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The braincase and neurosensory anatomy of an Early Jurassic marine crocodylomorph: implications for crocodylian sinus evolution and sensory transitions

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3 **The braincase and neurosensory anatomy of an Early Jurassic marine crocodylomorph:**
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5 **implications for crocodylian sinus evolution and sensory transitions**
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3 **ABSTRACT:** Modern crocodylians are a morphologically conservative group, but extinct
4 relatives (crocodylomorphs) experimented with a wide range of diets, behaviors, and body
5 sizes. Among the most unusual of these fossil groups is the thalattosuchians, an assemblage
6 of marine-dwellers that transitioned from semi-aquatic species (teleosaurids) into purely
7 open-ocean forms (metriorhynchids) during the Jurassic and Cretaceous Periods (ca. 191-125
8 million years ago). Thalattosuchians can give insight into the origin of modern crocodylian
9 morphologies and how anatomy and behavior changes during a major evolutionary transition
10 into a new habitat, but little is known about their brains, sensory systems, cranial sinuses, and
11 vasculature. We here describe the endocranial anatomy of a well-preserved specimen of the
12 Jurassic semi-aquatic teleosaurid *Steneosaurus* cf. *gracilirostris* using X-ray micro-CT. We
13 find that this teleosaurid still had an ear well attuned to hear on land, but had developed large
14 internal carotid and orbital arteries that likely supplied salt glands, which were previously
15 thought to be present in only the fully pelagic metriorhynchids. There is no great gulf in
16 endocranial anatomy between this teleosaurid and the metriorhynchids, and some of the
17 features that later permitted metriorhynchids to invade the oceanic realm were apparently first
18 developed in semi-aquatic taxa. Compared to modern crocodylians, *Steneosaurus* cf.
19 *gracilirostris* has a more limited set of pharyngotympanic sinuses, but it is unclear whether
20 this relates to its aquatic habitat or represents the primitive condition of crocodylomorphs that
21 was later elaborated.
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47 **Key words:** crocodylomorph, thalattosuchian, sensory evolution, pneumaticity, tympanic
48 sinuses, neuroanatomy
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3 Crocodilians are some of the most conspicuous animals in today's world, but they are not a
4 particularly diverse group. There are approximately 25 species of modern crocodilians, all of
5 which are semi-aquatic predators that predominately lurk in tropical-to-subtropical shallow
6 waters and use their powerful bites and conical teeth to subdue prey (e.g., Busbey, 1995;
7 McHenry et al., 2006; Pierce et al., 2008). This morphological and ecological conservatism
8 belies the long evolutionary history of crocodilians, which are survivors of about 250 million
9 years of evolution, spanning from when the crocodilian lineage split from its sister group,
10 which led to dinosaurs and birds, until the present day (Brusatte et al., 2010; Nesbitt, 2011).
11 Fossil crocodylomorphs—members of the wider group that includes modern crocodiles and
12 their closest extinct relatives—include a variety of plant-eating, fast-running, pug-nosed, and
13 swimming species of incredible morphological variety, ranging from the size of a dog to
14 longer than a bus. Studying these species can give insight into how the characteristic body
15 plan, sensory abilities, and behaviors of modern crocodilians developed over evolutionary
16 time.

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34 One of the most intriguing groups of extinct crocodylomorphs is the thalattosuchians,
35 a diverse assemblage of marine-dwellers that had a near global distribution during the
36 Jurassic Period and survived into the Early Cretaceous, a total time span ca. 191-125 million
37 years ago (e.g., Gasparini et al., 2000; Young et al., 2010; Chiarenza et al., 2015; Wilberg,
38 2015). The thalattosuchians are divided into two main subgroups: Teleosauridae, a clade of
39 long-snouted semi-aquatic forms that superficially resembled modern gharials, and
40 Metriorhynchidae, a group of pelagic species that could swim fast and hunt in the open
41 ocean, like living toothed whales. The metriorhynchids are some of the most aberrant reptiles
42 that ever existed, as they evolved from land-living ancestors but became specialized for a
43 fully aquatic existence by developing features such as large salt glands that allowed them to
44 drink seawater and expel excess salt from their food, hydrofoil-like forelimbs and a
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3 hypocercal tail that were used for swimming, and structural lightening of the skeleton and a
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5 loss of osteoderms that made them more buoyant and hydrodynamic in the water (Fraas,
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7 1902; Andrews, 1913; Hua and Buffrénil, 1996; Fernández and Gasparini, 2000, 2008;
8
9 Young et al., 2010; Herrera et al., 2013; Wilberg, 2015).

11 Thalattosuchians are important for two main reasons. First, the transition from land-
12
13 living or semi-aquatic species to the purely marine metriorhynchids was a major evolutionary
14
15 transformation, akin to the origin of whales from terrestrial mammals. It promises to give
16
17 insight into how anatomy, behavior, and physiology change as vertebrates invade new
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19 habitats and are modified for new lifestyles. Second, because thalattosuchians are relatively
20
21 basal members of Crocodylomorpha and are known from a wealth of fossil specimens, they
22
23 can give insight into the primitive crocodylian bauplan and how the modern species
24
25 developed their signature morphologies and behaviors from their fossil ancestors. Over the
26
27 last decade, reexamination of long-known fossils, phylogenetic analyses, histological studies,
28
29 and description of skull features relating to diet have helped to elucidate evolutionary patterns
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31 in thalattosuchians and cement their importance in untangling the early history of
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33 crocodylomorphs (e.g., Hua & Buffrénil, 1996; Fernández & Gasparini, 2008; Pierce et al.,
34
35 2009; Young et al., 2010; Wilberg, 2015).

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37 One area that has been poorly explored, however, is thalattosuchian neuroanatomy
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39 and sensory capabilities. Only a limited number of specimens have been examined in the
40
41 detail necessary to discuss these issues (e.g., Seeley, 1880; Wenz, 1968; Wharton, 2000;
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43 Holliday and Witmer, 2009; Fernández et al., 2011; Herrera et al., 2013; Herrera and
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45 Vennari, 2015). In particular, there has been very little study of the internal structure of the
46
47 thalattosuchian brain, sinuses, sensory organs, nerves, and vessels, which are key to
48
49 understanding the behaviors and senses of these animals, particularly with regard to their
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51 secondary adaptation to an aquatic environment. Recent papers have started to use computed
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3 tomography (CT) scanning to visualize the internal anatomy of some thalattosuchians (e.g.,
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5 Fernández and Herrera, 2009; Fernández et al., 2011; Herrera et al., 2013; Herrera and
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7 Vennari, 2015), but only a few specimens have been studied this way, and much of the focus
8
9 has been on the olfactory system and salt glands. The brain, sinuses, and inner ear of a
10
11 thalattosuchian have yet to be described in detail using CT data.
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14 We here describe the internal endocranial anatomy of a well-preserved specimen of a
15
16 Jurassic teleosaurid thalattosuchian using X-ray micro-CT (μ CT). We make comparisons
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18 between the brain, air sinus, vascular, and ear anatomy of this specimen and other fossil and
19
20 modern crocodylomorphs, and quantitatively compare the hearing capabilities of the fossil
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22 specimen (based on inner ear anatomical proxies) to that of modern crocodilians. We then
23
24 discuss the importance of the fossil data for understanding how modern crocodilians evolved
25
26 and how thalattosuchians transitioned from a terrestrial to an aquatic habitat.
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29 Institutional abbreviations—**FMNH**, Field Museum of Natural History, Chicago,
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31 Illinois, USA; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **NHMUK**,
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33 Natural History Museum, London, UK; **SMNS**, Staatliches Museum für Naturkunde
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35 Stuttgart, Baden-Württemberg, Germany.
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40 **MATERIALS AND METHODS**

41 **Fossil specimen**

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49 The braincase of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV
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51 OR 33095) forms the basis for this study (Figs. 1-2). It is from the Whitby Mudstone
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53 Formation of Whitby, Yorkshire, UK (lower Toarcian, Early Jurassic, ca. 183-178 million
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55 years ago). The specimen is relatively intact, comprising the neurocranium from the frontal
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3 posterior process posterior-wards, and exhibits little ventral distortion or lateral compression.

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5 The maximum preserved length is 115.26 mm and the maximum preserved width is 124 mm.

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7 As the skull is incomplete we cannot be completely certain of its species identification.

8
9 However, it shares numerous characteristics with the holotype (NHMUK PV OR 14792) and
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11 paratype (NHMUK PV OR 15500) of *Steneosaurus gracilirostris*, including: a large, sub-
12
13 triangular parietal dorsal 'table', which in dorsal view has a pronounced convexity at the
14
15 midline on its posterior margin; the anterior point of the parietal 'table' is almost on the same
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17 plane as the raised ridges that delimit the two muscular fossae within each supratemporal
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19 (=dorsotemporal) fenestra; and the dorsal surfaces of the frontal and parietal have poorly
20
21 defined ornamentation composed of large, irregularly-shaped ovals and elongate pits, which
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23 are irregularly spaced, with some being widely separated (note that much of the dorsal
24
25 surfaces of these bones are in fact worn and damaged, so this texture is not uniformly
26
27 visible).

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32 *Steneosaurus* is taxonomically problematic, with recent phylogenetic analyses finding
33
34 the genus to be either paraphyletic or polyphyletic (e.g., Young et al., 2012; Wilberg, 2015).
35
36 Therefore, what species actually belong in *Steneosaurus* is a major issue in thalattosuchian
37
38 taxonomy, one which is currently being investigated. As such, the description herein should
39
40 not be considered as representative of the entire genus *Steneosaurus*.

41 42 43 44 45 **Comparative Material**

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49 Three-dimensional virtual endocasts of the brain, inner ear, and sinuses reconstructed from
50
51 CT data have been published for the extant crocodylians *Crocodylus johnsoni* (Witmer et al.,
52
53 2008) and *Alligator mississippiensis* (Dufeu and Witmer, 2015). To add to the pool of
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55 comparative data for modern species, we also reconstructed the cranial endocast and inner ear
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3 of *Caiman crocodilus*, the spectacled caiman, based on a subadult specimen collected in
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5 Choco, Colombia, and accessioned into the collections of the Field Museum of Natural
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7 History (FMNH 73711). This is a well-preserved, three-dimensional specimen without any
8
9 obvious distortion or breaks.
10

11 12 13 14 **Computed Tomography and Visualization** 15

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18 The braincase of *Steneosaurus cf. gracilirostris* (NHMUK PV OR 33095) was μ CT scanned
19
20 at the Natural History Museum (London) using their Nikon XT H 225ST CT system in 2014.
21
22 It was scanned at 215kV and 150 μ A, with the following parameters: 1.0mm tin filter,
23
24 projections were made with an angle of 0.115° between projections. Isotropic voxel size =
25
26 89 μ m. Distance from source to detector = 1170mm. Distance from source to specimen =
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28 523mm. Mask radius = 89.33mm.
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32 The skull of *Caiman crocodilus* (FMNH 73711) was scanned at the High-Resolution
33
34 Scanning Facility of the University of Texas, Austin in 2002. It was scanned along the
35
36 coronal axis, and a total of 945 projections were made, each with a thickness of 0.142mm.
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38 The interslice spacing is also 0.142mm, and the field of reconstruction is 67 mm. Voxel
39
40 dimensions=65 (X) x 65 (Y) x 142 (Z). Further information on the specimen is available from
41
42 the open source DigiMorph digital library of CT scan data:
43
44 http://www.digimorph.org/specimens/Caiman_crocodilus/
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48 For both specimens, three-dimensional models of the cranial endocast, inner ear,
49
50 nerves and vessels, and sinuses were rendered by one of us (Muir) by digitally segmenting
51
52 the CT slice data using Materialise Mimics 17.0 at the University of Edinburgh, School of
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54 GeoSciences. The 3D Livewire and Calculate 3D tools were used, respectively.
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3 Standard linear measurements of the brain cavity endocast, associated nerve foramina
4 and vascular openings within the endocranium were made using the measuring tools in
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Standard linear measurements of the brain cavity endocast, associated nerve foramina and vascular openings within the endocranium were made using the measuring tools in Materialise Mimics 17.0. All measurements were taken from 3D voxel model data rather than polygon mesh models or across the tomograph stack. Angular and distance measurements were also recorded for the inner ear labyrinth.

We used the methods of Walsh et al. (2009) to estimate mean hearing frequency and hearing range of NHMUK PV OR 33095. This approach involves linear regression of measurements of the endosseous cochlear duct (ECD) length that have been scaled to basicranial length and log transformed, against hearing sensitivity data derived from audiogram analysis of living crocodylian, avian, squamate and chelonian taxa. The same transformed values derived from NHMUK PV OR 33095 are then used to determine the position of this taxon on the audiogram regression line (for full methods see Walsh et al., 2009). The calculation was made using measurements from the left labyrinth, as the right labyrinth could not be completely reconstructed.

