts of the brain are covered by overlaying venous sinuses (Hopson, 1979). Hence the brain endocast does not perfectly mirror the actual brain, which results in size and shape differences between the endocast and brain (the latter of which is not preserved in fossils, so we can never assess the quality of the match). However, it has been demonstrated that the difference between the actual brain and the endocast in alligators is comparable with intraspecific variation in brain shape and therefore endocasts can be used for large scale studies of brain morphology in archosaurs (Watanabe et al., 2019). In fossils it is challenging to study the actual neural organs as preservation allows us to study only their preserved bony cavities. However, some parts of the endocast more adequately reflect the actual size and shape of their corresponding brain structures, such as the olfactory bulbs and the cerebral hemispheres, whereas the hindbrain region does not show the same correspondence (Witmer et al., 2008; Watanabe et al., 2019). Thus, we are confident that the enlarged cerebral hemispheres that we note in NHMUK PV OR 32617 and other metriorhynchids is a genuine feature.

‘*Metriorhynchus*’ cf. ‘*M.*’ *brachyrhynchus* has the thalattosuchian synapomorphy of enlarged internal carotid canals and foramina (Pol and Gasparini, 2009; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018). It was suggested for metriorhynchids that the enlargement of the internal carotid canals and foramina indicates an increase in blood flow to salt glands (Herrera et al., 2013). Subsequently, based on CT scans of the teleosauroid *Plagiophthalmosuchus* cf. *gracilirostris*, Brusatte et al. (2016) hypothesised that the enlarged cerebral carotid arteries also supplied large nasal salt glands in this taxon. Thalattosuchians also evolved a hypertrophied venous sinus system. Based on the blood flow patterns of extant species (Porter et al., 2016), thalattosuchians would have had far greater blood flow entering and exiting the orbital and nasal regions. This corresponds to both their proportionally large orbits and salt glands, and hints that the salt glands evolved at the base of Thalattosuchia (Brusatte et al., 2016). It has been hypothesized that this enhanced blood supply was related to thermoregulation, as larger arteries can carry a larger amount of blood, which could then be used for heat exchange (Herrera et al., 2018; Porter et al., 2019). This could be linked to the hypothesis that metriorhynchids possibly evolved a non-homeothermic form of endothermy as an adaptation to active pelagic hunting (Séon et al., 2020).

Another interesting feature is that the lateral pharyngeal foramina are closed/absent in this specimen, as in most metriorhynchids (*Cricosaurus araucanensis*; the metriorhynchid specimen from Mörnsheim Formation (BSPG 1973 I195); *Purranisaurus potens*;

Thalattosuchus superciliosus; '*Metriorhynchus*' *westermanni*; see Herrera et al., 2018), while non-metriorhynchid thalattosuchians retain the plesiomorphic condition of having these foramina. The closure of these foramina would have limited the communication between the middle ear cavities and the pharynx to just the median pharyngeal foramen (Herrera et al., 2018). Loss of the lateral pharyngeal (Eustachian) foramina is significant in that the pharyngotympanic (Eustachian) tube is a highly conserved attribute that arises embryonically from the first pharyngeal pouch. In other tetrapods, this communication is used to equalize pressure of the middle ear and the surrounding environment, and hence losing the lateral plesiomorphic connection, leaving only the novel median connection, could be a physiological adaptation to the pelagic lifestyle.

Vestibular System

The vestibular system of the inner ear is the sensory system involved in balance and equilibrium (Sipla and Spoor, 2008). It is furthermore involved in important functions relating to environment such as head and gaze stabilization during body movements. For secondarily aquatic animals, such as metriorhynchids, the environment puts different demands on the vestibular system than is the case with their terrestrial relatives. Unlike in most terrestrial settings locomotion in an aquatic environment offers movements in all three dimensions of space. To adapt to such new environments, their body plan needs to change. Metriorhynchids, for example evolved flippers and lost their osteoderms to allow the animal more flexible body movements and possibly axial undulation (Massare, 1988). Strong buoyancy forces reduce the effects of weight and allow more complex body movements in a highly viscous aquatic medium and are some of the factors that might influence morphological changes in the labyrinth organ in a variety of secondarily aquatic vertebrates. Pelagic sauropterygians and sea turtles have more bulbous labyrinths with thicker semicircular canals than other reptiles (Georgi and Sipla, 2008; Neenan et al., 2017; Evers et al., 2019), cetaceans miniaturized their labyrinth drastically compared to their body size (Spoor et al., 2002), and other aquatic mammals such as sirenians and seals also reduced their semicircular canals but to a lesser degree (Hyrtl, 1845; Loza et al., 2017). Hence it is clear that specific aspects of their labyrinth morphologies convergently evolved in independent pelagic lineages.

In crocodylomorphs three different labyrinth morphologies have been recognized, each of which is characteristic of a particular habitat: terrestrial, semiaquatic, and pelagic (Schwab et al., 2020; Fig. 7). Schwab et al. (2020) used statistical tests to demonstrate the existence of distinctive ear morphologies for these three habitat categories, but only briefly described and figured representative inner ears of each type. We here describe and figure them in more detail (Fig. 7).

