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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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Running head instruction:

Schwab et al. —Braincase and inner ear of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus*

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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

125 and the current at 120 µA. A total of 3142 projections (4 frames per projection) were
126 collected during a 360° rotation, with each projection occurring over an exposure time of
127 250 ms.

128 Source to detector and source to object distances were set to 684.0 mm and 186.8 mm
129 respectively, resulting in a radiograph pixel-size of 54.6 µm and a field of view of c. 90 mm x
130 90 mm. Imaging of the whole specimen (W ≈ 65 mm, D ≈ 85 mm, H ≈ 128 mm) was
131 achieved in two halves as shown in (Fig. S1) allowing for an overlap of approximately 20%.
132 The raw projection data for each scan were reconstructed into 3D volumes (32-bit raw) using
133 an isotropic voxel-size (with an edge length) of 54.6 µm by means of Nikon's reconstruction
134 software (CT Pro 3D, v. XT 2.2 SP10), which uses a filtered back projection algorithm.

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

139 To allow for further analysis and segmentation the CT volumes were contrast-
140 enhanced using a custom-made algorithm, which was developed and optimised for this
141 specimen. The script was written in ImageJ macro language (IJ1 Macro), to generate and
142 apply a contrast and edge enhancement filter on a slice-by-slice basis. The macro 1.
143 duplicated the scan volume and run a bandpass filter (parameters: filter_large =15;
144 filter_small=5; source: https://imagej.nih.gov/ij/docs/menus/process.html#fft) on it. It then
145 ran a 3D median filter (2 x 2 x 2 pixel) to improve on signal to noise ratio, followed by an
146 unsharp mask (blur radius = 1 pixel; filter weighting = 0.7). The resulted "filter" volume was
147 then multiplied with the original in 32-bit domain to generate the enhanced "filtered" volume,
148 which was then sampled down to 16-bit to reduce size while maintaining a wide dynamic
149 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

175 posterolateral wall of the braincase, also contributing to the posterior and medial margins of
176 the supratemporal fenestrae. It is a single Y-shaped element, with the anterior process
177 forming the posterior half of the intertemporal bar and the two lateral processes diverge
178 posteriorly, where the supraoccipital fits between them (Fig. 2A, 3A). The parietal bears a
179 sagittal crest, as in most other thalattosuchians (e.g. Andrews, 1913; Young et al., 2013;
180 Brusatte et al., 2016; Herrera et al., 2018). The parietal contacts the frontal along its anterior
181 margin, and within the supratemporal fenestrae along its ventral margin, it contacts
182 laterosphenoid anteroventrally and the prootic posteroventrally (Fig. 2B, 3B). In occipital
183 view, the parietal contacts the otoccipital and the supraoccipital ventrally (Fig. 2C, 3F).

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

191 **Laterosphenoids**—The laterosphenoids form the lateral walls of the braincase (Fig.
192 2B, E, 3B, E). Internally, they house the cerebral hemispheres. The laterosphenoid forms the
193 anteromedial margin of the supratemporal fenestra. Ventrally, each laterosphenoid contacts
194 the basisphenoid, anterodorsally the frontal, posterodorsally the parietal, and posteriorly the
195 prootic. The laterosphenoid forms the anterior and anteroventral margins of the trigeminal
196 foramen (Fig. 2B, 3B). The trigeminal foramen is bilobate, or hour-glass-shaped, as is the
197 case in metriorhynchids generally (Herrera et al., 2018), differing from the more commonly
198 found circular foramen of other crocodylomorphs. Of the two lobes, the posterodorsal one is
199 smaller than the anteroventral one.