RESULTS

External cranial anatomy of NHMUK PV OR 33095

Frontal. The frontal is poorly preserved and largely incomplete (Figs. 1-2). Only the frontal's contributions to the intertemporal bar and anteromedial corners of the supratemporal fenestrae are preserved. Unfortunately, the external frontal-parietal suture is difficult to discern, and thus we cannot be sure of the sutural positions and the extent of the frontal. However, the visible morphology is very similar to that of other *Steneosaurus gracilirostris* skulls, and the morphology described by Jouve (2009) for *Teleosaurus cadomensis*. The

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2
3 external surface morphology of the frontal is worn and damaged, but poorly defined
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5 ornamentation consisting of large, irregularly-shaped ovals and elongate pits can be seen.
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8 There is a distinct 'platform' in the anteromedial corner of the supratemporal fenestra.
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10 This also occurs in other thalattosuchians (Fraas, 1902; Andrews, 1913; Lepage *et al.*, 2008;
11
12 Jouve, 2009; Young *et al.*, 2010; 2012, 2013, 2014a; Wilberg, 2015), and is primarily
13
14 composed by the frontal, with its outer edges contacting the parietal (and also the postorbitals
15
16 in metriorhynchoids, in which this platform is proportionally larger). Thus the 'platform'
17
18 likely is the maximal contribution of the frontal to the supratemporal fossa. This
19
20 interpretation is supported by the position of the parietal-laterosphenoid suture, which is
21
22 posteroventral to the 'platform' (best seen in right lateral view). This would result in the
23
24 parietal separating the frontal from the laterosphenoid, as in *Teleosaurus cadomensis*
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26 (MNHN.F AC 8746; Jouve, 2009).
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32 *Parietal.* The parietal is relatively well preserved (Figs. 1-2). It appears as a single element,
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34 without any signs of the interparietal suture on the external surface. In dorsal view, the
35
36 parietal should be 'T'-shaped, with an elongate anterior process and two lateral processes.
37
38 However, the two lateral processes are badly damaged, making their relationship with the
39
40 medial processes of the squamosals impossible to trace. The parietal forms the posterior and
41
42 medial margins of the supratemporal fenestrae and fossae. The anterior process forms most of
43
44 the intertemporal bar and contacts the frontal anteriorly.
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46

47
48 In dorsal view, the anterior process narrows dramatically as it extends posteriorly
49
50 towards the occiput, forming a sagittal crest, until it broadens out again to form the 'parietal
51
52 table'. The 'parietal table' is seen in all teleosaurids, being typically better developed in adult
53
54 specimens (Andrews, 1913; Westphal, 1961, 1962; Lepage *et al.*, 2008; Young *et al.*, 2014a).
55
56 It is a sub-triangular, flat surface, which makes up the region where the anterior and lateral
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3 processes of the parietal meet. Its external surface has a similar ornamentation as that of the
4
5 frontal. The 'table' is particularly large, similar in size to those in the holotype and paratype
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7 of *Steneosaurus gracilirostris*, with its anterior point being almost on the same plane as the
8
9 raised ridges at the laterosphenoid-prootic sutures on both sides of the skull, that delimit two
10
11 muscular fossae within the supratemporal fenestra on each side (see below). In dorsal view,
12
13 there is also a pronounced convexity at the midline of the posterior margin of the 'table',
14
15 which overhangs the supraoccipital slightly.
16
17

18
19 Within the supratemporal fenestra the parietal forms the dorsal half of the medial
20
21 supratemporal wall. The prootic and the laterosphenoid can be seen ventral to the anterior
22
23 process (Fig. 2), with the parietal separating the frontal from the laterosphenoid (see above).
24
25 The laterosphenoid contacts the ventral margin of the anterior process along the anterior-
26
27 middle regions of the anterior process, whereas the prootic contacts the ventral margin of the
28
29 anterior process immediately posterior to the laterosphenoid. The parietal is devoid of
30
31 ornamentation within the supratemporal fenestrae.
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33

34
35 In occipital view, the supraoccipital is ventral to the 'parietal table', which terminates
36
37 approximately level to the occipital tuberosities. The contacts between the parietal and the
38
39 exoccipital-opisthotic complex cannot be seen in occipital view because of the damage to the
40
41 lateral processes of the parietal.
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45 *Squamosal*. The squamosals appear to be missing. However, because of damage along the
46
47 postorbital-squamosal ridges (sensu Young et al., 2013) it is not possible to discern externally
48
49 whether or not the medial processes of the left and right squamosals are present. The dorsal
50
51 surfaces of these ridges are worn away, and as the supratemporal fenestrae are largely
52
53 incomplete and have damaged edges, we cannot ascertain whether a squamosal-postorbital
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55 suture is present.
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5 *Prootic*. Both prootics are fairly well preserved (Figs. 1-2). When observed within the
6
7 supratemporal fenestra, the prootic is a subtriangular bone that forms the posteromedial
8
9 corner of the supratemporal wall. Dorsally it contacts the parietal, posteroventrally the
10
11 quadrate, and anteriorly the laterosphenoid. The suture between the prootic and
12
13 laterosphenoid is expressed as a pronounced, raised, dorsoventrally-trending ridge that begins
14
15 slightly dorsal to the midpoint of the dorsal margin of the trigeminal foramen (cranial nerve
16
17 V). This ridge is seen in other thalattosuchians, including both teleosaurids and
18
19 metriorhynchids (Holliday and Witmer, 2009; Fernández et al., 2011). In NHMUK PV OR
20
21 33095, the ridge extends far dorsally, dividing the supratemporal fossa into attachments for
22
23 two muscles, as described by Holliday and Witmer (2009) in *Pelagosaurus typus*. The more
24
25 posterior fossa, located mostly on the prootic, is interpreted as an attachment site for the M.
26
27 adductor mandibulae externus profundus, whereas the more anterior fossa, located on the
28
29 laterosphenoid and the parietal, housed the M. pseudotemporalis superficialis (Holliday and
30
31 Witmer, 2009). Unfortunately, the dorsolateral corners of both prootics are damaged, and
32
33 thus we cannot determine the nature of the contact with the squamosals. CT data show that
34
35 the prootic and opisthotic forms the inner ear cavity.
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43 *Laterosphenoid*. The left and right laterosphenoids are well preserved (Figs. 1-2). This bone
44
45 has a ventral contact with the basisphenoid, and forms the ventral half of the medial
46
47 supratemporal wall and anteromedial corner of the supratemporal fenestra (Fig. 2). Where the
48
49 laterosphenoid forms the medial supratemporal wall, it contacts the anterior process of the
50
51 parietal dorsally. As the laterosphenoid curves and forms the anteromedial supratemporal
52
53 corner, it closely approaches the frontal (the anteromedial fossa 'platform'), but is separated
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1
2
3 by the parietal. Ventral to the contact with the prootic, the laterosphenoid has a posterior
4
5 suture with the quadrate in the region of the trigeminal foramen.
6

7 The trigeminal opening is a deep, funnel-like structure (Fig. 2, V). The surrounding
8
9 fossa would have housed the trigeminal ganglion, and thus the various branches of the
10
11 trigeminal nerve would have diverged from each other outside the endocranial cavity. This is
12
13 also the case in other modern and extinct crocodylomorphs, along with close outgroup taxa
14
15 (Holliday and Witmer, 2009), although some other archosaurs have evolved conditions in
16
17 which the trigeminal branches exit the endocranium separately and emerge through the bony
18
19 braincase walls via individual foramina (e.g., Brusatte and Sereno, 2007; Witmer and
20
21 Ridgely, 2009). In NHMUK PV OR 33095 the fossa extends only slightly posterior to the
22
23 foramen to excavate a portion of the external surface of the quadrate, which differs from the
24
25 expansive posterior extent of the fossa in metriorhynchids (Fernández et al., 2011). There is a
26
27 deep groove extending anteroventrally from the trigeminal foramen on the external surface of
28
29 the laterosphenoid, which transmitted the ophthalmic branch of the trigeminal nerve (CN V₁).
30
31 The groove extends far anteriorly before fanning out on the ventral surface of the frontal. A
32
33 smaller, shallower triangular fossa borders the anterodorsal corner of the trigeminal foramen,
34
35 which transmitted the maxillary branch of the trigeminal nerve (CN V₂). These two nerve
36
37 grooves are also seen in *Pelagosaurus typus* and metriorhynchids (Holliday and Witmer,
38
39 2009; Fernández et al., 2011), and the nerves exit the trigeminal foramen in a similar pattern
40
41 in modern crocodylians (Holliday and Witmer, 2009).
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47 Anterodorsal to the trigeminal foramen, and ventral to the pseudotemporalis fossa of
48
49 the supratemporal region, there is a shallow and elongate concavity, which we interpret as the
50
51 epipterygoid fossa. It is in the same location in *Pelagosaurus typus* and metriorhynchids
52
53 (Holliday and Witmer, 2009; Fernández et al., 2011). Although the epipterygoid itself is not
54
55 preserved in NHMUK PV OR 33095, the fossa indicates that it would have been present.
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3 Epipterygoids are present in most archosaurs, including many extinct crocodylomorphs, but
4
5 are lost in some eusuchians, including the modern species (Holliday and Witmer, 2009).
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8
9
10 *Supraoccipital*. The supraoccipital forms the dorsomedial part of the occipital region of the
11 skull (Figs. 1-2). In posterior view, the supraoccipital is trapezoid-shaped, broader dorsally
12 than ventrally. It has a pronounced concavity on its posterior surface, with a raised rim along
13 its lateral and dorsal margins. The lateral rims form part of the occipital tuberosities (along
14 with a raised region on the exoccipital-opisthotic complex) (Fig. 2, ot). The occipital
15 tuberosities are paired processes also seen in other teleosaurids, such as *Teleosaurus*
16 *cadomensis* (MNHN.F AC 8746; Jouve, 2009), *Steneosaurus heberti* (MNHN.F 1890-13),
17 *Steneosaurus obtusidens* (NHMUK PV R 3168; Andrews, 1913), and *Machimosaurus*
18 *buffetauti* (SMNS 91415; Martin and Vincent, 2013; Young et al., 2014a). They are
19 somewhat similar to the tuberosities seen in dyrosaurid crocodyliforms (e.g. MNHN.F ALG
20 1; Jouve, 2005), albeit less pronounced. Based on external examination, the supracoccipital of
21 NHMUK PV OR 33095 appears to lack a nuchal crest running along the midline of the
22 element, which would be unusual as the previously listed teleosaurids species all have this
23 crest. However, there is still some matrix adhering to the bone, and CT data shows that the
24 matrix is obscuring a low nuchal crest.
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43 The supraoccipital contacts the parietal along its dorsal margin and the exoccipital-
44 opisthotic complex along its lateral margins, and also has a slight ventral contact with the
45 exoccipital-opisthotic. In occipital view, the ventral margin of the supraoccipital forms the
46 medial portion of the dorsal margin of the foramen magnum. However, within the foramen
47 magnum there is a suture between the supraoccipital and the exoccipital-opisthotic,
48 demonstrating that the supraoccipital overlies the exoccipital-opisthotic in this region. This
49 overlapping morphology might explain why participation of the supraoccipital in the dorsal
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3 margin of the foramen magnum is so variable within Thalattosuchia, as independent
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5 regressions of this overlap in different lineages could explain how the exoccipital-opisthotic
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7 complex sometimes separates the supraoccipital from the foramen magnum.
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10 In dorsal view, the posterior surface of the supraoccipital is broadly exposed. This is
11
12 the result of a 'step'-like arrangement of the posterior skull, with the parietal terminating
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14 anterior to the supraoccipital, followed posteriorly by the exposure of the supraoccipital
15
16 posterior face, followed by the thickened ventral rim of the supraoccipital (i.e. the foramen
17
18 magnum dorsal rim), and finally the occipital condyle. This arrangement is seen in other
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20 teleosaurids, such as *Teleosaurus cadomensis* (MNHN.F AC 8746; Jouve, 2009), *S. heberti*
21
22 (MNHN.F 1890-13) and *Steneosaurus obtusidens* (NHMUK PV R 3168; Andrews, 1913),
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24 and is present in the basal metriorhynchoid *Pelagosaurus typus* (NHMUK PV OR 32599;
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26 Pierce and Benton, 2006). This differs markedly from the condition in metriorhynchids,
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28 which have verticalized the occipital surface, such that the supraoccipital is rarely visible in
29
30 dorsal view, or if it is, it is not as broadly exposed as in teleosaurids (e.g. Andrews, 1913;
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32 Young et al., 2010, 2012 2013; Fernández et al., 2011; Foffa and Young, 2014).
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39 *Exoccipital-opisthotic*. Based on examination of the occipital surface (Figs. 1-2), it is unclear
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41 whether the exoccipital and the opisthotic have fully fused to form an otoccipital. On the left
42
43 side of this complex, there may be a faint suture proceeding from the lateral margin of the
44
45 foramen magnum towards the hypoglossal foramen (= cranial nerve XII), then towards the
46
47 foramen for cranial nerves IX-XI. This is not the first time the potential lack of fusion
48
49 between these elements has been raised for thalattosuchians, as a possible suture between the
50
51 exoccipital and opisthotic was noted for the metriorhynchid *Torvoneustes coryphaeus* (Young
52
53 et al., 2013). If this is a suture, then the dorsal region would be the opisthotic (including the
54
55 paroccipital processes and the contact with the parietal and supraoccipital), and the ventral
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3 region would be the exoccipital (including the contact with the basioccipital and the
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5 contribution to the occipital condyle).
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7 The exoccipital-opisthotic complex contacts the supraoccipital along its medial
8
9 margin dorsally, and the parietal and squamosal along its dorsal margin lateral to the
10
11 supraoccipital. Ventral to its contact with the supraoccipital, the exoccipital-opisthotic forms
12
13 most of the foramen magnum, including the lateral walls, the dorsal wall (with the exception
14
15 of the supraoccipital overlap at the occipital surface), and the ventrolateral corners. These
16
17 paired ventrolateral projections form part of the occipital condyle, contacting the
18
19 basioccipital. The suture between the exoccipital-opisthotic and the basioccipital continues
20
21 ventrolaterally until it reaches the ventral margin of the skull. The exoccipital-opisthotic
22
23 contacts the quadrate along its ventrolateral margin. This can only be seen on the right-side,
24
25 as the left quadrate is incomplete. However, this suture is difficult to discern because of
26
27 numerous cracks in the vicinity. Overall, the exoccipital-opisthotic is devoid of
28
29 ornamentation, covers the majority of the occipital surface, and has a slightly convex external
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31 surface medial to the paroccipital processes.
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36 Both paroccipital processes are preserved, although they are missing their distal ends.
37
38 They are large, pronounced, and oriented horizontally in posterior view. The dorsal surface is
39
40 slightly concave, with this concavity extending from the exoccipital-opisthotic contribution to
41
42 the occipital tuberosities medially along the dorsal surface of the exoccipital-opisthotic
43
44 complex. The ventral margin of this concave surface is sharply delimited by a ridge, which is
45
46 contiguous with the thickened ventral rim of the supraoccipital.
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49 There are several foramina for nerves and vessels on the posterior surface of the
50
51 exoccipital-opisthotic. These are better preserved on the left side. The foramen magnum is
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53 the largest opening on the occipital surface, situated at the skull midline between the
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55 supraoccipital, the exoccipital-opisthotic, and the basioccipital. It is oval-shaped, at least
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3 twice as wide mediolaterally than tall dorsoventrally. Lateral to the foramen magnum, and
4
5 level with the dorsal margin of the occipital condyle, is a sub-circular foramen that
6
7 transmitted the hypoglossal nerve (CN XII).
8

