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Rostral neurovasculature indicates sensory trade-offs in Mesozoic pelagic crocodylomorphs

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ABSTRACT

Metriorhynchoid thalattosuchians were a marine clade of Mesozoic crocodylomorphs that evolved from semi-aquatic, "gharial"-like species into the obligately pelagic subclade Metriorhynchidae. To explore whether the sensory and physiological demands of underwater life necessitates a shift in rostral anatomy, both in neurology and vasculature, we investigate the trigeminal innervation and potential somatosensory abilities of metriorhynchoids by digitally segmenting the rostral neurovascular canals in CT scans of 10 extant and extinct crocodyliforms. The dataset includes the terrestrial, basal crocodyliform *Protosuchus haughtoni*, two semi-aquatic basal metriorhynchoids, four pelagic metriorhynchids and three extant, semi-aquatic crocodylians. In the crocodylian and basal metriorhynchoid taxa, we find three main neurovascular channels running parallel to one another posteroanteriorly down the length of the snout, whereas in metriorhynchids there are two, and in *P. haughtoni* only one. Crocodylians appear to be unique in their extensive trigeminal innervation, which is used to supply the integumentary sensory organs (ISOs) involved with their facial somatosensory abilities. Crocodylians have a far higher number of foramina on the maxillary bones than either metriorhynchoids or *P. haughtoni*, suggesting that the fossil taxa lacked the somatosensory abilities seen in extant species. We posit that the lack of ISO osteological correlates in metriorhynchoids is due to their basal position in Crocodyliformes, rather than a pelagic adaptation. This is reinforced by the hypothesis that extant crocodyliforms, and possibly some neosuchian clades, underwent a long "nocturnal bottleneck"—hinting that their complex network of ISOs evolved in Neosuchia, as a sensory trade-off to compensate for poorer eyesight.

Institutional Abbreviations: BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; GLAHM, Hunterian Museum, Glasgow, Scotland, UK; MJML, Museum of Jurassic Marine Life, Kimmeridge, UK; MLP, Museo de La Plata, La Plata, Argentina; MM, Minden Museum, Minden, Germany; MNB, Musée du Nouveau-Brunswick (Brunswick Museum), New Brunswick, Canada; NHMUK, Natural History Museum, London, UK; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; TMM, Texas Memorial Museum, Austin, Texas, USA; UF, Florida Museum of Natural History, Gainesville, Florida, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA

Anatomical Abbreviations: acIS, alveolar canals supplying neurovasculature to the integumentary systems; Alv, dental alveoli; cIS, canals supplying neurovasculature to the integumentary systems; cPA, canals supplying neurovasculature to the palate; DAC, dorsal alveolar canal.

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KEYWORDS
Crocodylomorpha, Metriorhynchidae, neurovasculature, somatosensation, Thalattosuchia

1 | INTRODUCTION

Thalattosuchian crocodyliforms underwent a major evolutionary transition during the Jurassic and evolved from semi-aquatic, nearshore predators to pelagic forms which lived in the open oceans (Fernández & Gasparini, 2000, 2008; Young, Brusatte, Ruta, & Andrade, 2010; Wilberg, 2015; Brusatte et al., 2016). Thalattosuchia is composed of two subgroups: the Teleosauroidea, which evolved a diverse range of semi-aquatic morphologies but never made the transition to being fully pelagic (Johnson, Young, & Brusatte, 2020); and the Metriorhynchoidea, where the pelagic transition did occur (Wilberg, 2015; Young et al., 2010). The obligate marine metriorhynchoid subgroup Metriorhynchidae evolved a wide range of osteological adaptations well-suited to their pelagic lifestyle, including hydrofoil-like forelimbs, a hypocercal tail, loss of bony armour (osteoderms), and an osteoporotic-like lightening of the skull, femora, and ribs (e.g., Andrews, 1913; Fraas, 1902; Hua & De Buffrénil, 1996; Young et al., 2010). Physiologically, metriorhynchids are known to have had hypertrophied salt exocrine glands (Fernández & Gasparini, 2000, 2008; Fernández & Herrera, 2009; Gandola, Buffetaut, Monaghan, & Dyke, 2006; Herrera, Fernández, & Gasparini, 2013), a rearrangement and expansion of the pelvic girdle suggesting they evolved some form of viviparity (see Herrera et al., 2017; Young et al., 2010), and possibly evolved a nonhomeothermic form of endothermy (Séon et al., 2020).

Recently, computed tomography (CT) has been used to analyze the internal anatomy of thalattosuchian skulls, investigating their brains, sinuses, vasculature, and bony labyrinths (Brusatte et al., 2016; Fernández, Carabajal, Gasparini, & Chong, 2011; Fernández & Herrera, 2009; Herrera et al., 2013; Herrera, Leardi, & Fernández, 2018; Pierce, Williams, & Benson, 2017; Schwab et al., 2020). Thus, we are now beginning to understand the adaptations that occurred when thalattosuchians adapted to life in marine ecosystems, in particular during the metriorhynchoid shift into being obligately pelagic animals.