The terrestrial morphology is present in early crocodylomorphs, such as sphenosuchian-grade taxa like *Junggarsuchus sloani* (Fig. 7A-D). It is characterised by very long, thin and round semicircular canals and a thin crus commune. The anterior and posterior canals embay the characteristic 'M' shape and the anterior canal extends higher dorsally. The cochlear duct is relatively long compared to the rest of the labyrinth and medially bends in *Junggarsuchus sloani*, but is straight in other non-crocodyliform crocodylomorphs.

The semiaquatic labyrinth morphology is seen in modern crocodylians as well as non-metriorhynchid thalattosuchians like teleosauroids. This labyrinth morphology is an intermediate form with thicker semicircular canals and wider crus commune, and it is overall dorsoventrally shorter than in the terrestrial forms (Fig. 7E-H, M-P). Non-metriorhynchid thalattosuchians have a reduced curvature and triangular shaped semicircular canals compared to modern crocodylians, where the curvature appears more rounded and the overall canal is oval in cross section. Teleosauroids have the 'M' shape which is mostly lost in modern crocodylians. The cochlear duct is straight and shorter than in the terrestrial morphology, but longer than in the pelagic one. Modern crocodylians have a twisted cochlear duct.

The third labyrinth morphology is seen in pelagic taxa, including the NHMUK PV OR 32617 specimen that we describe here. This unique labyrinth morphology is present in all sampled metriorhynchids and characterised by a dorsoventrally compact labyrinth, thick semicircular canals, an enlarged vestibule and a presumably short cochlear duct (the end of the cochlear duct is not enclosed by bone and hence just a minimum length can be estimated). This morphology is most extreme in the derived metriorhynchids, like *Cricosaurus* (Fig. 7I-L) and *Torvoneustes*. The canals have more pronounced curvature compared to non-metriorhynchid thalattosuchians and the anterior ampulla is more bulbous. Unlike the terrestrial and semiaquatic labyrinths, the anterior canal of the pelagic labyrinths becomes smaller and just slightly exceeds the posterior canal dorsally.

One possible explanation for the change in morphology in the labyrinths of pelagic species (which evolved from semiaquatic ancestors) is their wider range of body movements in a three-dimensional aquatic context, not simply because they lived in the water. For example, cetaceans are highly agile and reduced their semicircular canals, however sirenians (manatees and dugongs) are also fully aquatic but are not very agile and hence do not have reduced canals (Ekdale, 2013). The reduced cetacean semicircular canals may also prevent overstimulation during exaggerated head movements associated with swimming and diving, as it is generally assumed that longer and more arching semicircular canals are more sensitive to rotations in space (Spoor et al., 2002; Ekdale, 2016). This could also be the case for marine reptiles such as metriorhynchids. Another explanation could be that because of neck shortening in metriorhynchids (they had five instead of seven postaxial cervical vertebrae; Andrews, 1913; Young and Andrade, 2009) head and gaze stabilization (vestibulo-ocular and vestibulo-collic reflexes) became less important, which resulted in a reduction of the semicircular canals, as has been suggested for cetaceans and plesiosaurs (Spoor et al., 2002; Neenan et al., 2017). A third hypothesis for the morphological shift seen in pelagic labyrinths relates to diving. Thickening of the semicircular canals could have been driven by either an increased membranous duct diameter or an increased perilymphatic space (space between the membranous and bony labyrinth, filled with perilymphatic fluid). Diving results in changes in hydrostatic pressure, which must be compensated for via fluid movement within the perilymphatic duct system. Thicker canals could have increased the perilymphatic space and functioned as a buffer to protect the sensory system. This hypothesis has been proposed for pelagic deep diving turtles (Evers et al., 2019). Hence, the change in morphology could have been a response to changing sensory requirements as secondarily aquatic vertebrates, such as metriorhynchids, moved into deeper, more open waters.

CONCLUSION

Our computed tomography (CT) study of the braincase of the marine thalattosuchian '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* provides one of the best looks yet at the neurosensory system and internal cranial anatomy of a fully aquatic, pelagic, fast-swimming metriorhynchid. Key neuroanatomical features described herein include a unique flexure in the brain endocast that has not been noted in other thalattosuchians or marine reptiles, the function of which is currently unknown. NHMUK PV OR 32617 also had enlarged cerebral hemispheres to potentially process increased sensory input and a more rounded pituitary fossa that could be related to water regulation in the ocean or housed an enlarged venous sinus. The well-developed vasculature system noted here has previously been reported for other metriorhynchids as well as basal thalattosuchians, suggesting it evolved early in thalattosuchian history. Whether it functioned to support salt glands and/or for aide thermoregulation is currently unclear. Furthermore, a pelagic bony labyrinth morphology is present, with an overall dorsoventrally short morphology, thick semicircular canals and an enlarged vestibule. This might have allowed the animal to better interact with its three dimensional aquatic environment, it may have helped with pressure changes during diving or might be due to reduced neck and head and gaze stabilisation. These new insights into the endocranial evolution of thalattosuchians allow us to better understand their transition into the open oceans. Some of these features (e.g., salt glands) seem to have evolved prior to metriorhynchids becoming fully pelagic, and were thus 'exaptations' that helped transition them to life in the water, whereas others (e.g., pelagic labyrinth morphology) apparently developed only after metriorhynchids moved into the open oceans.