9
10 Further lateral to the hypoglossal opening is a large foramen situated ventral to the
11 proximal paroccipital process. We interpret this as transmitting either the vagus nerve (CN X)
12 or a combination of the vagus, accessory (CN XI), and possibly glossopharyngeal (CN IX)
13 nerves and associated vessels. Different workers have considered varying combinations of
14 these nerves as passing through this foramen in other thalattosuchians (e.g., Wenz, 1968;
15 Jouve, 2009; Fernández *et al.*, 2011; Young *et al.*, 2012, 2013; Herrera & Vennari, 2015).
16 Unfortunately, in NHMUK PV OR 33095 the μ CT data are not helpful in tracing this
17 opening far internally into the endocranium, because the canal extending from the foramen
18 enters the otoccipital sinus, disappears into this pneumatic chamber, and doesn't clearly
19 reconnect with the endocast. This indicates that the neurovascular bundle would have been
20 surrounded by the sinus, as is also the case in *Alligator mississippiensis* (Dufeu and Witmer,
21 2015). The lack of other large foramina on the occipital surface (except for a small one above
22 the carotid opening, see below) suggests that the large foramen underneath the paroccipital
23 process was most likely a multipurpose opening that transmitted more than just the vagus
24 nerve.
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43 Ventrally and slightly laterally to the hypoglossal foramen, at the level of the ventral
44 base of the paroccipital process, is a smaller, slit-like foramen. We suggest that if this small
45 opening did transmit a cranial nerve, it most likely was for the hypoglossal nerve, although
46 this is not clear because the slit can only be traced a few millimeters internally before
47 disappearing in the CT slices. A much larger foramen opens immediately below the slit. This
48 is for the internal carotid artery and it takes the form of a large, funnel-like structure that
49 opens posteroventrally (Fig. 2, ic). It is located immediately along the ventral margin of the
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3 braincase and lateral to the suture between the exoccipital-opisthotic and basioccipital. The
4
5 internal carotid foramen is larger than the aforementioned openings for the cranial nerves.
6
7 Unfortunately, the braincase is broken laterally on each side, so the cranioquadrate opening,
8
9 which can often be large in thalattosuchians and is connected to the tympanic sinuses (e.g.,
10
11 Fernández *et al.*, 2011), is not preserved.
12
13

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15 There is some potentially phylogenetically useful variation in the orientation of the
16
17 nerve foramina in thalattosuchians. The presence of a large vagus (or multipurpose) foramen
18
19 near the base of the paroccipital processes in NHMUK PV OR 33095 is shared with the
20
21 teleosaurid *Teleosaurus cadomensis* (MNHN.F AC 8746; Jouve, 2009) and the basal
22
23 metriorhynchoid *Pelagosaurus typus* (NHMUK PV OR 32599). Metriorhynchids lack a
24
25 foramen at this location, but instead have a large opening for the vagus nerve positioned
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27 dorsolateral in relation to the internal carotid artery foramen (see Fernández *et al.*, 2011;
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29 Young *et al.*, 2013; Herrera and Vennari, 2015). It therefore appears that the position of the
30
31 foramen shifts from a dorsolateral position (near the paroccipital process) in basal
32
33 thalattosuchians to a ventromedial one (closer to the internal carotid artery foramen) in
34
35 metriorhynchids.
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39 Furthermore, it has been suggested that the large external opening for the carotids on
40
41 the posterior braincase is a synapomorphy of metriorhynchids (Pol and Gasparini 2009;
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43 Fernández *et al.*, 2011). However, the opening is also enlarged in NHMUK PV OR 33095, as
44
45 well as other teleosaurids (e.g., *Teleosaurus cadomensis*: Jouve, 2009:fig. 3) and basal
46
47 metriorhynchoids (e.g., *Pelagosaurus typus*: Pierce and Benton, 2006), suggesting it is a
48
49 wider thalattosuchian feature. The large size and position of the foramina at the ventral edge
50
51 of the braincase in thalattosuchians does differ from the much smaller, more dorsally
52
53 positioned openings in early crocodylomorphs such as *Junggarsuchus sloani* (Clark *et al.*,
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3 2004:fig. 2), *Dibothrosuchus elaphros* (Wu and Chatterjee, 1993:fig. 3), and *Almadasuchus*
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5 *figarii* (Pol et al., 2013:fig. 1).
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10 *Occipital condyle*. The occipital condyle is sub-circular in posterior view, slightly
11
12 mediolaterally wider at its dorsal margin than ventrally (Figs. 1-2). There is a deep depression
13
14 at the center of the posterior surface. The condyle is mostly formed by the basioccipital, with
15
16 the exoccipital–opisthotics contributing only to the dorsolateral corners. The gap between the
17
18 corners, filled by the basioccipital, comprises most of the dorsal margin of the condyle and
19
20 the ventral margin of the foramen magnum. This is the normal condition within
21
22 Thalattosuchia, and is seen in other teleosaurids, basal metriorhynchoids, metriorhynchine
23
24 metriorhynchids and basal geosaurine metriorhynchids (Andrews, 1913; Pierce and Benton,
25
26 2006; Lepage et al., 2008; Jouve, 2009; Foffa and Young, 2014). In derived geosaurine
27
28 metriorhynchids, however, the exoccipital–opisthotic forms the entire dorsal margin of the
29
30 occipital condyle (*Plesiosuchus manselii* Young et al., 2012; *Torvoneustes coryphaeus*
31
32 Young et al., 2013).
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39 *Basioccipital*. In addition to constituting the majority of the occipital condyle, the
40
41 basioccipital forms the ventromedial part of the occipital region of the skull (Figs. 1-2). The
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43 suture between the exoccipital–opisthotic and the basioccipital is clearly seen on the occipital
44
45 condyle, and is also visibly laterally and ventrally to the condyle. Here, the lateral contact
46
47 between the exoccipital–opisthotic and basioccipital is expressed as a subtle suture that
48
49 projects ventrolaterally from the occipital condyle to the lateral margin of the basal tuber
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51 (=basioccipital tuberosity) (Fig. 2, bt). The left and right tubera extend ventrolaterally from
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53 the ventral edge of the braincase in posterior view. Between the tubera is a deep fossa, which
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55 houses a foramen that transmitted the medial pharyngeal tube and leads into a recess
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3 underneath the occipital condyle that is part of the median pharyngeal sinus system (Fig. 2,
4 mpf). This opening has various names in the literature, including the median Eustachian
5 foramen (e.g., Jouve, 2009) and foramen intertympanicum (e.g., Pol et al., 2013). We prefer
6 the simple term median pharyngeal foramen (e.g., Fernández et al., 2011). In ventral view,
7 the tuber contacts the quadrate along much of its lateral margin. Also in ventral view, what
8 remains of the basisphenoid can be seen contacting the ventral margins of both tubera.
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18 *Basisphenoid.* The basisphenoid is poorly preserved, but in ventral view it clearly contacts
19 the basioccipital along its dorsal margin and the orbital process of the quadrate along its
20 anterolateral margin (Figs. 1-2). Posteriorly, the basisphenoid broadens laterally and develops
21 a ‘trident’ shape on its exposed ventral surface, consisting of three distinct prongs with
22 notches between them. These house the medial pharyngeal canal and lateral (true) Eustachian
23 tubes. A portion of the basisphenoid is also visible in occipital view, as the bone immediately
24 ventral to the basal tubera of the basioccipital. The basisphenoid continues anteriorly as an
25 elongate and narrow structure along the skull midline, which is broadly visible in ventral
26 view. It is unclear if there is a separate parasphenoid or not in this region, so we are referring
27 to this portion of the braincase as the basisphenoid for simplicity. Dorsally this region of the
28 basisphenoid contacts the laterosphenoid. Anteriorly, the basisphenoid is damaged and
29 reveals a hollow passage that housed the orbital arteries after they emerged from the pituitary
30 fossa (see below).
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49 *Quadrate.* The quadrates are incompletely preserved (Figs. 1-2), with the right one much
50 more complete than the left. The condylar region is oriented posteroventrally. The medial
51 hemicondyle is noticeably smaller than the lateral hemicondyle, with a deep sulcus separating
52 them. The articular surfaces of both hemicondyles are almost parallel and are oriented
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3 dorsolaterally. In ventral view, the quadrate contacts the basal tuber along its medial margin.
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5 The orbital process of the quadrate overlaps the basisphenoid, and as with other
6
7 thalattosuchians, this process remains free of bony attachment at its anteromedial surface
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9 (Holliday and Witmer, 2009; Jouve, 2009; Fernández et al., 2011). There is also a prominent
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11 crest ('crest B' of Iordansky, 1973) on the ventral surface of the bone, running from the
12
13 lateral hemicondyle distally towards the orbital process. Within the supratemporal fenestra
14
15 the quadrate forms the ventral half of the posterior supratemporal wall (Fig. 2). Dorsally the
16
17 quadrate contacts the squamosals (although the squamosals are damaged for much of the
18
19 contact), medially the prootic, and anteriorly and anteromedially the laterosphenoid. Because
20
21 of damage, we cannot describe how the quadrate participates in the external otic aperture,
22
23 cranioquadrate canal or infratemporal (= laterotemporal) fenestra, nor can we describe the
24
25 sutural contacts with the jugal, quadratojugal, or pterygoid. CT data show that the quadrate
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27 forms much of the middle ear cavity.
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34 **Internal cranial anatomy of *Caiman crocodylius***

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38 A three-dimensional model of the cranial endocast, inner ear, and associated nerves and
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40 vessels is shown in Figure 3. As the primary purpose of this reconstruction is to provide data
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42 from an extant taxon to which we can compare the *Steneosaurus* fossil braincase, we do not
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44 present a detailed verbal description of it here, but rather rely on our images to present the
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46 morphology.
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51 **Internal cranial anatomy of NHMUK PV OR 33095**

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3 Our CT-based reconstruction of the cranial endocast, inner ear endocast (endosseous
4 labyrinth and columella), associated nerves and vessels, and pneumatic cavities in NHMUK
5 PV OR 33095 is shown in Figures 4-5. Because the brain of extant crocodiles and other
6 reptiles does not entirely fill the endocranial cavity, the resulting cranial endocast is more
7 accurately considered a cast of the dural envelope (including many dural venous sinuses)
8 rather than the brain itself (e.g., Jerison, 1973; Hopson, 1979; Rogers, 1999; Witmer et al.,
9 2008). However, although the exact size and shape of the brain are unclear, many portions of
10 the brain (such as the cerebral hemispheres and pituitary fossa) are identifiable, as are some
11 of the cranial nerves and vessels that emanate from the brain. For ease of description we refer
12 to these structures using Anglicized terms for the neuroanatomy under discussion, although it
13 should be noted that these terms actually refer to endocranial osteological correlates of the
14 neural structures.
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32 *Cranial endocast.* The endocast of NHMUK PV OR 33095 is incomplete, due to the
33 breakage of the specimen anteriorly (Figs. 4-5). The break is located somewhere near the
34 forebrain-midbrain juncture, meaning that the midbrain and hindbrain are present but the
35 olfactory tracts and bulbs and other features of the forebrain are not preserved. The preserved
36 portion of the endocast is long and narrow, similar to the shape in another teleosaurid
37 specimen from which a latex endocast was constructed (Wharton, 2000), a teleosaurid
38 specimen in which the endocranial cavity is visible in cross section (Owen, 1842: 83; Seeley,
39 1880:pl. XXIV; Wilberg, 2015:fig. 7), and the metriorhynchids '*Metriorhynchus*' cf.
40 *westermanni* (Fernández et al., 2011), *Dakosaurus* cf. *andiniensis* (Herrera and Vennari,
41 2015), and *Cricosaurus araucanensis* (Herrera et al., 2013). Modern crocodylians have a
42 similar shape, although with greater flexures between the midbrain and hindbrain (cephalic
43 flexure) and within the hindbrain (pontine flexure) (Colbert, 1946a; Witmer et al., 2008;
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3 Dufeu and Witmer, 2015; Fig. 3). Because they have very subtle flexures, thalattosuchian
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5 endocasts appear tubular in shape, compared to the more kinked, sigmoidal endocasts of
6
7 extant species.
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10 The cerebral hemispheres can be clearly located on the endocast (Fig. 5, cer) . They
11
12 are large, bulbous structures that project laterally, although not to the same extent as in
13
14 modern crocodilians (Witmer et al., 2008; Fig. 3). The optic lobes are visible as subtle
15
16 swellings directly posterior to the cerebral region. In most modern adult crocodilians, the
17
18 optic lobes typically do not appear as discrete swellings on the endocast (e.g., *Crocodylus*
19
20 *johnsoni*; Witmer et al., 2008), but in young specimens the optic lobes protrude further
21
22 laterally (e.g., *Caiman crocodilus*: Fig. 3; *Alligator mississippiensis*: Dufeu and Witmer,
23
24 2015). Ventral to the cerebrum is the pituitary fossa (Figs. 4-5, pf), which is anteroposteriorly
25
26 elongate and dorsoventrally low, as in modern crocodilians (e.g., Witmer et al., 2008) and
27
28 other thalattosuchians (e.g., Seeley, 1880; Fernández et al., 2011). The fossa is larger relative
29
30 to the rest of the endocast than in extant taxa. In NHMUK PV OR 33095 and other
31
32 thalattosuchians the pituitary fossa is oriented roughly parallel to the main axis of the
33
34 endocast (with the lateral semicircular canal of the ear oriented horizontally for reference),
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36 whereas in modern crocodilians the fossa is often angled obliquely, in a posteroventral-
37
38 anterodorsal direction (Fig. 3; Witmer et al., 2008; Dufeu and Witmer, 2015). This may be
39
40 related to the more flexed endocasts of these species, or a geometric consequence of the
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42 pituitary fossa being somewhat larger in thalattosuchians than in extant crocodiles.
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48 The internal carotid arteries are the most salient arterial vessels associated with the
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50 endocast (Figs. 4-5, ic). The carotid canals extend from the large foramina on the posterior
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52 surface of the braincase, one on each side ventrolateral to the foramen magnum, and then
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54 continue posteriorly into the braincase, where their internal tracts are temporarily lost in the
55
56 CT data as they pass through the pharyngotympanic sinus, as in extant crocodylians (Dufeu
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3 and Witmer, 2015). The carotid tracts reemerge ventral to the endosseous labyrinth, where
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5 each carotid sharply deflects medially. The left and right carotid canals converge at the
6
7 posterior end of the pituitary fossa (in the region of the hypophyseal recess) and continue into
8
9 the fossa as a single large midline vessel. This architecture is similar to that known in other
10
11 thalattosuchians (e.g., Fernández et al., 2011) and modern crocodylians (Fig. 3; e.g., Colbert,
12
13 1946a; Witmer et al., 2008; Dufeu and Witmer, 2015).