In extant crocodylians, CT datasets have been used to examine the facial neurovasculature (e.g., see Lessner, 2020; Lessner and Holliday, 2020a). Extant crocodylians have numerous specialized integumentary sensory organs (ISOs), primarily located across their rostrum (although crocodylids and gavialids also have postcranial ISOs), which are used to detect changes in water pressure, water temperature, and pH (Di-Poï & Milinkovitch, 2013; Leitch & Catania, 2012; Soares, 2002). The neurosensory component needed for the rostral ISOs is supplied by the trigeminal system. The presence of a highly branched trigeminal system is associated with the presence of ISOs in crocodylians, and it is more highly branched than the trigeminal system of animals that lack the same level of high somatosensation (Lessner and Holliday, 2020a, 2020b). Extant crocodylians also have a high number of foramina where the neurovascular canals meet the surface of the bone, which is considered another osteological correlate for ISOs (Barker, Naish, Newham, Katsamenis, & Dyke, 2017; Carr, Varricchio, Sedlmayr, Roberts, & Moore, 2017; Morhardt, 2009).

The trigeminal system is comprised of the trigeminal ganglion which splits into three rami: the ophthalmic ramus (innervating much of the orbit, nasal cavity, and dorsomedial portion of the cranium), the maxillary ramus (innervating the lateral portion of the snout and much of the palate), and the mandibular ramus (innervating all the jaw adductor muscles and carrying sensory information from the lower jaw region) (Leitch & Catania, 2012). Many of these trigeminal nerves travel through canals in the bone, meaning there are clear osteological correlates for these nerves and associated vasculature. Using CT datasets, we digitally segmented the neurovascular canals that transmitted the trigeminal maxillary rami through the snouts of semi-aquatic basal metriorhynchoids and derived pelagic metriorhynchids. We used these data to ascertain differences in the trigeminal systems of terrestrial, semi-aquatic, and fully pelagic species. These observations were compared to the complexly branched trigeminal innervation of modern crocodylians, and an outgroup, the terrestrial crocodyliform *Protosuchus haughtoni*, which we consider to be a suitable model for the ancestral condition of the trigeminal system in crocodyliforms.

2 | MATERIALS

The dataset used herein consists of CT scans of 12 skull specimens across 10 species (see Figure 1 and Table S1). Our metriorhynchoid ingroup includes two basal metriorhynchoids, *Pelagosaurus typus* (NHMUK PV OR 32599) and *Eoneustes gaudryi* (NHMUK PV R 3263), and four metriorhynchids, *Thalattosuchus superciliosus* (NHMUK PV R 11999), *Cricosaurus araucanensis* (MLP 72-IV-7-1), *Cricosaurus schroederi* (MM uncatalogued), and *Torvoneustes coryphaeus* (MJML K1863). The metriorhynchoid specimens occur from sediments ranging across most of the known timespan of the clade, from the Toarcian (Early Jurassic: *Pe. typus*) to the Valanginian (Early Cretaceous: *Cri. schroederi*). Apart from *Cri. araucanensis*, which is nearly complete, all the metriorhynchoid specimens are missing the anterior portion of the rostrum (comprising the premaxilla and anterior end of the maxilla).

The extant crocodylian outgroup sample consists of two species with convergent longirostrine morphology to that of thalattosuchians, *Gavialis gangeticus* (UF 118998 and TMM M-5490) and *Tomistoma schlegelii* (USNM 211322 and TMM M-6342), and one species exhibiting a platyrostral morphology typical of most extant crocodylians, *Crocodylus rhombifer* (NMB AB50.0171). For *Gavialis* and *Tomistoma*, adult (UF 118998 and USNM 211322) and subadult specimens (TMM M-5490 and TMM M-6342) were included. In the extant crocodylians, our observations are focused on the posterior end of the snout, lateral to the nasal bone, as this is homologous to the portion preserved in the metriorhynchoids.

The extinct crocodyliform selected as the outgroup taxon to both Thalattosuchia and Crocodylia is *Pr.*