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

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

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

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

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

247 **Basisphenoid**—The basisphenoid is partially preserved. In ventral view, the
248 basisphenoid contacts the basioccipital along its posterior margin. The basisphenoid forms
249 the anterior margin of the median pharyngeal foramen (Fig. 2D, 3D). Here the lateral

250 pharyngeal foramina (pharyngotympanic or Eustachian tube) are absent, as in *Cricosaurus*
251 *araucanensis* and other metriorhynchids (e.g. *Purranisaurus potens*, *Thalattosuchus*
252 *superciliosus*, supporting the hypothesis that metriorhynchids lacked these foramina, at least
253 in morphologically mature individuals, see Herrera et al., 2018). The basisphenoid is partially
254 visible in occipital view, ventral to basal tubera of the basioccipital (Fig. 2C, 3F). The
255 basisphenoid continues anteriorly as a narrow structure along the midline. The basisphenoid
256 is expected to house the orbital arteries, but the braincase is broken in this region.
257
258 **Internal Cranial Anatomy**
259 Three-dimensional models of the brain endocast, pneumatic sinuses, bony labyrinth,
260 cranial nerves and vasculature are described in detail below (Figs. 4–7, S3).
261 **Cranial Endocast**—The cranial endocast is incomplete due to a break in the anterior
262 part. The break is located in the forebrain region and hence the olfactory tract and bulbs are
263 missing. NHMUK PV OR 32617 shows a concave dorsal curvature in lateral view in the
264 forebrain/midbrain region and it seems that the dorsal surface of the cerebellum forms a dural
265 peak, which might be part of the venous sinus (Fig. 5). Other thalattosuchian brain endocasts
266 have been generally described as elongated, straight and narrow, however *Cricosaurus*
267 *araucanensis* shows a slight curvature in its forebrain region as well (Wharton, 2000;
268 Fernández et al., 2011; Herrera, 2015; Herrera and Vennari, 2015; Brusatte et al., 2016;
269 Pierce et al., 2017; Herrera et al., 2018).Extant crocodylians, in contrast, have greater flexure
270 between the midbrain and hindbrain (cephalic flexure) and between the midbrain and
271 hindbrain (pontine flexure) (Colbert, 1946; Witmer et al., 2008; Dufeau and Witmer, 2015).
272 Outside of Crocodylomorpha, cephalic and pontine flexure has also been found in
273 ornithosuchids, aetosaurs, erpetosuchids and phytosaurs (Baczko and Desojo, 2016;
274 Lautenschlager and Butler, 2016; Baczko et al., 2018; Nesbitt et al., 2018). The cerebrum is

275 enlarged laterally, symmetrical, positioned behind the olfactory tract and is more laterally
276 expanded than in other thalattosuchians (Brusatte et al., 2016; Pierce et al., 2017; Herrera et
277 al., 2018). Metriorhynchids generally have larger cerebral hemispheres than teleosauroids and
278 basal metriorhynchoids such as *Pelagosaurus typus* (Brusatte et al., 2016; Pierce et al., 2017;
279 Herrera et al., 2018). The optic lobes are positioned posterior to the cerebral region. They are
280 not discrete in modern adult crocodylians but are more defined in juveniles (Dufeau and
281 Witmer, 2015; Brusatte et al., 2016). The cerebellum starts at the level of cranial nerve V and
282 extends to the anterior semicircular canal of the bony labyrinth (Fig. 5B, E). The pituitary
283 fossa is ventral to the midbrain and posteroventral to the cerebrum, and the anterior part is
284 connected to the brain cavity in the region of the cerebrum (Fig. 5B, E). In most other
285 thalattosuchians it is elongated anteroposteriorly and dorsoventrally low (Brusatte et al.,
286 2016; Pierce et al., 2017). In NHMUK PV OR 32617 it appears more bulbous and rounded
287 than in other thalattosuchians. It is positioned parallel to the brain endocast, but in extant
288 crocodylians it is oriented anterodorsally, such that the internal carotid vessels are noticeably
289 ventral to where the orbital vessels would exit anteriorly. The brain endocast is ventrally
290 more bulbous than in other thalattosuchians (Fig. 5D), but this shape also characterises
291 modern crocodylians. The rostral middle cerebral vein forms a ridge at the dorsal region of
292 the brain endocast, in the midbrain region (Fig. 5A–C, D–E). It exits the braincase through
293 the trigeminal foramen, contributing to its hour-glass shape.