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16 All of the cranial nerves are visible in the CT data, although these are usually most
17
18 discernable either near the external braincase surface (where they traverse the braincase
19
20 through foramina) or near the endocast (where they emerge from the brain). The largest and
21
22 most distinctive nerve is the trigeminal (cranial nerve V), the large ganglion of which would
23
24 have been located outside of the endocranial cavity, within the huge fossa on the lateral
25
26 surface of the braincase (see above) (Figs. 4-5). A large external trigeminal ganglion was also
27
28 present in other thalattosuchians (e.g., Holliday and Witmer, 2009; Fernández et al., 2011),
29
30 other early crocodylomorphs (e.g., *Sphenosuchus acutus*: Walker 1990), close
31
32 crocodylomorph outgroups (e.g., *Gracilisuchus stipanicorum*: Holliday and Witmer, 2009),
33
34 and the extant crocodylians (e.g., Colbert, 1946a; Witmer et al., 2008; Dufeu and Witmer,
35
36 2015). This is therefore a plesiomorphic feature of crocodylomorphs that they retained from
37
38 their distant archosaurian ancestors.
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43 The major nerves extending from the ventrolateral portion of the midbrain and
44
45 passing near the pituitary fossa are difficult to trace. There is a set of narrow, paired nerves
46
47 emerging from the ventral surface of the endocast anterior to the endosseous labyrinth, which
48
49 extend anteriorly and are partially covered in ventral view by the large pituitary fossa (Fig.
50
51 5). The oculomotor (CN III), trochlear (CN IV), and abducens (CN VI) nerves emerge from
52
53 this region in *Crocodylus johnsoni* (Witmer et al., 2008). These structures in NHMUK PV
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55 OR 33095 could potentially be the oculomotor nerves, as large oculomotor nerves have been
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3 identified in this area in '*Metriorhynchus*' cf. *westermanni* (Fernández et al., 2011).
4
5 However, they are located in a similar position to the abducens nerves in *Pelagosaurus typus*
6
7 (Dufeu, 2011), and therefore we consider this to be the most likely identification. The nerves
8
9 exiting the posterior surface of the braincase—CN IX to CN XII—can be traced in the CT
10
11 data. We illustrate the best-preserved regions, where small portions of their tracts are seen to
12
13 extend internally from the external foramina before becoming less distinct further internally
14
15 (Figs. 4-5). As explained above, the neurovascular bundle leading internally from the vagus
16
17 (or multipurpose) opening can be traced in the CT data, but disappears into the otoccipital
18
19 sinus and is not seen to reemerge to meet the endocast.
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22
23 There is a single midline hollow structure extending anteriorly from the basisphenoid
24
25 sinus in the region where the carotids meet the pituitary fossa (Figs. 4,5, mpsd). It would have
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27 continued further anteriorly, as its internal tract is exposed at the broken anterior surface of
28
29 the braincase. The identity of this structure is somewhat uncertain, as it is not present in
30
31 *Alligator mississippiensis*, whose internal sinus system has been the subject of detailed
32
33 description (Dufeu and Witmer, 2015), but is likely an anterior pneumatic diverticulum of
34
35 this sinus (which is part of the median pharyngeal sinus system and pneumatized by the
36
37 median pharyngeal tube between the basioccipital and basisphenoid posteriorly) or
38
39 vasculature leading into the sinus. A similar sinus diverticulum has been noted in the
40
41 thalattosuchian *Pelagosaurus typus* (Dufeu, 2011).
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46 Furthermore, there are large, thick, paired vessels extending anteriorly from the
47
48 pituitary fossa (Figs. 4-5, oa). These continue to the broken anterior surface of the specimen,
49
50 so they would have extended further anteriorly in life. These are not present (or at least not as
51
52 large) in modern crocodylians (Colbert, 1946a; Witmer et al., 2008; Dufeu and Witmer,
53
54 2015) and are not visible in recently studied thalattosuchians whose braincases are either not
55
56 well preserved or are broken too far posteriorly to contain these vessels (e.g., Wharton, 2000;
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3 Fernández et al., 2011; Herrera and Vennari, 2015). They were, however, noticed by Seeley
4
5 (1880:pl. XXIV) in his study of a teleosaurid skull in which the endocranial cavity was
6
7 visible in cross section. He identified them as the optic nerves (CN II), but recent work on
8
9 modern crocodylians shows that the optic nerves actually project from the endocranium much
10
11 further anterodorsally, in front of the cerebrum and far anterior to the pituitary fossa (e.g.,
12
13 Witmer et al., 2008; Dufeu and Witmer, 2015). Instead, we interpret these structures as the
14
15 orbital arteries, because these vessels extend anteriorly out of the pituitary fossa in extant
16
17 diapsids (Porter, 2015). These large vessels extending anteriorly from the pituitary fossa are
18
19 approximately the same size as the internal carotids from which they branch posteriorly
20
21 within the fossa.
22
23

24
25 There is a large paired venous sinus above the hindbrain that is continuous with the
26
27 dural space (Figs. 4-5, dvs). This represents a portion of the dural venous sinus system that
28
29 was described in a teleosaurid by Wharton (2000) and subsequently noted in metriorhynchid
30
31 thalattosuchians (Fernández et al., 2011; Herrera and Vennari, 2015), but is not present in
32
33 such a hypertrophied form in modern crocodylians (Fig. X; Witmer et al., 2008; Dufeu and
34
35 Witmer, 2015). In NHMUK PV OR 33095 the venous sinus on each side connects to the
36
37 dorsal portion of the endocranium in the region between the endosseous labyrinth and trigeminal
38
39 foramen. This venous structure is the posterior portion of the transverse sinus (middle
40
41 cerebral vein) system that is a very consistent element of the encephalic venous drainage
42
43 system in archosaurs, albeit reduced in extant crocodylians (Wharton, 2000; Sampson and
44
45 Witmer, 2007; Witmer et al., 2008; Witmer and Ridgely, 2009; Porter and Witmer, 2015). In
46
47 thalattosuchians, this posterior branch (the posterior middle cerebral vein) is hypertrophied.
48
49 In *Pelagosaurus typus* (LMW, pers. obs.), the vein has a branch that reaches the occiput,
50
51 which is very common in archosaurs; this is probably also the case in NHMUK PV OR
52
53 33095, although the CT data are not entirely clear on this point. However, the major portion
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3 of this vein in the thalattosuchians '*Metriorhynchus*' cf. *westermanni* (Fernández et al., 2011)
4 and *Pelagosaurus typus* (pers. obs.) is directed laterally to open into the supratemporal fossa
5 via a large aperture and then continues on to open into the middle-ear region. The branch
6 leading to the supratemporal opening would correspond to the dorsal head vein of other
7 diapsids (Sampson and Witmer, 2007; Witmer et al. 2008) or the temporoorbital vein of
8 extant crocodylians (Porter, 2015). Although not fully illustrated here, the CT data for
9 NHMUK PV OR 33095 do indeed show that posterior middle cerebral vein does open via a
10 large dorsal head vein aperture in the posterior portion of the supratemporal fossa. However,
11 unlike in '*Metriorhynchus*' cf. *westermanni* (Fernández et al., 2011) and *Pelagosaurus typus*
12 (LMW, pers. obs.), there is no evidence that vein reaches the middle-ear space or any of its
13 pneumatic diverticula.
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30 *Pneumatic sinuses.* The braincase of NHMUK PV OR 33095 is pneumatic, with internal
31 sinuses filling many of the bones surrounding the endocast. Most of these sinuses are in the
32 same positions as those identified in modern crocodylians by Dufeu and Witmer (2015), and
33 therefore we use their terminology here. As in the extant taxa, the braincase sinuses of
34 NHMUK PV OR 33095 can be divided into two systems: a median pharyngeal sinus system
35 underneath the endocast that communicates with the pharynx via a midline median
36 pharyngeal tube (sometimes called the 'median Eustachian tube'), and a pharyngotympanic
37 sinus system on each side of the endocast, which communicates with the pharynx via a lateral
38 (true) Eustachian tube and is intimately associated with the middle ear (Witmer et al. 2008;
39 Dufeu and Witmer 2015).
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51
52 The median pharyngeal sinus excavates the interior of the basisphenoid (Fig. 4, mps).
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54 The median pharyngeal tube enters the recess by passing through the medial pharyngeal
55 foramen, the large opening on the ventral surface of the braincase between the basioccipital
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3 and basisphenoid (Fig. 4, mpt). The sinus fills nearly the entire posterior portion of the
4
5 basisphenoid, terminating anteriorly where the internal carotids meet the endocast.
6

7
8 Extensions of the sinus, the subcarotid recesses, extend laterally to underlie the carotids in the
9
10 region where they curve medially to enter the pituitary fossa (Fig. 4, scr). The subcarotid
11
12 recesses are greatly expanded in NHMUK PV OR 33095. These recesses become larger
13
14 during ontogeny in *Alligator* (Dufeu and Witmer, 2015). A median pharyngeal sinus system
15
16 is also present in '*Metriorhynchus*' cf. *westermanni* (Fernández et al., 2011) and *Dakosaurus*
17
18 cf. *andiniensis* (Herrera and Vennari, 2015), and the large median pharyngeal foramen seen
19
20 in many other early crocodylomorphs, visible externally without the aid of CT, indicates that
21
22 this sinus system is a common feature of crocodylomorphs (e.g., Nesbitt, 2011; Pol et al.,
23
24 2013).
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28 The pharyngotympanic sinus system is much more extensive and complex than the
29
30 relatively simple midline medial pharyngeal sinus. Dufeu and Witmer (2015) have shown
31
32 that the pharyngotympanic system consists of seven main diverticula in modern *Alligator*,
33
34 which throughout ontogeny generally become larger, begin to coalesce, and ultimately merge
35
36 together into an expansive sinus. Some, but not all, of these diverticula are present in
37
38 NHMUK PV OR 33095. These recesses are discussed individually below.
39