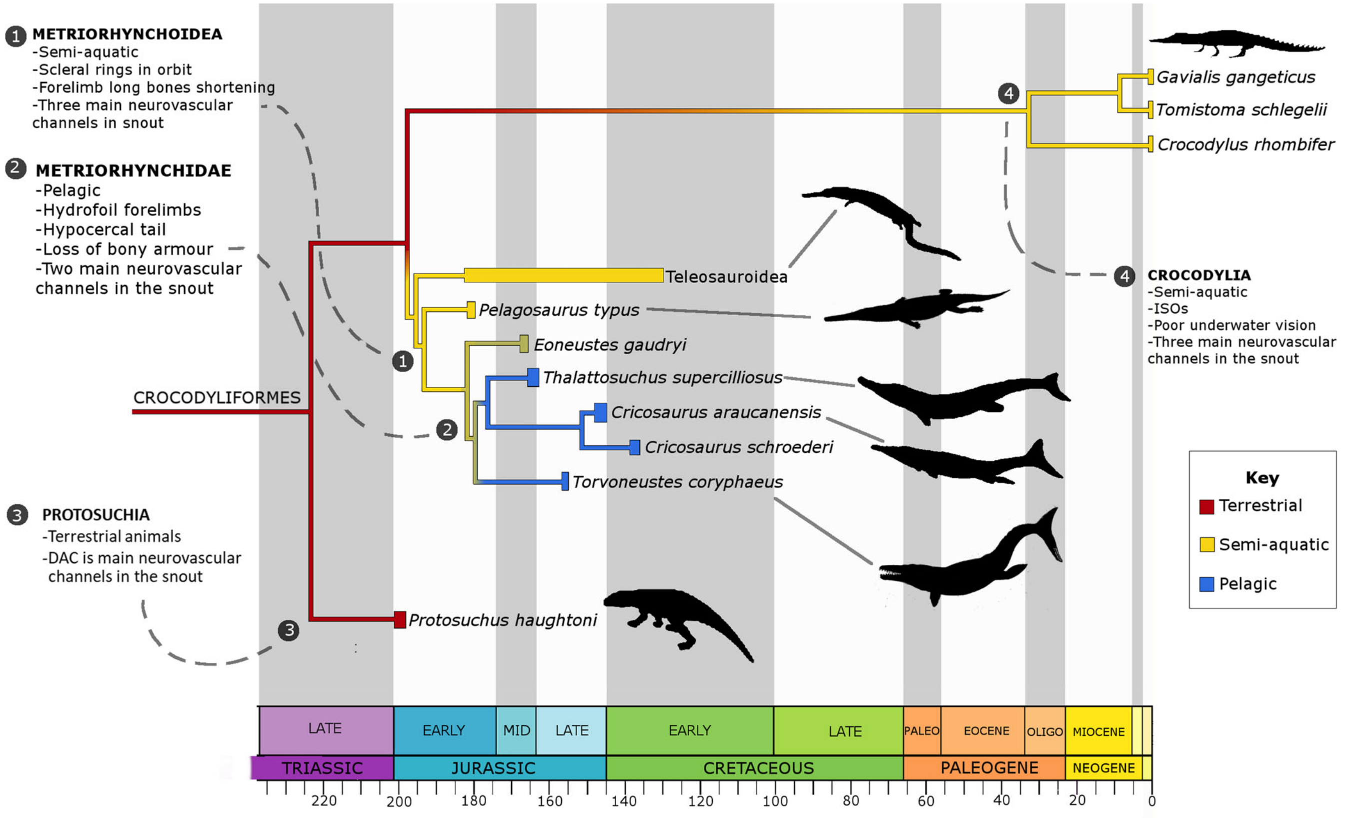

FIGURE 1 Phylogenetic relationships of the species in this study, based on the results of Young et al. (2021). Red lines indicate terrestrial taxa, yellow lines semi-aquatic taxa, and blue lines are for pelagic taxa. Silhouettes are sourced from Phylopic.org and were created by Tamura, N., Hartmann, S., Kimmel, B., Monger, G., and Bogdanov, D

haughtoni (BP/1/4770). *Protosuchus haughtoni* was sampled because it provides an example of both the plesiomorphic condition in Crocodyliformes and therefore approximates the morphology in a terrestrial species prior to the marine transition. The *Pr. haughtoni* skull is near-complete, but is slightly compressed on its left side (Gow, 2000).

All skull specimens were subjected to CT scanning prior to analysis in this study at various facilities with different scanning parameters (see Table S1). The scans of the two basal metriorhynchoids, *Pe. typus* and *E. gaudryi*, had the best density separation between the fossil bone, endosseous cavities, and enclosing rock matrix. In the metriorhynchids, due to matrix densities in *Th. superciliosus* and *Tor. coryphaeus*, and the low resolution of the *Cri. araucanensis* scan, the finer details of the neurovascular canals branching to the surface of the snout or the roof of the mouth were unclear, leaving only the thicker neurovascular channels to be segmented. The scan of *Cri. schroederi* had a better contrast to those of the other metriorhynchoids but lacked the high level of detail seen in basal metriorhynchoids.

The data for all models of the segmented neurovascular canals has been uploaded to MorphoSource (https://www.morphosource.org/) and can be accessed here: [https://www.morphosource.org/projects/000366884?locale=en].

3 | METHODS

Three-dimensional reconstructions of the rostral neurovasculature canals for all specimens were created by digital segmentation of CT slices in Materialise Mimics 20.0 and 23.0 using the livewire and ellipse tools. The morphology was examined and described.