294 **Dorsal Dural Venous Sinus**—Above the hindbrain, there is a pair of large venous
295 sinuses. They merge with the brain endocast dorsally, between the where cranial nerve V
296 emerges and the anterior semicircular canal of the bony labyrinth (Fig. 5). The sinuses are
297 positioned dorsal to the crus commune of the bony labyrinth, then bend ventrolaterally to exit
298 the braincase through the temporo-orbital foramen. The parietal forms the dorsal, the prootic
299 the ventral and the squamosal the lateral margins of the temporo-orbital foramen, which leads

300 into the supratemporal fenestra. Based on comparisons with extant crocodylians (Porter et al.,
301 2016), this canal would have housed the caudal middle cerebral vein. The hypertrophy of this
302 venous sinus system is present in all other digitally segmented and natural endocasts of
303 thalattosuchians (Fernández et al., 2011; Brusatte et al., 2016; Pierce et al., 2017; Herrera et
304 al., 2018), and is never seen in this hypertrophied form in modern crocodylians (Witmer et
305 al., 2008; Dufeau and Witmer, 2015).

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

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

319 The pharyngotympanic sinus is the more extensive system, being located lateral to the
320 brain endocast and connected to the median pharyngeal sinus. It is less extensive compared to
321 teleosauroids (Brusatte et al., 2016; Herrera et al., 2018) and the basal metriorhynchoid
322 *Pelagosaurus typus* (Pierce et al., 2017). This sinus system has been divided into eight main
323 diverticula in the modern crocodylian species *Alligator mississippiensis* (Dufeau and Witmer,
324 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.

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

383 **Vasculature**—The internal carotid canals were completely visible and reconstructed in
384 the scan (Fig. 5). These hypertrophied canals enter at the posterior surface of the braincase,
385 ventrolateral to the foramen magnum in occipital view. Anteriorly from their exit foramina,
386 the internal carotid canals are visible through the entire scan and contacting the
387 pharyngotympanic sinus. Having the internal carotids pass through the pharyngotympanic
388 sinus has only been reported previously for metriorhynchids in *Cricosaurus araucanensis*
389 previously (Herrera et al., 2018), but modern crocodylians (Dufeau and Witmer, 2015) and
390 non-metriorhynchoid thalattosuchians (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al.,
391 2018) also have the medial portion of these canals pass through the pharyngotympanic sinus.
392 The internal carotid canals run parallel to the brain until the cochlear duct where they turn in
393 a ventromedial direction. The canals then pass over into the upper posterior end of the
394 pituitary fossa, with the left and right canals entering the fossa through a single midline
395 foramen. However, in most other thalattosuchians (Fernández et al., 2011; Brusatte et al.,
396 2016; Pierce et al., 2017; Herrera et al., 2018) and modern crocodylians (Dufeau and Witmer,
397 2015) the carotid canals enter the pituitary fossa through two separate foramina anteriorly.
398 The orbital vessels are not preserved due to the break in the braincase but, it seems that the
399 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