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FIGURE CAPTIONS

FIGURE 1. Phylogenetic relationships of crocodylomorphs with ‘*Metriorhynchus*’ cf. ‘*M.*’ *brachyrhynchus* (NHMUK PV OR 32617) in blue. Phylogeny based on Young et al. (2020). Size (182x125mm)

FIGURE 2. Photographs and line drawing of the braincase of ‘*Metriorhynchus*’ cf. ‘*M.*’ *brachyrhynchus* (NHMUK PV OR 32617). **A**, dorsal; **B**, right lateral; **C**, posterior; **D**, ventral; **E**, left lateral. **Abbreviations: bo**, basioccipital; **bs**, basisphenoid; **cf**, carotid

foramen; **fm**, foramen magnum; **fr**, frontal; **ls**, laterosphenoid; **mpf**, median pharyngeal foramen; **oc**, occipital condyle; **ot**, otoccipital; **pa**, parietal; **pro**, prootic; **so**, supraoccipital; **tof**, temporo-orbital foramen. Roman numerals designate cranial nerve openings. Roman numerals designate cranial nerves. Scale bar equals 5cm. Size (182x100mm)

FIGURE 3. Digital reconstruction of the braincase of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617). **A**, dorsal; **B**, right lateral; **C**, anterior; **D**, ventral; **E**, left lateral; **F**, posterior. **Abbreviations: bo**, basioccipital; **bs**, basisphenoid; **cf**, carotid foramen; **fm**, foramen magnum; **fr**, frontal; **ls**, laterosphenoid; **mpf**, median pharyngeal foramen; **oc**, occipital condyle; **ot**, otoccipital; **pa**, parietal; **pro**, prootic; **so**, supraoccipital; **tof**, temporo-orbital foramen. Roman numerals designate cranial nerve openings. Scale bar equals 5cm. Size (182x106.17mm)

FIGURE 4. Internal endocranial anatomy of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617). **A**, dorsal; **B**, right lateral; **C**, anterior; **D**, ventral; **E**, left lateral; **F**, posterior. **Abbreviations: bl**, bony labyrinth; **cer**, cerebrum; **dvs**, dural venous sinus; **ic**, internal carotid artery; **mps**, median pharyngeal sinus; **mpt**, median pharyngeal tube; **mpsd**, median pharyngeal sinus diverticulum; **otd**, otoccipital diverticulum; **pf**, pituitary fossa; **ptd**, pterygoid diverticulum; **pts**, pharyngotympanic sinus; **ptt**, pharyngotympanic tubes; **shc**, second hypoglossal canal. Roman numerals designate cranial nerves. Scale bar equals 5cm. Size (182x112mm)

FIGURE 5. Internal endocranial anatomy of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617). **A**, dorsal; **B**, right lateral; **C**, anterior; **D**, ventral; **E**, left lateral; **F**, posterior. **Abbreviations: bl**, bony labyrinth; **cer**, cerebrum; **dvs**, dural venous sinus; **ic**,

internal carotid artery; **oa**, orbital artery; **pf**, pituitary fossa; **rmcv**, rostral middle cerebral vein; **shc**, second hypoglossal canal. Roman numerals designate cranial nerves. Scale bar equals 5cm. Size (182x112mm)

FIGURE 6. Right bony labyrinth of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* (NHMUK PV OR 32617). **A**, lateral; **B**, medial; **C**, anterior; **D**, posterior; **E**, dorsal. **Abbreviations: asc**, anterior semicircular canal; **cc**, crus commune; **cd**, cochlear duct; **lsc**, lateral semicircular canal; **psc**, posterior semicircular canal; **ve**, vestibule. Scale bar equals 1cm. Size (182x54.61mm)

FIGURE 7. Comparative right bony labyrinths. **A-D**, *Junggarsuchus sloani* (IVPP V14010); **E-H**, *Osteolaemus tetraspis* (FMNH 98936); **I-L**, *Cricosaurus araucanensis* (MLP 72-IV-7-1); **M-P**, *Plagiophthalmosuchus* cf. *gracilirostris* (NHMUK PV OR 33095). Orientations of the labyrinths are lateral, anterior, posterior and dorsal from left to right. Coloured boxes indicate habitat, red, terrestrial; orange, semiaquatic; blue, pelagic. Scale bars equal 1cm. Size (182x90mm)