Using the three-dimensional reconstructions of the cranium, we were able to count foramina associated with the trigeminal system (Figure 2). In order to quantify the extent of the snout surface innervated by the trigeminal system, we counted the number of foramina on the maxillae. As many of the skulls only had partial snouts, only the foramina lateral to the nasals were counted (Table 1). Scans with voxel sizes larger than the neurovascular canals and foramina were excluded (*Cri. araucanensis* and the subadult *Gavialis*). We then compared the number of foramina on the ventral surface of the maxillae (i.e., within the oral cavity) with the number of foramina on the lateral surfaces. The counts were analyzed in groups (e.g., metriorhynchoids vs. extant crocodylians) with one-way analysis of variance (ANOVA) tests to determine if there were differences in foramina counts between different groups of specimens. We also measured the maximum diameter of the trigeminal fossa as a proxy for the diameter of the trigeminal ganglion in each specimen (see Table 1,

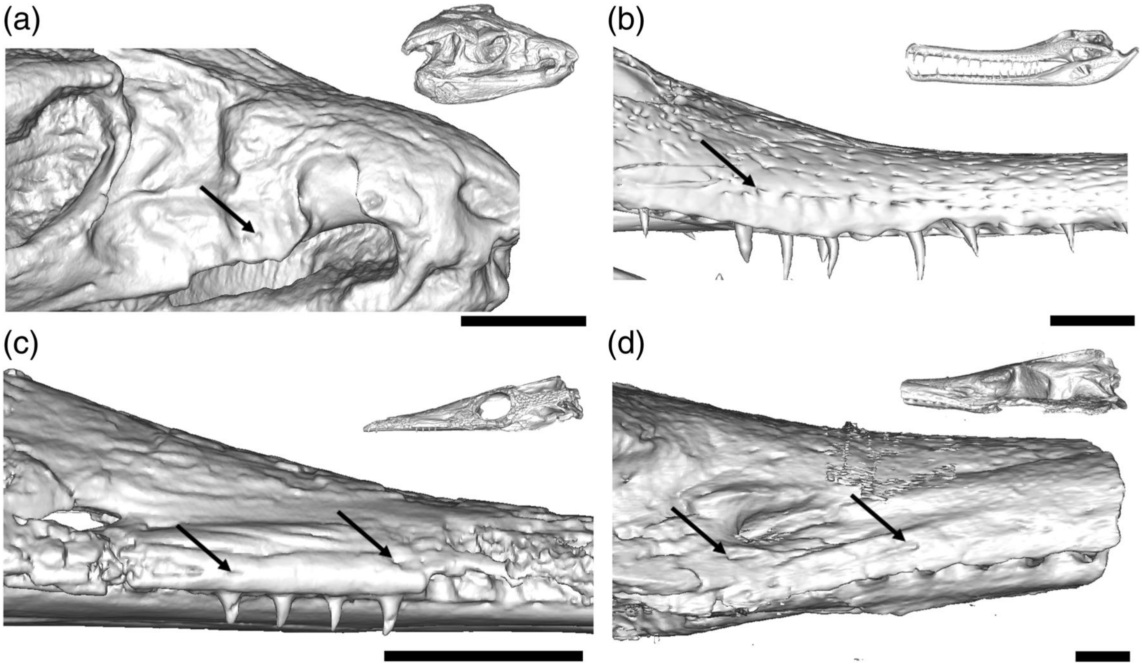

FIGURE 2 Surface of the maxillary bones showing foramina, with arrows highlighting a few foramina visible from this angle. (a) *Protosuchus haughtoni* (BP/1/4770). (b) *Tomistoma schlegelii* (TMM M-6342). (c) *Pelagosaurus typus* (NHMUK PV OR 32599). (d) *Torvoneustes coryphaeus* (MJML K1863). Scale bars 10 mm (a), 20 mm (b–d)

TABLE 1 Data gathered from the scans; the number of foramina on the maxillae of the specimens and the diameters of the trigeminal ganglia and the location at which the ganglia were measured (image or slice number on the coronal view of the scan on Materialize Mimics)

			Number of foramina				**Left ganglion**		**Right ganglion**	
Species	**Specimen ID**	**Distance between vestibules (mm)**	**Left maxilla external surface**	**Left maxilla ventral surface**	**Right maxilla external surface**	**Right maxilla ventral surface**	**Diameter (mm)**	**Slice location**	**Diameter (mm)**	**Slice location**
Pr. haughtoni	BP/1/4770	5.89	11	0	8	0	Unclear		Unclear	
Cro. rhombifer	NMB AB50.017	19.84	54	22	58	25	7.93	101	7.96	101
G. gangeticus (adult)	UF 118998	22.23	48	29	50	32	7.57	139.6590	7.98	139.6590
G. gangeticus (subadult)	TMM M-5490	12.90	Low resolution				3.99	37.0346	3.69	37.0346
Tom. schlegelii (adult)	USNM 211322	26.78	57	9	51	9	12.61	246.25	12.86	246.25
Tom. schlegelii (subadult)	TMM M-6342	20.84	118	26	88	18	7.13	86.48	8.04	86.48
Pe. typus	NHMUK PV OR 32599	16.77	8	20	3	12	1.54	453	1.41	461
E. gaudryi	NHMUK PV R 3263	N/A	3	4	7	8	Not preserved			
Th. superciliosus	NHMUK PV R 11999	29.68	14	2	2	Unclear	10.49	74.2800	10.89	74.2800
Cri. araucanensis	MLP 72-IV-7-1	23.95	Low resolution				10.85	40	10.71	40
Cri. schroederi	MM uncatalogued	33.05	4	4	5	5	Not preserved		9.43	152.5
Tor. coryphaeus	MJML K1863	38.61	6	Unclear	3	Unclear	10.06	100.8815	11.49	100.8815