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41 (1) The basioccipital diverticulum that fills the basal tubera and part of the
42
43 surrounding bone is absent, as the basioccipital is solid internally. (2) The recessus
44
45 epitubericus, a finger-like cavity that fits between the trigeminal ganglion (above) and
46
47 internal carotid (below) and extends anterior to the internal carotids in ventral view, is also
48
49 absent. (3) Because the pterygoid is unknown in NHMUK PV OR 33095, it is not clear if
50
51 there was a pterygoid diverticulum. However, as this extends from the recessus epitubericus
52
53 into the pterygoid in *Alligator*, the lack of the recessus epitubericus in NHMUK PV OR
54
55 33095 suggests that, if present, a pterygoid diverticulum must have emerged from another
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3 source. (4) The intertympanic diverticulum, which pervades the prootic and supraoccipital
4 above the foramen magnum and occasionally extends into the parietal in *Alligator*, is absent.
5
6 The enlarged dorsal dural venous sinus occupies a similar position (although it has a different
7 source), so this may be precluding the development of an intertympanic sinus.
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11 (5) There is a large prootic diverticulum filling much of the prootic posterior to
12 trigeminal ganglion and immediately anterior to the inner ear canals (Fig. 4, ptspd). This
13 appears to be equivalent to what Fernández et al. (2011) refer to as the ‘middle ear cavity’ in
14 ‘*Metriorhynchus*’ cf. *westermanni*, as it occupies the same part of the prootic surrounding the
15 inner ear and posterior to the ganglion. Unlike the case in *Alligator*, there is no external fossa
16 on the prootic leading into this recess (Dufeu and Witmer, 2015: fig. 9).
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25 (6) There is limited pneumaticity in the quadrate, the result of a suspensorium
26 diverticulum (Fig. 4, ptssd). Dufeu and Witmer (2015) described how this diverticulum
27 consists of two separate but convergent diverticula in *Alligator*: an infundibular diverticulum
28 filling much of the main body of the quadrate and a quadrate diverticulum that hollows out
29 the quadrate condyles and sends a thin extension, the siphonium, out through an external
30 foramen on the condyles and into the articular bone. The infundibular diverticulum is clearly
31 present in NHMUK PV OR 33095. It pervades most of the ventral portion of the quadrate
32 body, and communicates with the prootic diverticulum anteriorly and dorsally, otoccipital
33 diverticulum posteriorly and medially, and medial pharyngeal sinus ventrally. This is
34 equivalent to ‘cavity 2’ of Fernández et al. (2011), which they identified in ‘*Metriorhynchus*’
35 cf. *westermanni*. However, there is no sign of a quadrate diverticulum in NHMUK PV OR
36 33095. The quadrate condyles are solid internally and there is no external foramen for
37 transmitting the siphonium.
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54 (7) There is a large otoccipital diverticulum that fills the otoccipital lateral to the
55 foramen magnum, completely surrounding the neurovascular bundle for nerves IX-XI (Fig. 4,
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3 ptsod). This recess occupies only the ventral half of the paroccipital process, making it much
4
5 less extensive than the condition in all stages of *Alligator* ontogeny, in which the recess fills
6
7 the entire depth of the otoccipital (Dufeu and Witmer, 2015). '*Metriorhynchus*' cf.
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9 *westermanni* also has an otoccipital diverticulum limited to the ventral half of the paroccipital
10
11 process, which may indicate that this is a common feature of thalattosuchians (Fernández et
12
13 al., 2011). In NHMUK PV OR 33095 the otoccipital recess is divided into dorsal and ventral
14
15 partitions, which are separate from each other posteriorly but merge anteriorly. The bundle
16
17 for the vagus nerve and associated structures leads into the dorsal partition. Based on the
18
19 condition in '*Metriorhynchus*' cf. *westermanni*, it is likely this dorsal partition communicated
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21 with the expansive dorsal dural venous sinus above the endocast (Fernández et al., 2011).
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27 *Inner ear.* The endosseous labyrinth is similar in shape to that of modern crocodilians, with a
28
29 triangular vestibular apparatus dorsally (consisting of the semicircular canals and sacculus)
30
31 and an elongate cochlear (lagena) duct ventrally, which is dorsoventrally deeper than the
32
33 vestibular apparatus (Fig. 4-6; Owen, 1850; Colbert, 1946b; Witmer et al., 2008; Dufeu and
34
35 Witmer, 2015). As in most living species, the cochlear duct is directed medially, with a slight
36
37 curvature along the posterior margin. The three semicircular canals are approximately
38
39 orthogonal to each other, and the anterior and posterior canals meet at the common crus,
40
41 which is approximately the same diameter as the canals themselves (Table 1). The anterior
42
43 semicircular canal is expanded very slightly further anteriorly than the posterior canal is
44
45 posteriorly. As a result, there is a slightly larger gap between the anterior canal and the
46
47 common crus than there is between the posterior canal and the crus. Unlike in modern
48
49 crocodilians (Fig. 7) and most other archosaurs, however, the anterior and posterior
50
51 semicircular canals extend to the same level dorsally when seen in lateral view (e.g., Witmer
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53 et al., 2008: fig. 6.5). It should be noted that modern crocodilians are unusual among fossil
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3 and extant archosaurs in having an anterior canal that is only marginally expanded dorsally
4
5 relative to the posterior canal.
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7 Using the methods of Walsh et al. (2009), we estimate that NHMUK PV OR 33095
8
9 had a mean hearing sensitivity (MHS) of 1500 Hz, and a hearing range (HR) of 2400 Hz (Fig.
10
11 8). These values are towards the higher end of the spectrum of hearing sensitivity known in
12
13 living crocodylian species (*Crocodylus acutus*: MHS 1650 Hz, HR 2700 Hz [Wever, 1978];
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15 *Alligator mississippiensis*: MHS 550 Hz, HR 900 Hz [Wever, 1978]; *Caiman crocodylus*:
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17 MHS 1150 Hz, HR 1700 Hz [Manley, 1990]).
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20 21 22 23 **DISCUSSION**

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27 The CT data for *Steneosaurus cf. gracilirostris* (NHMUK PV OR 33095) provide important
28
29 new information on the ears, cranial sinuses, and cranial vascularization of extinct
30
31 crocodylomorphs. This, in turn, provides insight into the origin of modern crocodylian
32
33 morphologies and helps reveal how the peculiar extinct thalattosuchians were modifying their
34
35 senses and cranial systems as they transitioned into an aquatic habitat.
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41 *Hearing and balance.* Some of the most striking evidence comes from the endosseous
42
43 labyrinth, which would have housed the membranous inner ear in life. NHMUK PV OR
44
45 33095 has a relatively elongate cochlear duct, the part of the inner ear related to hearing. An
46
47 elongate cochlear duct is known to have been present in the Permian basal diapsid reptile
48
49 *Youngina capensis*, pointing to an early origin for enhanced hearing frequency sensitivity in
50
51 terrestrially-adapted diapsids (Walsh et al., 2014), the larger group of reptiles to which
52
53 lizards, crocodylomorphs, and birds belong. However, extant diapsid clades (e.g., squamates,
54
55 rhynchocephalians and, if included within Diapsida, turtles) possess relatively short cochlear
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3 ducts (Walsh et al., 2009), and the trend toward duct elongation appears to be largely
4
5 confined to Archosauromorpha (the diapsid subclade including crocodylomorphs, dinosaurs,
6
7 pterosaurs, and birds). This elongation was presumably present in fully terrestrial stem
8
9 archosauromorphs, and the relatively elongate cochlear duct in *Steneosaurus* cf. *gracilirostris*
10
11 must therefore be retained from a fully terrestrial crocodylian ancestor. This fits with our
12
13 current understanding of crocodylomorph phylogenetics, as the oldest and most primitive
14
15 members of the group are terrestrial species such as *Sphenosuchus* and *Terrestrisuchus* (e.g.,
16
17 Nesbitt, 2011).
18
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21 The length of the cochlear duct is strongly correlated with, and thus predictive of, best
22
23 hearing range and mean hearing frequency in extant birds and reptiles (Walsh et al., 2009).
24
25 When we add NHMUK PV OR 33095 to a dataset with a variety of modern taxa, we estimate
26
27 its hearing sensitivity to be towards the known upper range of living crocodylian auditory
28
29 sensitivity values (Fig. 8). Furthermore, the cochlear duct length of NHMUK PV OR 33095
30
31 is located within a point cloud of many other taxa, meaning that it is not an outlier and not
32
33 greatly different in relative length to the cochleae of modern reptiles and birds. This strongly
34
35 suggests that hearing in air remained important to *Steneosaurus* cf. *gracilirostris*, and that
36
37 only limited, if any, adaptation to sound transmission in water had occurred in this
38
39 thalattosuchian. Further information from the middle ear ossicle would be useful for
40
41 determining whether there are differences in impedance matching between terrestrial (fossil)
42
43 and aquatic/semi-aquatic crocodylians, but to our knowledge this has yet to be tested
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45 quantitatively.
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50 As with the auditory region of the labyrinth, the vestibular apparatus of NHMUK PV
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52 OR 33095 is not greatly different to that seen in living crocodylians. The vestibular system in
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54 extinct archosaurs has received a great deal of attention in recent years thanks to the advent of
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56 μ CT approaches, but much of this has centered on birds and dinosaurs, with far fewer studies
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3 of fossil crocodylians and stem archosaurs (Walsh et al., 2014). Although variation in
4
5 vestibular system morphology over archosaur evolution is presently incompletely known, a
6
7 strong trend toward anterior semicircular canal expansion is clearly apparent in bipedal
8
9 archosaurs (Georgi et al., 2013), and also in pterosaurs (Witmer et al., 2003). This has been
10
11 attributed to sensitivity to the pitching motion of the head (Sipla, 2007), but some expansion
12
13 of the anterior canal is also apparent in quadrupedal dinosaurs and crocodiles (Witmer et al.,
14
15 2008). The reason for this is unclear, but anterior canal expansion may also be positively
16
17 correlated with head mass (Georgi et al., 2013).
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21 In NHMUK PV OR 33095, the anterior semicircular canal is only slightly longer than
22
23 the posterior canal (Table 1), suggesting sensitivity to pitching was less important for this
24
25 taxon. This may be consistent with a more aquatic lifestyle involving reduced head rotation
26
27 along the sagittal plane. However, although the lateral semicircular canal is slightly longer
28
29 than the anterior canal, its larger cross sectional diameter (Table 1) and relatively straight and
30
31 uncurved morphology around the sacculus seem poorly optimized for sensitivity. Another
32
33 possibility is that the neck of *Steneosaurus* cf. *gracilirostris* was less flexible than the neck of
34
35 most living crocodiles, removing some of the requirement for sensitivity to pitch and yaw
36
37 through increased coupling with the trunk (but see Spoor et al., 2002 for an alternative view
38
39 of this situation in cetaceans). However, the cervical flexibility of teleosaurids appears to
40
41 have been comparable with that of living crocodylians, and reduction in flexibility would have
42
43 had important implications for feeding behavior in this longirostrine taxon. We suspect that
44
45 this canal circumference reduction instead relates to lower head mass relative to other
46
47 crocodylians, due to a more gracile and lighter rostrum. This possibility is supported by the
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49 reduced canal expansion in the longirostrine *Tomistoma* and *Gavialis*, relative to broad-
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51 snouted living crocodylians (Fig. 7).
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3 *Cranial pneumaticity*. NHMUK PV OR 33095 possesses some, but not all, of the standard
4 pharyngotympanic sinuses of modern crocodylians (Dufeu and Witmer, 2015). The
5 basioccipital diverticulum, recessus epitubericus, and intertympanic diverticulum are absent.
6
7 Furthermore, the suspensorium diverticulum is greatly reduced compared to modern species,
8 such that it only occupies a portion of the quadrate and does not extensively hollow out the
9 bone and extend posteriorly from the braincase, out through the siphoneal opening on the
10 quadrate condyle and into the articular, as in the extant taxa. Only the prootic and otoccipital
11 diverticula are similar in their position and large sizes to the same recesses in the living
12 species. What is particularly interesting is that all of the recesses lacking in NHMUK PV OR
13 33095 appear very early in the ontogeny of *Alligator* and are uniformly present in all studied
14 specimens (Dufeu and Witmer, 2015), meaning that their absence in the teleosaurid
15 specimen is not likely due to ontogeny or individual variation.
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30 It is difficult to explain why NHMUK PV OR 33095 had limited pneumaticity
31 compared to modern crocodylians, but there are several possibilities. It may be that a more
32 limited set of pharyngotympanic sinuses is the ancestral condition for Crocodylomorpha, and
33 thus *Steneosaurus cf. gracilirostris* is exhibiting this morphology because of its relatively
34 basal position in the family tree. Perhaps extensive sinuses evolved in concert with a quadrate
35 that is more firmly sutured to the remainder of the braincase (see discussion in Dufeu and
36 Witmer [2015]), which occurred later in crocodylomorph evolutionary history. Alternatively,
37 it is possible that NHMUK PV OR 33095 evolved from ancestors with a more extensive
38 array of pharyngotympanic sinuses similar to modern crocodylians, but it (and possibly other
39 thalattosuchians) apomorphically lost some of the diverticula. If so, this could potentially be
40 related to lifestyle, perhaps due to changes resulting from the transition to a more aquatic
41 habitat such as increased reliance on diving to catch prey, changes in buoyancy, or alterations
42 to the hearing system. Third, there may be a link with diet, as Dufeu and Witmer (2015)
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3 observed that feeding specialists with long snouts and enlarged adductor chambers, like
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5 modern gharials, exhibit a reduction in the number and extent of diverticula, whereas feeding
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7 generalists, like the extinct sebecids, have more expansive sinuses. Although the functional
8
9 link between sinus morphology and diet is unclear, it is noteworthy that teleosaurids are
10
11 gharial-like in morphology, and probably had a similar diet, so this could explain the
12
13 moderate sinuses. Finally, it may be that NHMUK PV OR 33095 is simply an unusual
14
15 individual in a species or clade that is rife with variation. This may be unlikely, but we note
16
17 that modern *Alligator* exhibits more extensive pneumaticity than *Crocodylus* (Witmer et al.,
18
19 2008; Dufeau and Witmer, 2015). Testing these hypotheses will require CT-based sinus
20
21 reconstructions for other thalattosuchians and, critically, other basal crocodylomorphs such as
22
23 'sphenosuchians' that will give insight into the primitive conditions of the clade and
24
25 variability among closely related taxa.
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32 *Vasculature and salt glands.* Among the most noticeable internal features of NHMUK PV
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34 OR 33095 are the enlarged internal carotid and orbital arteries. These two vessels are
35
36 functionally linked, as the carotids enter the pituitary fossa posteriorly, and then the orbital
37
38 arteries emerge from the fossa and continue anteriorly towards the snout. Therefore, the large
39
40 size of one is probably linked to the enlargement of the other.
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43 Previously, it has been suggested that enlarged internal carotids (as indicated by large
44
45 foramina on the posterior surface of the braincase) are diagnostic of metriorhynchids, but
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47 here we show that they are also present in teleosaurids. Thus, large internal carotids appear to
48
49 be a thalattosuchian feature. Why are these arteries so large in thalattosuchians? Branches of
50
51 the internal carotids supply the salt glands in some modern vertebrates, and the large size of
52
53 the carotids in metriorhynchids has been explained as a mechanism for increasing blood flow
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55 to the glands, which are known to have been present based on CT data (e.g., Herrera et al.,
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3 2013). We therefore suggest that these large vessels in NHMUK PV OR 33095 also supplied
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5 large salt glands. This can be tested further by CT scanning teleosaurid specimens with more
6
7 complete snouts, to determine whether the osteological correlates of metriorhynchid salt
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9 glands are also present.
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12 Previous studies have considered large salt glands to be a unique adaptation of
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14 metriorhynchids among basal crocodylomorphs, an integral component of their transition to a
15
16 fully marine existence (e.g., Fernández and Gasparini, 2000, 2008; Gandola et al., 2006;
17
18 Fernández and Herrera, 2009; Herrera et al., 2013). If teleosaurids like *Steneosaurus* cf.
19
20 *gracilirostris* also possessed large salt glands, this would indicate that the glands evolved first
21
22 in semi-aquatic thalattosuchians that were still well adapted for hearing sounds on land (see
23
24 above), not just in the fully marine species. Or, perhaps the salt glands evolved even earlier in
25
26 crocodylomorph phylogeny, in terrestrial taxa, and thus were a 'pre-adaptation' that helped
27
28 thalattosuchians become so successful in semi-aquatic and pelagic niches. This can be tested
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30 by CT scanning a wider range of basal crocodylomorphs to determine if osteological
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32 correlates of salt glands are present.
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40 *Transition from semi-aquatic to aquatic habitats.* Teleosaurid thalattosuchians like
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42 *Steneosaurus* cf. *gracilirostris* were semi-aquatic animals, closely related to the pelagic
43
44 metriorhynchids and proxies for the ancestral morphologies and behaviors that were modified
45
46 as metriorhynchids transitioned into a fully aquatic niche. CT data for NHMUK PV OR
47
48 33095 indicate that teleosaurids had already developed several signature cranial features of
49
50 metriorhynchids, such as a large dorsal dural venous sinus, enlarged internal carotids, and
51
52 potentially a salt gland. Furthermore, in overall morphology, the braincase of *Steneosaurus*
53
54 cf. *gracilirostris* is remarkably similar to those of metriorhynchids (e.g., Pol and Gasparini,
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56 2009; Fernández et al., 2011). This indicates that there was no great morphological gulf in
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2
3 endocranial anatomy between these two groups of thalattosuchians, and some of the features
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5 that later permitted metriorhynchids to successfully invade the aquatic realm were first
6
7 developed in the semi-aquatic teleosaurids and other basal thalattosuchians.
8