425 metabolism (Heller, 1942, 1950) and hence an enlarged pituitary fossa in thalattosuchians
426 might be correlated with their water regulation to prevent dehydration (Pierce et al., 2017).
427 An alternative hypothesis is that the pituitary fossa was enlarged due to hypertrophy of the
428 cavernous sinus, as the cavernous sinus is located within the pituitary fossa in extant
429 crocodylians (see Porter et al., 2016). Given the hypertrophy of the transverse sinus and
430 stapedial canals in thalattosuchians (Fernández et al., 2011; Brusatte et al., 2016; Pierce et al.,
431 2017; Herrera et al., 2018), hypertrophy of the cavernous sinus would not be unexpected.
432 The cerebral hemispheres appear enlarged, as in other metriorhynchids (Herrera et al.,
433 2018). In birds, enlarged cerebral hemispheres have been interpreted as an adaptation to
434 process increased sensory inputs, and to coordinate increasingly complex behaviours (Rogers,
435 1999; Walsh and Milner, 2011; Balanoff et al., 2013). The enlarged cerebral hemispheres in
436 NHMUK PV OR 32617 and other metriorhynchids could be linked to the pelagic lifestyle, as
437 these animals had to deal with more complex body movements and a greater sensory input
438 than terrestrial and semiaquatic relatives, because they lived and moved in a three-
439 dimensional environment.
440 It should also be noted that the brain endocast does not accurately represent the actual
441 brain morphology. The brain does not fill the entire endocranial cavity in crocodylomorphs,
442 as parts of the brain are covered by overlaying venous sinuses (Hopson, 1979). Hence the
443 brain endocast does not perfectly mirror the actual brain, which results in size and shape
444 differences between the endocast and brain (the latter of which is not preserved in fossils, so
445 we can never assess the quality of the match). However, it has been demonstrated that the
446 difference between the actual brain and the endocast in alligators is comparable with
447 intraspecific variation in brain shape and therefore endocasts can be used for large scale
448 studies of brain morphology in archosaurs (Watanabe et al., 2019). In fossils it is challenging
449 to study the actual neural organs as preservation allows us to study only their preserved bony

450 cavities. However, some parts of the endocast more adequately reflect the actual size and
451 shape of their corresponding brain structures, such as the olfactory bulbs and the cerebral
452 hemispheres, whereas the hindbrain region does not show the same correspondence (Witmer
453 et al., 2008; Watanabe et al., 2019). Thus, we are confident that the enlarged cerebral
454 hemispheres that we note in NHMUK PV OR 32617 and other metriorhynchids is a genuine
455 feature.

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

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

475 *Thalattosuchus superciliosus*; '*Metriorhynchus*' *westermanni*; see Herrera et al., 2018), while
476 non-metriorhynchid thalattosuchians retain the plesiomorphic condition of having these
477 foramina. The closure of these foramina would have limited the communication between the
478 middle ear cavities and the pharynx to just the median pharyngeal foramen (Herrera et al.,
479 2018). Loss of the lateral pharyngeal (Eustachian) foramina is significant in that the
480 pharyngotympanic (Eustachian) tube is a highly conserved attribute that arises embryonically
481 from the first pharyngeal pouch. In other tetrapods, this communication is used to equalize
482 pressure of the middle ear and the surrounding environment, and hence losing the lateral
483 plesiomorphic connection, leaving only the novel median connection, could be a
484 physiological adaptation to the pelagic lifestyle.
485
486 **Vestibular System**
487 The vestibular system of the inner ear is the sensory system involved in balance and
488 equilibrium (Sipla and Spoor, 2008). It is furthermore involved in important functions
489 relating to environment such as head and gaze stabilization during body movements. For
490 secondarily aquatic animals, such as metriorhynchids, the environment puts different
491 demands on the vestibular system than is the case with their terrestrial relatives. Unlike in
492 most terrestrial settings locomotion in an aquatic environment offers movements in all three
493 dimensions of space. To adapt to such new environments, their body plan needs to change.
494 Metriorhynchids, for example evolved flippers and lost their osteoderms to allow the animal
495 more flexible body movements and possibly axial undulation (Massare, 1988). Strong
496 buoyancy forces reduce the effects of weight and allow more complex body movements in a
497 highly viscous aquatic medium and are some of the factors that might influence
498 morphological changes in the labyrinth organ in a variety of secondarily aquatic vertebrates.
499 Pelagic sauropterygians and sea turtles have more bulbous labyrinths with thicker

500 semicircular canals than other reptiles (Georgi and Sipla, 2008; Neenan et al., 2017; Evers et
501 al., 2019), cetaceans miniaturized their labyrinth drastically compared to their body size
502 (Spoor et al., 2002), and other aquatic mammals such as sirenians and seals also reduced their
503 semicircular canals but to a lesser degree (Hyrtl, 1845; Loza et al., 2017). Hence it is clear
504 that specific aspects of their labyrinth morphologies convergently evolved in independent
505 pelagic lineages.