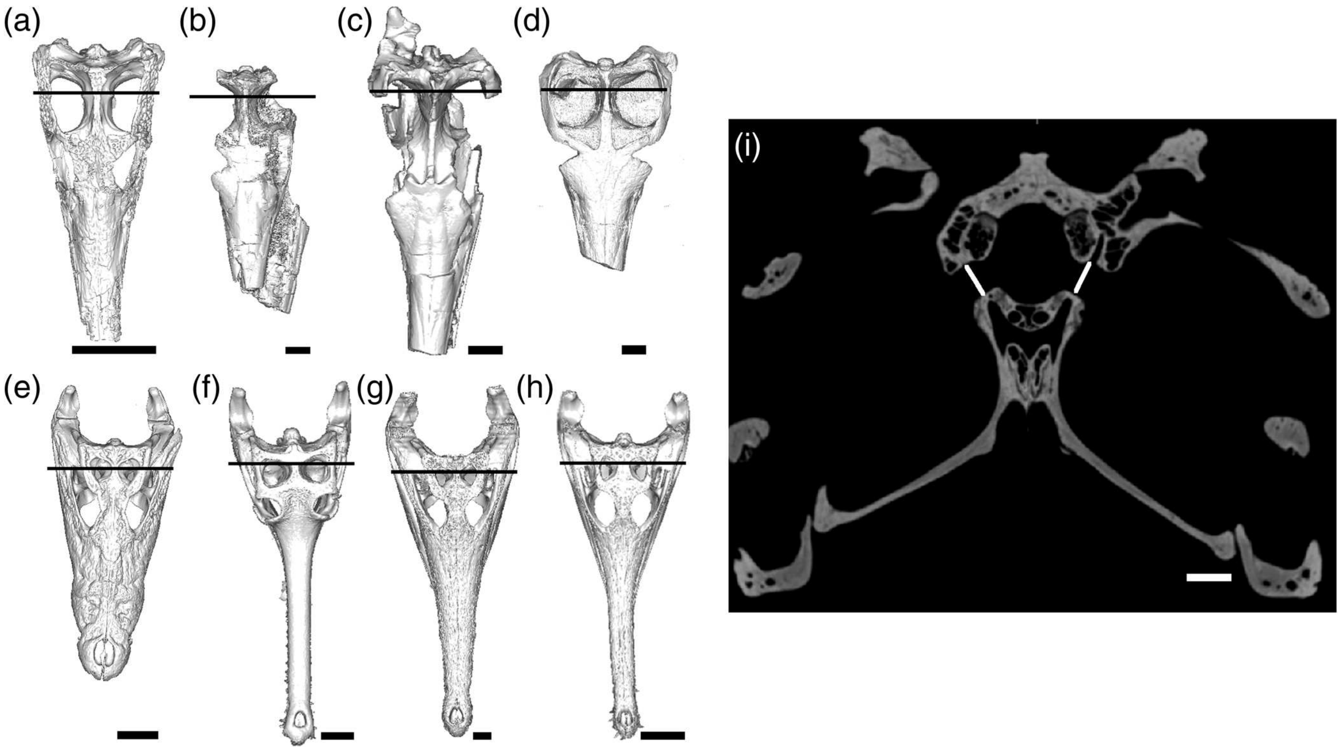

FIGURE 3 Position of the trigeminal fossa in each skull, which was measured it a homologous point in each specimen. The specimens are sized to best compare the relative position of the trigeminal fossa and are not to scale. (a) *Pelagosaurus typus* (NHMUK PV OR 32599); (b) *Thalattosuchus superciliosus* (NHMUK PV R 11999); (c) Cricosaurus schroederi (MM uncatalogued); (d) *Torvoneustes coryphaeus* (MJML K1863); (e) *Crocodylus rhombifer* (NMB AB50.017); (f) *Gavialis gangeticus* adult (UF 118998); (g) *Tomistoma schlegelii* adult (USNM 211322); (h) *Tomistoma schlegelii* subadult (TMM M-5490); (i) *Cro. rhombifer* (NMB AB50.017) in coronal view, white bars indicating where the trigeminal fossa diameter measurement was taken. Scale bars 50 mm (a–h), 10 mm (i)

Figure 3). George and Holliday (2013) found that the size of the trigeminal fossa may indicate the sensory magnitude of the trigeminal nerves, so we thought it was pertinent to investigate this relationship. The diameter of the trigeminal fossa was compared with the distance between the vestibular labyrinths (a proxy for body size developed by Schwab et al., 2020). We then compared the trigeminal fossa: body size proxy ratios of the crocodylians to those of the metriorhynchoids using a one-way ANOVA.