9
10 Future work should focus on detailed internal endocranial descriptions of
11
12 metriorhynchid braincases, using CT data. This will hold the key to determining how other
13
14 features of the skull and sensory systems were modified as metriorhynchids moved into the
15
16 open water. Most problematically, little is currently known about the inner ears and
17
18 pharyngotympanic sinuses of metriorhynchids, so it is unclear whether they shared with
19
20 NHMUK PV OR 33095 an ear that was still well attuned to hear on land, and if not when an
21
22 ear better equipped to function in the water evolved. Likewise, changes in semicircular canal
23
24 circumference may be expected in metriorhynchids as their heads became increasingly
25
26 coupled with their bodies as cervical flexibility was lost. It is also uncertain whether
27
28 metriorhynchids shared with NHMUK PV OR 33095 the same limited array of
29
30 pharyngotympanic sinuses relative to modern crocodylians, and if there were detailed
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32 differences between the sinus systems of teleosaurids and metriorhynchids that could be
33
34 explained by the latter's unusual habitat. As more CT data become available for teleosaurids
35
36 and metriorhynchids, these thalattosuchians may emerge as something of a model system for
37
38 understanding how anatomy changes during major evolutionary transitions in deep time.
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45 **ACKNOWLEDGEMENTS**

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12
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14
15
16
17

18 LITERATURE CITED

19
20
21
22
23 Andrews CW. 1913. A descriptive catalogue of the marine reptiles of the Oxford Clay, Part
24
25 Two. British Museum (Natural History), London.

26
27 Brusatte SL, Benton MJ, Desojo JB, Langer MC. 2010. The higher-level phylogeny of
28
29 Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology* 8:3-47.

30
31 Brusatte SL, Sereno PC. 2007. A new species of *Carcharodontosaurus* (Dinosauria:
32
33 Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of*
34
35 *Vertebrate Paleontology* 27:902-916.
36
37

38 Busbey AB. 1995. The structural consequences of skull flattening in crocodylians. In:
39
40 Thomason JJ, editor. *Functional morphology in vertebrate paleontology*. Cambridge:
41
42 University Press, p 173–192.
43
44

45 Chiarenza A, Foffa D, Young MT, Insacco G, Cau A, Carnevale G, Catanzariti R. 2015. The
46
47 youngest record of metriorhynchid crocodylomorphs, with implications for the
48
49 extinction of Thalattosuchia. *Cretaceous Research* 56:608–616.
50
51

52 Clark JM, Xu X, Forster CA, Wang Y. 2004. A Middle Jurassic 'sphenosuchian' from China
53
54 and the origin of the crocodylian skull. *Nature* 430:1021-1024.
55
56
57
58
59
60

- 1
2
3 Colbert EH. 1946a. *Sebecus*, representative of a peculiar suborder of fossil Crocodylia from
4 Patagonia. Bulletin of the American Museum of Natural History 87:221–270.
5
6
7 Colbert EH. 1946b. The eustachian tubes in crocodiles. Copeia 1946:12–14.
8
9
10 Dufeu DL. 2011. The evolution of cranial pneumaticity in Archosauria: patterns of
11 paratympanic sinus development. Unpublished PhD dissertation. Athens (OH): Ohio
12 University, 174 pp.
13
14
15
16 Dufeu DL, Witmer LM. 2015. Ontogeny of the middle-ear air-sinus system in *Alligator*
17 *mississippiensis* (Archosauria: Crocodylia). PLoS ONE 10(9):e0137060.
18
19 doi:10.1371/journal.pone.0137060
20
21
22
23 Fernández MS, Carabajal AP, Gasparini Z, Chong Diaz G. 2011. A metriorhynchid
24 crocodyliform braincase from northern Chile. Journal of Vertebrate Paleontology
25
26 31:369–377.
27
28
29
30 Fernández M, Gasparini Z, 2000. Salt glands in a Tithonian metriorhynchid crocodyliform
31 and their physiological significance. Lethaia 33:269–276.
32
33
34 Fernández M, Gasparini Z, 2008. Salt glands in the Jurassic metriorhynchid *Geosaurus*:
35 implications for the evolution of osmoregulation in Mesozoic crocodyliforms.
36
37 Naturwissenschaften 95:79–84.
38
39
40
41 Fernández M, Herrera Y. 2009. Paranasal sinus system of *Geosaurus araucanensis* and the
42 homology of the antorbital fenestra of metriorhynchids (Thalattosuchia:
43 Crocodylomorpha). Journal of Vertebrate Paleontology 29:702–714.
44
45
46
47 Foffa D, Young MT. 2014. The cranial osteology of *Tyrannoneustes lythrodectikos*
48 (Crocodylomorpha: Metriorhynchidae) from the Middle Jurassic of Europe. PeerJ
49
50 2:e608. <http://dx.doi.org/10.7717/peerj.608>
51
52
53
54 Fraas E. 1902. Die Meer-Krocodilier (Thalattosuchia) des oberen Jura unter specieller
55
56
57
58
59
60

- 1
2
3 Gandola R, Buffetaut E, Monaghan N, Dyke G. 2006. Salt glands in the fossil crocodile
4
5 *Metriorhynchus*. *Journal of Vertebrate Paleontology* 26:1009-1010.
6
7
8 Gasparini ZB, Vignaud P, Chong G. 2000. The Jurassic Thalattosuchia (Crocodyliformes) of
9
10 Chile: a paleobiogeographic approach. *Bulletin de la Société Géologique de France*
11
12 171:657–664.
13
14 Georgi JA, Sipla JS, Forster CA 2013. Turning Semicircular Canal Function on Its Head:
15
16 Dinosaurs and a Novel Vestibular Analysis. *PLoS ONE* 8(3):e58517. doi:
17
18 10.1371/journal.pone.0058517.
19
20
21 Herrera Y, Fernández MS, Gasparini Z. 2013. The snout of *Cricosaurus araucanensis*: a case
22
23 study in novel anatomy of the nasal region of metriorhynchids. *Lethaia* 46:331–340.
24
25 Herrera Y, Vennari VV. 2015. Cranial anatomy and neuroanatomical features of a new
26
27 specimen of Geosaurini (Crocodylomorpha: Metriorhynchidae) from west-central
28
29 Argentina. *Historical Biology* 27:33–41.
30
31
32 Holliday CM, Witmer LM. 2009. The epipterygoid of crocodyliforms and its significance for
33
34 the evolution of the orbitotemporal region of eusichians. *Journal of Vertebrate*
35
36 *Paleontology* 29:715–733.
37
38
39 Hopson JA. 1979. Paleoneurology. In: Gans C, editor. *Biology of the Reptilia*, Vol 9,
40
41 *Neurology*. New York: Academic Press, p 39-146.
42
43 Hua S, Buffrénil V. de. 1996. Bone histology as a clue in the interpretation of functional
44
45 adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate*
46
47 *Paleontology* 16:703–717.
48
49
50 Iordansky NN. 1973. The skull of the Crocodilia. In: Gans C, Parsons TS, editors. *Biology of*
51
52 *the Reptilia*, Volume 4. New York: Academic Press, p 201–262.
53
54
55 Jerison HJ. 1973. *Evolution of the brain and intelligence*. New York: Academic Press.
56
57
58
59
60

- 1
2
3 Jouve S. 2005. A new description of the skull of *Dyrosaurus phosphaticus* (Thomas, 1893)
4
5 (Mesoeucrocodylia: Dyrosauridae) from the Lower Eocene of North Africa. Canadian
6
7 Journal of Earth Science 42:323–337.
8
9
10 Jouve S. 2009. The skull of *Teleosaurus cadomensis* (Crocodylomorpha; Thalattosuchia), and
11
12 phylogenetic analysis of Thalattosuchia. Journal of Vertebrate Paleontology 29:88–
13
14 102.
15
16 Lepage Y, Buffetaut E, Hua S, Martin JE, Tabouelle J. 2008. Catalogue descriptif,
17
18 anatomique, géologique et historique des fossiles présentés à l'exposition « Les
19
20 Crocodiliens fossiles de Normandie » (6 novembre–14 décembre 2008). Bulletin de la
21
22 Société Géologique de Normandie et des Amis du Muséum du Havre 95:5–152.
23
24
25 McHenry CR, Clausen PD, Daniel WJT, Meers MB, Pendharkar A. 2006. Biomechanics of
26
27 the rostrum in crocodylians: a comparative analysis using finite-element modeling.
28
29 The Anatomical Record Part A 288A:827–849.
30
31
32 Manley GA. 1990. Peripheral hearing mechanisms in reptiles and birds. Berlin, Germany:
33
34 Springer.
35
36
37 Martin JE, Vincent P. 2013. New remains of *Machimosaurus hugii* von Meyer, 1837
38
39 (Crocodylia, Thalattosuchia) from the Kimmeridgian of Germany. Fossil Record
40
41 16:179–196.
42
43
44 Nesbitt SJ. 2011. The early evolution of archosaurs: relationships and the origin of major
45
46 clades. Bulletin of the American Museum of Natural History 352:1-292.
47
48
49 Owen R. 1842. Report on British fossil reptiles, part II. Report of the British Association for
50
51 the Advancement of Science 11:60–204.
52
53
54 Owen R. 1850. On the communications between the cavity of the tympanum and the palate in
55
56 the Crocodylia (gavials, alligators and Crocodiles). Philosophical Transactions of the
57
58 Royal Society 140:521–527.
59
60

- 1
2
3 Porter WR. 2015. Physiological implications of dinosaur cephalic vascular systems.
4
5 Unpublished PhD dissertation. Athens (OH): Ohio University.
6
7 Porter WR, Witmer, LM. 2015. Vascular patterns in iguanas and other squamates: blood
8
9 vessels and sites of thermal exchange. PLOS ONE 10(10):e0139215.
10
11 doi:10.1371/journal.pone.0139215.
12
13
14 Pierce SE, Angielczyk KD, Rayfield EJ. 2008. Patterns of morphospace occupation and
15
16 mechanical performance in extant crocodylian skulls: a combined geometric
17
18 morphometric and finite element modeling approach. Journal of Morphology 269:840–
19
20 864.
21
22
23 Pierce SE, Angielczyk KD, Rayfield EJ. 2009. Shape and mechanics in thalattosuchian
24
25 (Crocodylomorpha) skulls: implications for feeding behaviour and niche partitioning.
26
27 Journal of Anatomy 215:555-576.
28
29
30 Pierce SE, Benton MJ. 2006. *Pelagosaurus typus* Bronn, 1841 (Mesoeucrocodylia:
31
32 Thalattosuchia) from the Upper Lias (Toarcian, Lower Jurassic) of Somerset,
33
34 England. Journal of Vertebrate Paleontology 26:621–635.
35
36
37 Pol D, Gasparini Z. 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia:
38
39 Crocodylomorpha) and the phylogenetic position of Thalattosuchia. Journal of
40
41 Systematic Palaeontology 7:163-197.
42
43
44 Pol D, Rauhut OWM, Lecuona A, Leardi JM, Xu X, Clark JM. 2013. A new fossil from the
45
46 Jurassic of Patagonia reveals the early basicranial evolution and the origins of
47
48 Crocodyliformes. Biological Reviews 88:862-872.
49
50
51 Rogers SW. 1999. *Allosaurus*, crocodiles, and birds: evolutionary clues from spiral computed
52
53 tomography of an endocast. The Anatomical Record 257:162–173.
54
55
56 Sampson SD, Witmer, LM. 2007. Craniofacial anatomy of *Majungasaurus crenatissimus*
57
58 (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Memoirs of the
59
60