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

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

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

525 modern crocodylians. The cochlear duct is straight and shorter than in the terrestrial
526 morphology, but longer than in the pelagic one. Modern crocodylians have a twisted cochlear
527 duct.

528 The third labyrinth morphology is seen in pelagic taxa, including the NHMUK PV OR
529 32617 specimen that we describe here. This unique labyrinth morphology is present in all
530 sampled metriorhynchids and characterised by a dorsoventrally compact labyrinth, thick
531 semicircular canals, an enlarged vestibule and a presumably short cochlear duct (the end of
532 the cochlear duct is not enclosed by bone and hence just a minimum length can be estimated).
533 This morphology is most extreme in the derived metriorhynchids, like *Cricosaurus* (Fig. 7I-
534 L) and *Torvoneustes*. The canals have more pronounced curvature compared to non-
535 metriorhynchid thalattosuchians and the anterior ampulla is more bulbous. Unlike the
536 terrestrial and semiaquatic labyrinths, the anterior canal of the pelagic labyrinths becomes
537 smaller and just slightly exceeds the posterior canal dorsally.

538 One possible explanation for the change in morphology in the labyrinths of pelagic
539 species (which evolved from semiaquatic ancestors) is their wider range of body movements
540 in a three-dimensional aquatic context, not simply because they lived in the water. For
541 example, cetaceans are highly agile and reduced their semicircular canals, however sirenians
542 (manatees and dugongs) are also fully aquatic but are not very agile and hence do not have
543 reduced canals (Ekdale, 2013). The reduced cetacean semicircular canals may also prevent
544 overstimulation during exaggerated head movements associated with swimming and diving,
545 as it is generally assumed that longer and more arching semicircular canals are more sensitive
546 to rotations in space (Spoor et al., 2002; Ekdale, 2016). This could also be the case for marine
547 reptiles such as metriorhynchids. Another explanation could be that because of neck
548 shortening in metriorhynchids (they had five instead of seven postaxial cervical vertebrae;
549 Andrews, 1913; Young and Andrade, 2009) head and gaze stabilization (vestibulo-ocular and

550 vestibulo-collic reflexes) became less important, which resulted in a reduction of the
551 semicircular canals, as has been suggested for cetaceans and plesiosaurs (Spoor et al., 2002;
552 Neenan et al., 2017). A third hypothesis for the morphological shift seen in pelagic labyrinths
553 relates to diving. Thickening of the semicircular canals could have been driven by either an
554 increased membranous duct diameter or an increased perilymphatic space (space between the
555 membranous and bony labyrinth, filled with perilymphatic fluid). Diving results in changes in
556 hydrostatic pressure, which must be compensated for via fluid movement within the
557 perilymphatic duct system. Thicker canals could have increased the perilymphatic space and
558 functioned as a buffer to protect the sensory system. This hypothesis has been proposed for
559 pelagic deep diving turtles (Evers et al., 2019). Hence, the change in morphology could have
560 been a response to changing sensory requirements as secondarily aquatic vertebrates, such as
561 metriorhynchids, moved into deeper, more open waters.
562
563 CONCLUSION
564
565 Our computed tomography (CT) study of the braincase of the marine thalattosuchian
566 '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus* provides one of the best looks yet at the
567 neurosensory system and internal cranial anatomy of a fully aquatic, pelagic, fast-swimming
568 metriorhynchid. Key neuroanatomical features described herein include a unique flexure in
569 the brain endocast that has not been noted in other thalattosuchians or marine reptiles, the
570 function of which is currently unknown. NHMUK PV OR 32617 also had enlarged cerebral
571 hemispheres to potentially process increased sensory input and a more rounded pituitary fossa
572 that could be related to water regulation in the ocean or housed an enlarged venous sinus. The
573 well-developed vasculature system noted here has previously been reported for other
574 metriorhynchids as well as basal thalattosuchians, suggesting it evolved early in