4 | RESULTS

4.1 | Trigeminal canal morphology

In basal metriorhynchoids (Figures 4 and 5) and extant crocodylians (Figures 6–8), there are three parallel neurovascular canals running posteroanteriorly along the length of the snout: (a) the dorsal alveolar canal (DAC); (b) a canal running ventral to the DAC that likely supplied the neurovasculature to the gingivae and palate (the cPA); and (c) a canal running lateral to the DAC that likely supplied neurovasculature to the integumentary systems on the surface of the snout (the cIS). These three canals are distinctly separated by bone and can be identified by their position relative to either the dental alveoli or to the DAC. Although trigeminal nerve branches ran through the cPA and cIS, branching off the main maxillary nerve trunk in the DAC on their way to their targets, branches of the accompanying maxillary blood vessels anastomosed longitudinally along the snout (Porter, Sedlmayr, & Witmer, 2016), giving the appearance of discrete canals. Extant crocodylians have a complex branching system of trigeminal neurovascular canals (Lessner, 2020; Lessner and Holliday, 2020a, 2020b), whereas the metriorhynchoids have fewer branches (Figures 4,5,9, and 10). In metriorhynchids, there are two main neurovascular canals running parallel to each other: (a) the DAC and (b) the canal running ventral to the DAC which would have supplied neurovasculature to the gingivae (Figures 9 and 10). Canals which would have supplied neurovasculature to the lateral surface of the snout bud from the dental alveoli rather than interacting with a discrete posteroanterior canal—these lateral branches to the skin connected to the DAC through the dental alveoli

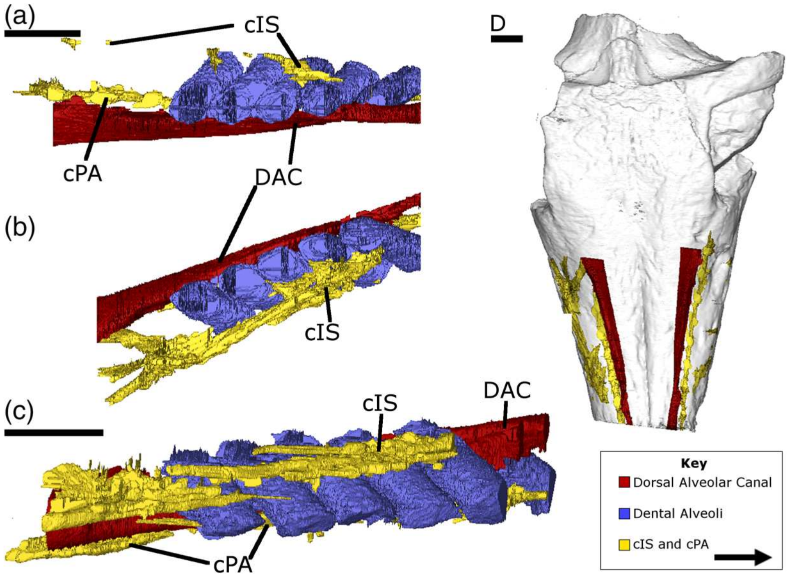

FIGURE 4 Rostral neurovascular canals of the basal metriorhynchoid *Eoneustes gaudryi* (NHMUK PV R 3263). (a) Dorsal view of segmented neurovascular canals (left side); (b) dorsal view of segmented neurovascular canals (right side); (c) lateral view of segmented neurovascular canals on the right; (d) dorsal view of whole specimen. Arrow in key indicates anterior direction for a–c. Scale bars equal 20 mm