- 1
2
3 Society of Vertebrate Paleontology, Journal of Vertebrate Paleontology
4
5 27(Supplement to 2):32–102.
6
7 Seeley HG. 1880. Note on the cranial characters of a large teleosaur from the Whitby Lias
8 preserved in the Woodwardian Museum of the University of Cambridge, indicating a
9 new species, *Teleosaurus eucephalus*. Quarterly Journal of the Geological Society,
10 London. 36:627–634.
11
12 Sipla JS. 2007. The semicircular canals of birds and non-avian dinosaurs. Unpublished PhD
13 dissertation. Stony Brook (NY): State University of New York, Stony Brook.
14
15 Spoor F, Bajpai S, Hussain ST, Kumar K, Thewissen JGM 2002. Vestibular evidence for the
16 evolution of aquatic behaviour in early cetaceans. Nature 417:163–166.
17
18 Walker AD. 1990. A Revision of *Sphenosuchus acutus* Houghton, a Crocodylomorph Reptile
19 from the Elliot Formation (Late Triassic or Early Jurassic) of South Africa.
20 Philosophical Transactions of the Royal Society of London, Series B 330:1–120.
21
22 Walsh SA, Barrett PM, Milner AC, Manley GA, Witmer LM. 2009. Inner ear anatomy is a
23 proxy for deducing auditory capability and behaviour in reptiles and birds. Proceedings
24 of the Royal Society B 276:1355–1360.
25
26 Walsh SA, Zhe-Xi L, Barrett P. 2014. Modern imaging techniques as a window to prehistoric
27 auditory worlds. In: Köppl C, Manley G, editors. Insights from Comparative Hearing
28 Research. Springer Handbook of Auditory Research 49, Springer Verlag. p. 227-261.
29
30 Wever EG. 1978. The reptile ear: its structure and function. Princeton, NJ: Princeton
31 University Press.
32
33 Wenz S. 1968. Contribution à l'étude du genre *Metriorhynchus*. Crâne et moulage
34 endocrânien de *Metriorhynchus superciliosus*. Annales de Paléontologie 54:149–183.
35
36 Westphal F. 1961. Zu Systematik der deutschen und englischen Lias-Krokodilier. Neues
37 Jahrbuch für Geologie und Paläontologie, Abhandlungen, 113:207–218.
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 Westphal F. 1962. Die Krokodilier des Deutschen und Englischen Oberen Lias.
4
5 Palaeontographica Abteilung A 118:23–118.
6
7
8 Wharton DS. 2000. An enlarged endocranial venous system in *Steneosaurus pictaviensis*
9
10 (Crocodylia: Thalattosuchia) from the Upper Jurassic of Les Lourdines, France.
11
12 Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science
13
14 331:221–226.
15
16 Wilberg EW. 2015. What's in an outgroup? The impact of outgroup choice on the
17
18 phylogenetic pPosition of Thalattosuchia (Crocodylomorpha) and the origin of
19
20 Crocodyliformes. Systematic Biology 64:621-637.
21
22
23 Witmer LM, Ridgely RC. 2009. New insights into the brain, braincase, and ear region of
24
25 tyrannosaurs, with implications for sensory organization and behavior. Anatomical
26
27 Record 292:1266–1296.
28
29
30 Witmer LM, Ridgely RC, Dufeu DL, Semones MC. 2008. Using CT to peer into the past:
31
32 3D visualization of the brain and ear regions of birds, crocodiles, and nonavian
33
34 dinosaurs. In: Frey R, Endo H, editors. Anatomical Imaging: Towards a New
35
36 Morphology. Tokyo: Springer-Verlag, p 67-87.
37
38
39 Wu X-C, Chatterjee S. 1993. *Dibothrosuchus elaphros*, a crocodylomorph from the Lower
40
41 Jurassic of China and the phylogeny of the Sphenosuchia. Journal of Vertebrate
42
43 Paleontology 13:58-89.
44
45
46 Young MT, Andrade MB, Etches S, Beatty BL. 2013. A new metriorhynchid
47
48 crocodylomorph from the Lower Kimmeridge Clay Formation (Late Jurassic) of
49
50 England, with implications for the evolution of dermatocranium ornamentation in
51
52 Geosaurini. Zoological Journal of the Linnean Society 169:820–848.
53
54
55 Young MT, Brusatte SL, Andrade MB, Desojo JB, Beatty BL, Steel L, Fernández MS,
56
57 Sakamoto M, Ruiz-Omeñaca JI, Schoch RR. 2012. The cranial osteology and feeding
58
59
60

1
2
3 ecology of the metriorhynchid crocodylomorph genera *Dakosaurus* and *Plesiosuchus*
4
5 from the Late Jurassic of Europe. PLOS ONE 7:e44985.
6

7 Young MT, Brusatte SL, Ruta M, Andrade MB. 2010. The evolution of Metriorhynchoidea
8
9 (Mesoeucrocodylia, Thalattosuchia): an integrated approach using geometrics
10
11 morphometrics, analysis of disparity and biomechanics. Zoological Journal of the
12
13 Linnean Society 158:801–859.
14

15
16 Young MT, Hua S, Steel L, Foffa D, Brusatte SL, Thüring S, Mateus O, Ruiz-Omeñaca JI,
17
18 Havlik P, Lepage Y, Andrade MB. 2014. Revision of the Late Jurassic teleosaurid
19
20 genus *Machimosaurus* (Crocodylomorpha, Thalattosuchia). Royal Society Open
21
22 Science 1:140222.
23
24
25
26
27
28
29
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31
32
33
34
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37
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FIGURE CAPTIONS

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Fig. 1. Braincase of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095) in dorsal (A), ventral (B), posterior (C), anterior (D), right lateral (E), and left lateral (F) views. Scale bar equals 5 cm.

Fig. 2. Photos and line drawings of the braincase of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095) in posterior (A), right lateral (B), and right ventrolateral oblique (C) views. Scale bar equals 5 cm. Abbreviations: bo, basioccipital; bs, basisphenoid; bt, basal tubera; fr, frontal; ic, internal carotid foramen; ls, laterosphenoid; mpf, median pharyngeal foramen; ot, occipital tuberosity; par, parietal; pr, prootic; q, quadrate; so, supraoccipital. Roman numerals designate cranial nerves.

Fig. 3. Internal endocranial anatomy of the extant spectacled caiman, *Caiman crocodilus* (FMNH 73711). Endocranial features illustrated inside transparent skull (A), with scale bar equaling 2 cm. Endocranial features illustrated in anterior (B), posterior (C), right lateral (D), left lateral (E), dorsal (F), and ventral (G) views. Abbreviations: cd, cochlear duct; cer, cerebrum; col, columella (=stapes); el, endosseous labyrinth; ic, internal carotid artery; pf, pituitary fossa; vc, venous canal. Roman numerals designate cranial nerves.

Fig. 4. Internal endocranial anatomy of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095), derived from CT scan data. The specimen is illustrated in dorsal (A), ventral (B), posterior (C), anterior (D), right lateral (E), and left lateral (F) views. Scale bar equals 5 cm. Abbreviations: dvs, dorsal dural venous sinus; el, endosseous labyrinth; en, cranial endocast; ic, internal carotid artery; mpts, median

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3 pharyngeal sinus; mpt, median pharyngeal tube; oa, orbital artery; pf, pituitary fossa; ptsod,
4 pharyngotympanic sinus otoccipital diverticulum; ptspd, pharyngotympanic sinus prootic
5 diverticulum; ptssd, pharyngotympanic sinus suspensorium diverticulum; scr, subcarotid
6 recess extension of the median pharyngeal sinus. Roman numerals designate cranial nerves.
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14 Fig. 5. Cranial endocast, endosseous labyrinth, and endocranial nerve and vascular structures
15 of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris* (NHMUK PV OR 33095),
16 derived from CT scan data. Figures are in dorsal (A), ventral (B), posterior (C), anterior (D),
17 right lateral (E), and left lateral (F) views. Scale bar equals 5 cm. Abbreviations: cer,
18 cerebrum; dvs, dorsal dural venous sinus; el, endosseous labyrinth; ic, internal carotid artery;
19 oa, orbital artery; pf, pituitary fossa. Roman numerals designate cranial nerves.
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30 Fig. 6. Endosseous labyrinth of the teleosaurid thalattosuchian *Steneosaurus* cf. *gracilirostris*
31 (NHMUK PV OR 33095), derived from CT scan data. Scale bar equals 1 cm. Abbreviations:
32 asc, anterior semicircular canal; cc, common crus; cd, cochlear duct; lsc, lateral semicircular
33 canal; psc, posterior semicircular canal.
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41 Fig. 7. Comparative selection of left endosseous labyrinths segmented from extant
42 crocodylian taxa using CT data. A, *Alligator mississippiensis*; B, *Caiman crocodilus*; C,
43 *Gavialis gangeticus*; D, *Tomistoma schlegelii*; E, *Crocodylus acutus*; F, *C. intermedius*; G, *C.*
44 *johnsoni*; H, *C. moreletii*.
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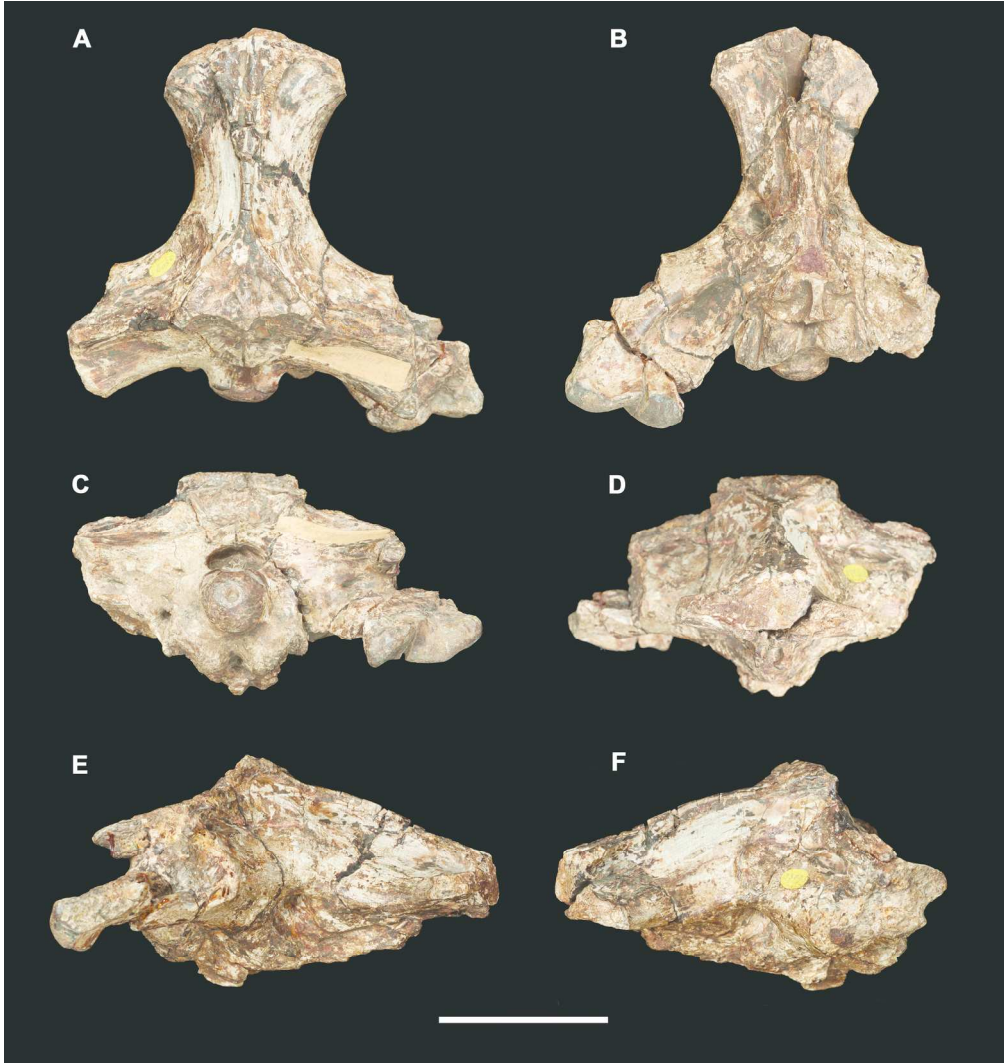
50
51
52 Fig. 8. Hearing sensitivity estimates for *Steneosaurus* cf. *gracilirostris* derived from the
53 methods of Walsh et al. (2009).
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TABLES

Table 1. Dimensions and angular measurements of the brain cavity endocast and endosseous inner ear. Abbreviations: ASSC, anterior semicircular canal; ASSC/PSSC, intersection angle between the canals; ASSC/BA, intersect angle between ASSC and BA; BA, main (sagittal) brain axis; BCE, brain cavity endocast; ECD, endosseous cochlear duct; LAB, whole labyrinth; LSSC, lateral semicircular canal; OW, oval window; PSSC, posterior semicircular canal; PSSC/BA, intersect angle between PSSC and BA; All linear measurements are in millimeters, rounded to tenths of a millimeter and collected using Materialise Mimics 17.0. Measurements marked with an asterisk are averages of left and right labyrinth values.

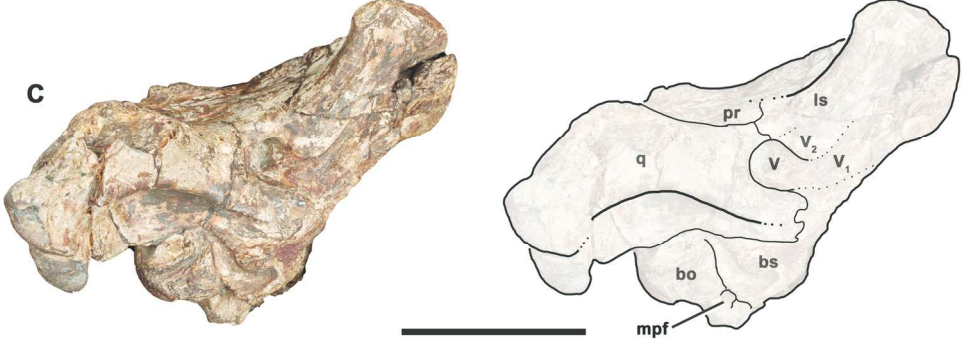
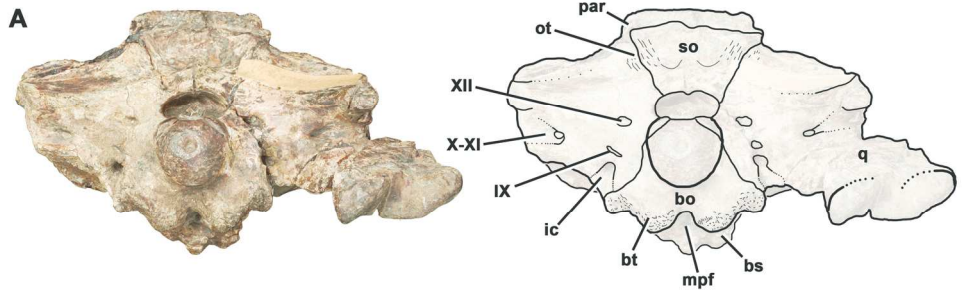
	Length	Width	Depth	Diameter	Deg.	Volume
BCE	76.5 mm	22.8 mm	22.8 mm	—	—	8612.7 mm ³
ASSC	18.1 mm	—	—	2.0 mm	—	—
LSSC	20.4 mm	—	—	3.8 mm	—	—
PSSC	16.0 mm	—	—	2.0 mm	—	—
ASSC/PSSC	—	—	—	—	94	—
ASSC/BA*	—	—	—	—	51	—
PSSC/BA*	—	—	—	—	70	—
ECD	13.8 mm	—	—	—	—	—
OW*	—	—	—	5.9 mm	—	—
LAB	—	—	—	—	—	885.7 mm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