575 thalattosuchian history. Whether it functioned to support salt glands and/or for aide
576 thermoregulation is currently unclear. Furthermore, a pelagic bony labyrinth morphology is
577 present, with an overall dorsoventrally short morphology, thick semicircular canals and an
578 enlarged vestibule. This might have allowed the animal to better interact with its three
579 dimensional aquatic environment, it may have helped with pressure changes during diving or
580 might be due to reduced neck and head and gaze stabilisation. These new insights into the
581 endocranial evolution of thalattosuchians allow us to better understand their transition into
582 the open oceans. Some of these features (e.g., salt glands) seem to have evolved prior to
583 metriorhynchids becoming fully pelagic, and were thus 'exaptations' that helped transition
584 them to life in the water, whereas others (e.g., pelagic labyrinth morphology) apparently
585 developed only after metriorhynchids moved into the open oceans.
586

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588

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596

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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

818 foramen; **fm**, foramen magnum; **fr**, frontal; **ls**, laterosphenoid; **mpf**, median pharyngeal
819 foramen; **oc**, occipital condyle; **ot**, otoccipital; **pa**, parietal; **pro**, prootic; **so**, supraoccipital;
820 **tof**, temporo-orbital foramen. Roman numerals designate cranial nerve openings. Roman
821 numerals designate cranial nerves. Scale bar equals 5cm. Size (182x100mm)
822
823 FIGURE 3. Digital reconstruction of the braincase of '*Metriorhynchus*' cf. '*M.*'
824 *brachyrhynchus* (NHMUK PV OR 32617). **A**, dorsal; **B**, right lateral; **C**, anterior; **D**, ventral;
825 **E**, left lateral; **F**, posterior. **Abbreviations: bo**, basioccipital; **bs**, basisphenoid; **cf**, carotid
826 foramen; **fm**, foramen magnum; **fr**, frontal; **ls**, laterosphenoid; **mpf**, median pharyngeal
827 foramen; **oc**, occipital condyle; **ot**, otoccipital; **pa**, parietal; **pro**, prootic; **so**, supraoccipital;
828 **tof**, temporo-orbital foramen. Roman numerals designate cranial nerve openings. Scale bar
829 equals 5cm. Size (182x106.17mm)
830
831 FIGURE 4. Internal endocranial anatomy of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus*
832 (NHMUK PV OR 32617). **A**, dorsal; **B**, right lateral; **C**, anterior; **D**, ventral; **E**, left lateral; **F**,
833 posterior. **Abbreviations: bl**, bony labyrinth; **cer**, cerebrum; **dvs**, dural venous sinus; **ic**,
834 internal carotid artery; **mps**, median pharyngeal sinus; **mpt**, median pharyngeal tube; **mpsd**,
835 median pharyngeal sinus diverticulum; **otd**, otoccipital diverticulum; **pf**, pituitary fossa; **ptd**,
836 pterygoid diverticulum; **pts**, pharyngotympanic sinus; **ptt**, pharyngotympanic tubes; **shc**,
837 second hypoglossal canal. Roman numerals designate cranial nerves. Scale bar equals 5cm.
838 Size (182x112mm)
839
840 FIGURE 5. Internal endocranial anatomy of '*Metriorhynchus*' cf. '*M.*' *brachyrhynchus*
841 (NHMUK PV OR 32617). **A**, dorsal; **B**, right lateral; **C**, anterior; **D**, ventral; **E**, left lateral; **F**,
842 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)