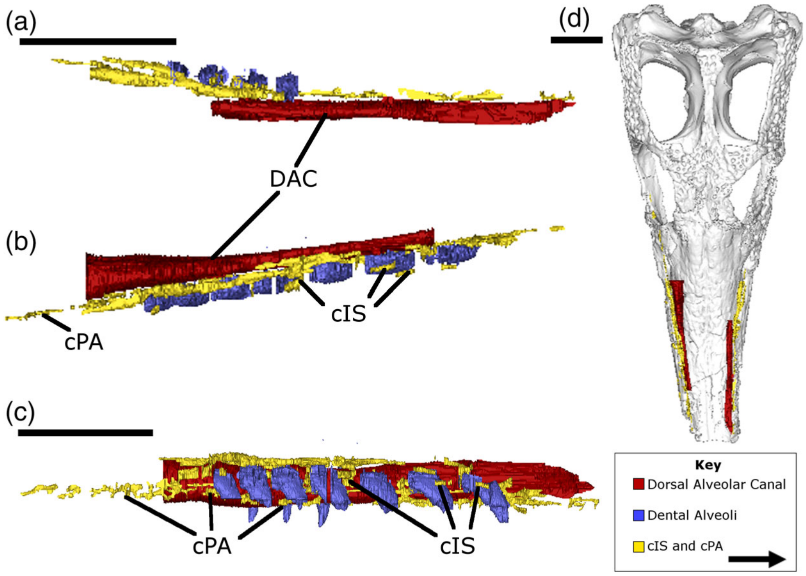

FIGURE 5 Rostral neurovascular canals of the basal metriorhynchoid *Pelagosaurus typus* (NHMUK PV OR 32599). (a) Dorsal view of the segmented neurovascular canals on the right; (b) dorsal view of the segmented neurovascular canals on the left; (c) lateral view of segmented neurovascular canals on the right; (d) dorsal view of whole specimen. Arrow in key indicates anterior direction for a–c. Scale bars equal 20 mm

(acIS in Figures 9,10, and 11c,d). Metriorhynchids are unique among the specimens studied for having these alveolar neurovascular canals rather than a trigeminal neurovascular canal dorsal to the dental alveoli.

The morphology in metriorhynchoids and extant crocodylians is distinct from the condition in *Pr. haughtoni*. Whereas the other crocodyliforms have up to three main canals running parallel to each other, *Pr. haughtoni* only exhibits the DAC, which terminates in a notch between the maxilla and the premaxilla, in an anteriorly facing foramen previously noted by Gow (2000). In *Pr. haughtoni*, there are branches from the dorsal alveoli to the lateral surface of the snout, but no clear evidence of the neurovascular canals to the gingivae (Figure 12). However, for most of the length of the snout, *Pr. haughtoni* lacks a secondary bony palate, so the neurovascular system supplying the roof of the mouth may have been in soft tissue rather than bony canals.

4.2 | Foramina density

We performed a one-way ANOVA to compare the counts of snout surface foramina on all metriorhynchoids (excluding *Cri. araucanensis*) versus extant crocodylians (excluding the subadult *Gavialis*), which found that metriorhynchoids had significantly fewer foramina than crocodylians ($p = .01 \cdot 10^{-6}$). This suggests that these two groups had different distributions of facial neurovasculature. There was no difference in the number of foramina in basal metriorhynchoids compared to the

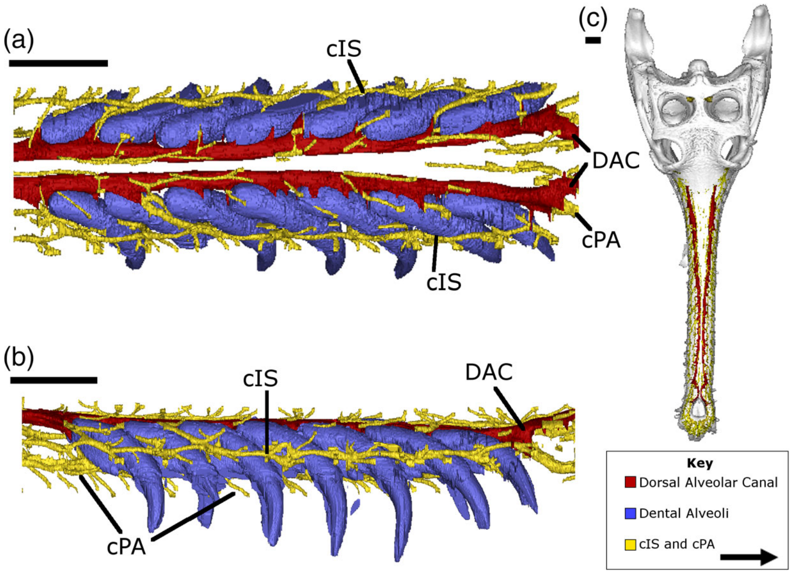

FIGURE 6 Rostral neurovascular canals of the longirostrine crocodylian *Gavialis gangeticus* (UF-herp-118998). (a) Dorsal view of segmented neurovascular canals; (b) lateral view of segmented neurovascular canals on the right; (c) dorsal view of whole specimen. Arrow in key indicates anterior direction for a and b. Scale bars equal 20 mm