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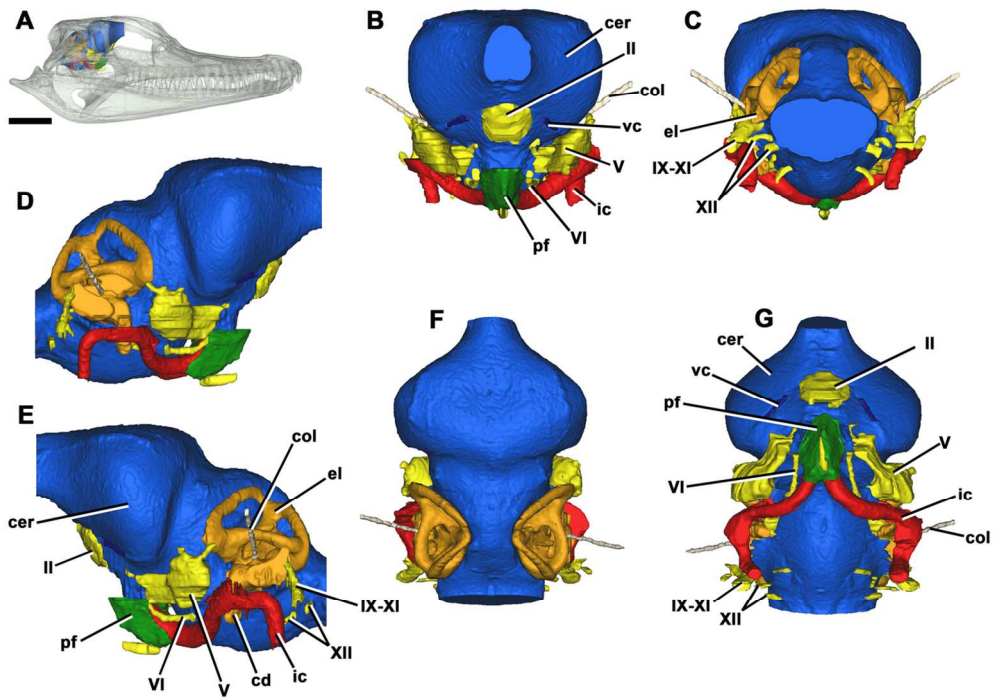
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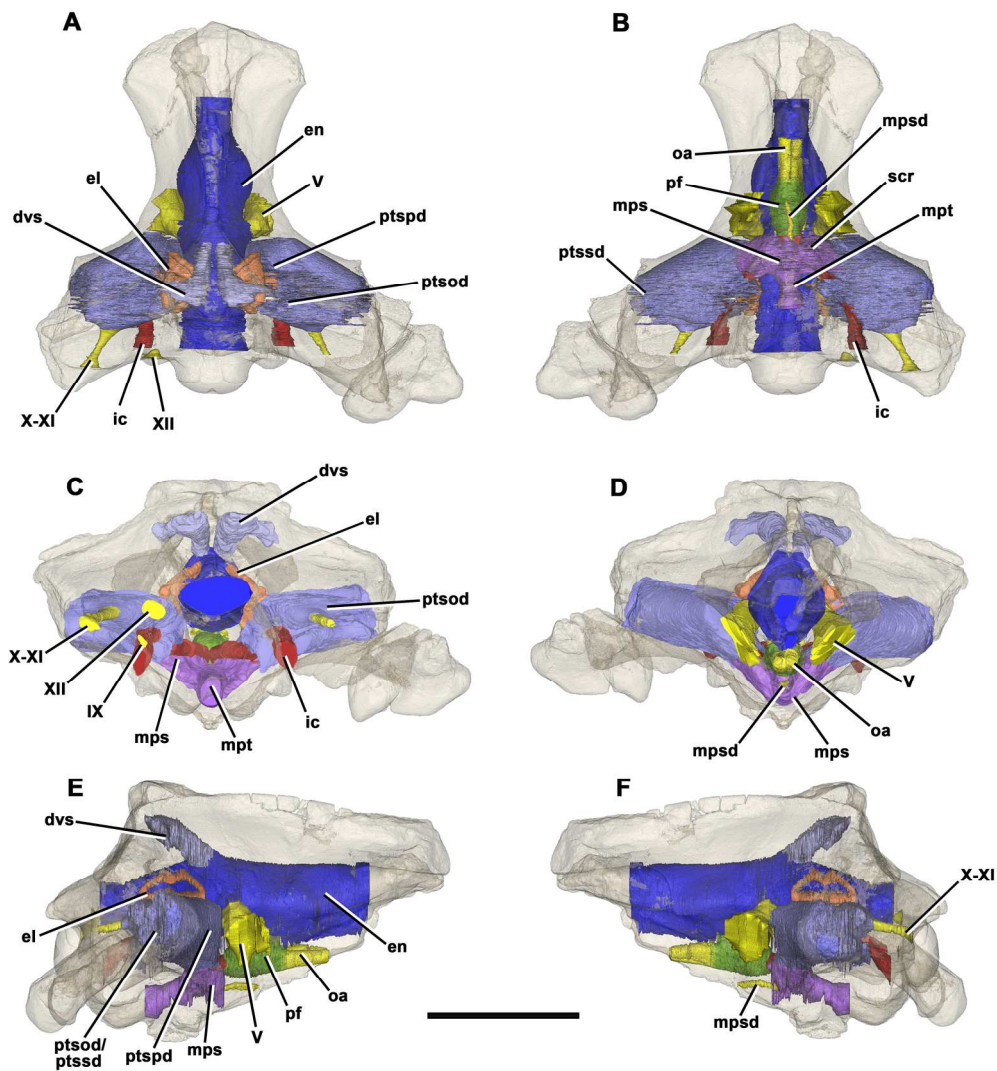


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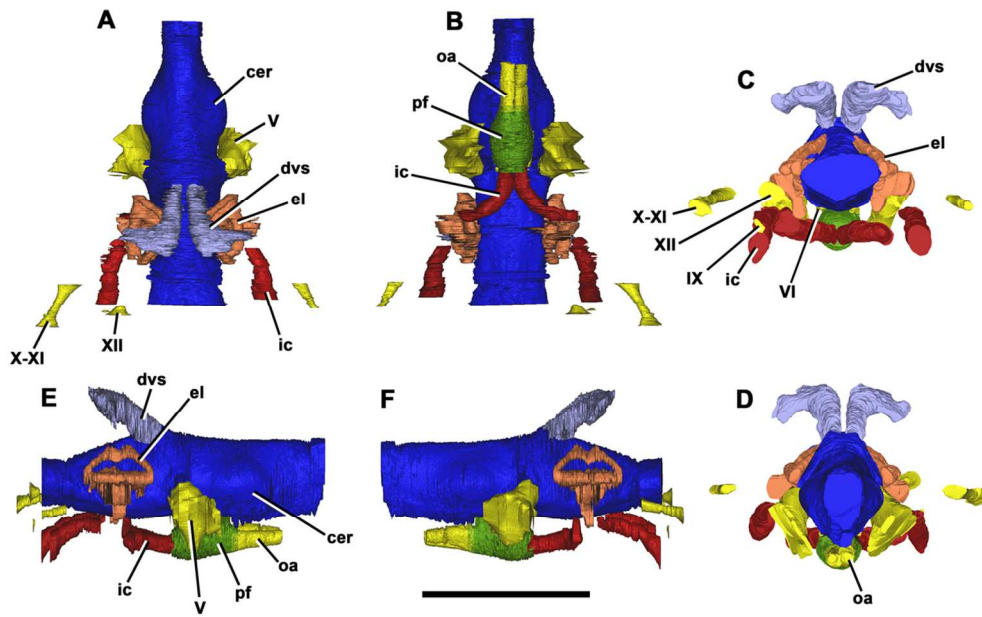
Review

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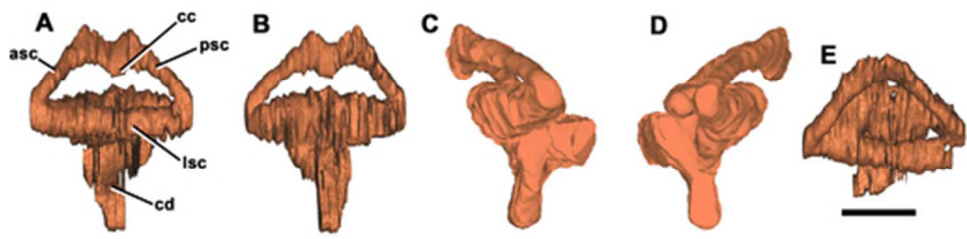


184x201mm (300 x 300 DPI)



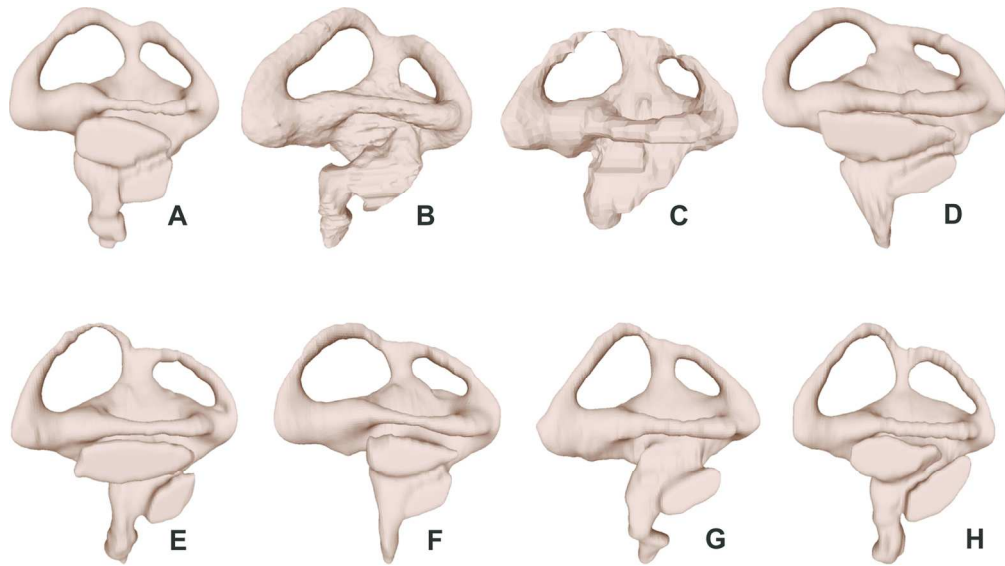
107x68mm (300 x 300 DPI)

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45x12mm (300 x 300 DPI)

For Peer Review

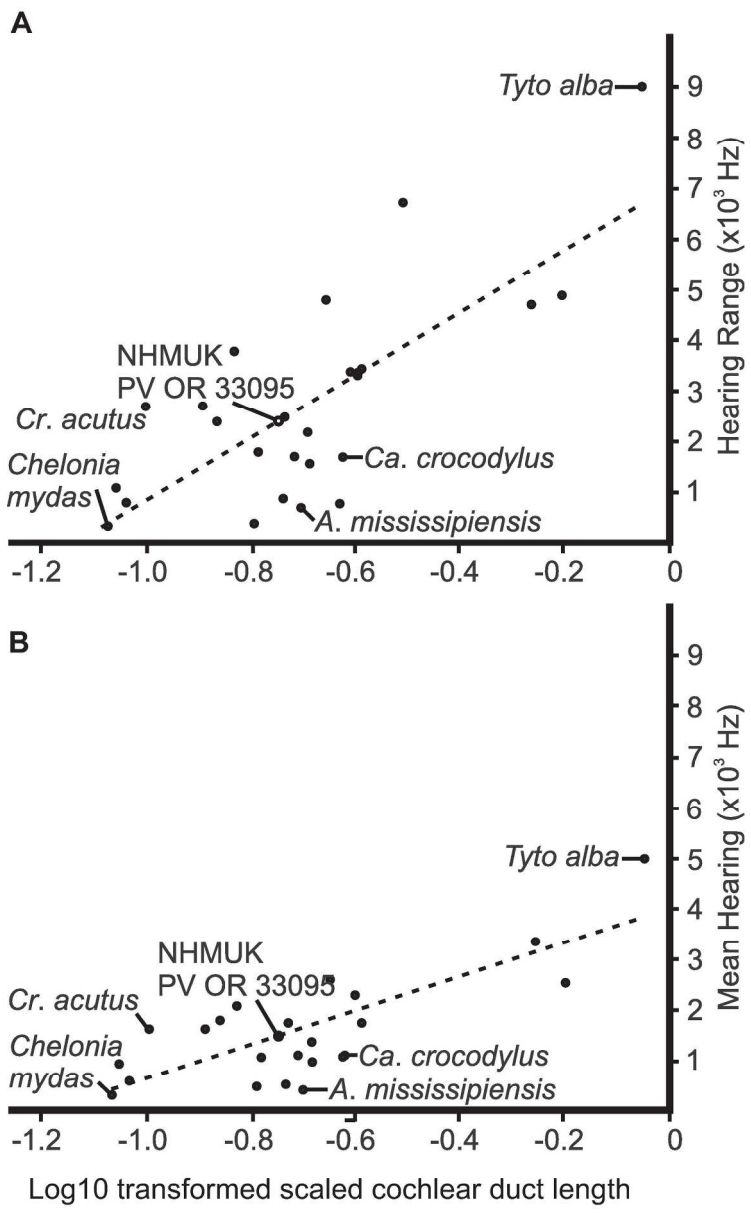


143x79mm (300 x 300 DPI)

Peer Review

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170x278mm (300 x 300 DPI)