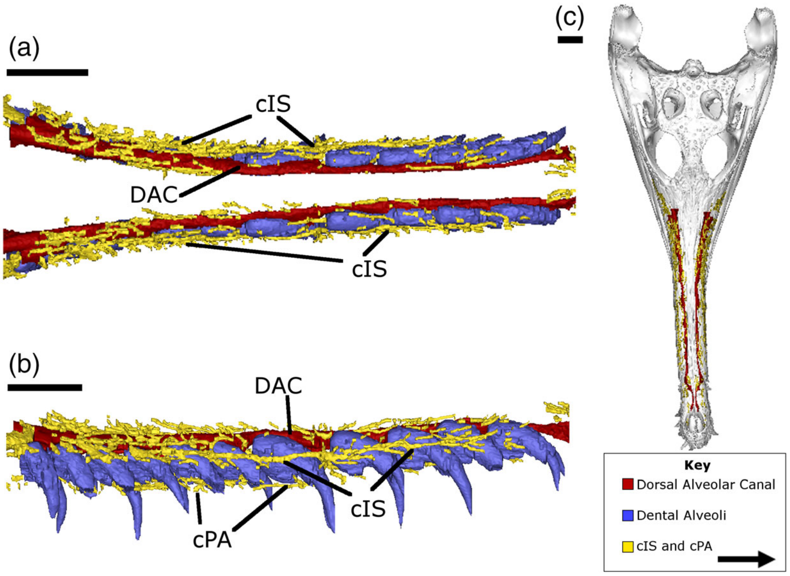

FIGURE 7 Rostral neurovascular canals of the longirostrine crocodylian *Tomistoma schlegelii* (TMM M-6342). (a) Dorsal view of segmented neurovascular canals; (b) lateral view of segmented neurovascular canals on the right; (c) dorsal view of whole specimen. Arrow in key indicates anterior direction for a and b. Scale bars equal 20 mm

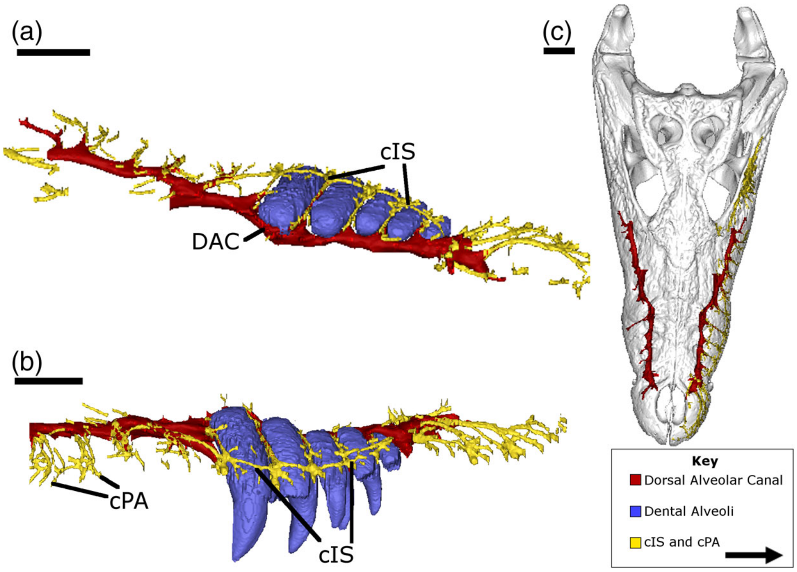

FIGURE 8 Rostral neurovascular canals of the broad snouted crocodylian *Crocodylus rhombifer* (NMB AB50.017). (a) Dorsal view of segmented neurovascular canals on the left; (b) lateral view of segmented neurovascular canals on the left; (c) dorsal view of whole specimen. Arrow in key indicates anterior direction for a and b. Scale bars equal 20 mm

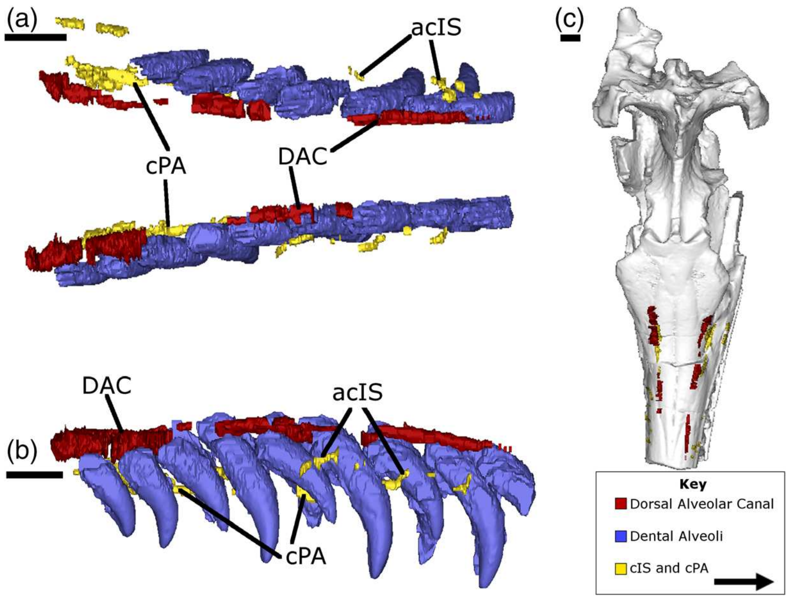

FIGURE 9 Rostral neurovascular canals of the metriorhynchid *Cricosaurus schroederi* (MM uncatalogued). (a) Dorsal view of segmented neurovascular canals; (b) lateral view of segmented neurovascular canals on the right; (c) dorsal view of whole specimen. Arrow in key indicates anterior direction for a and b. Scale bars equal 20 mm

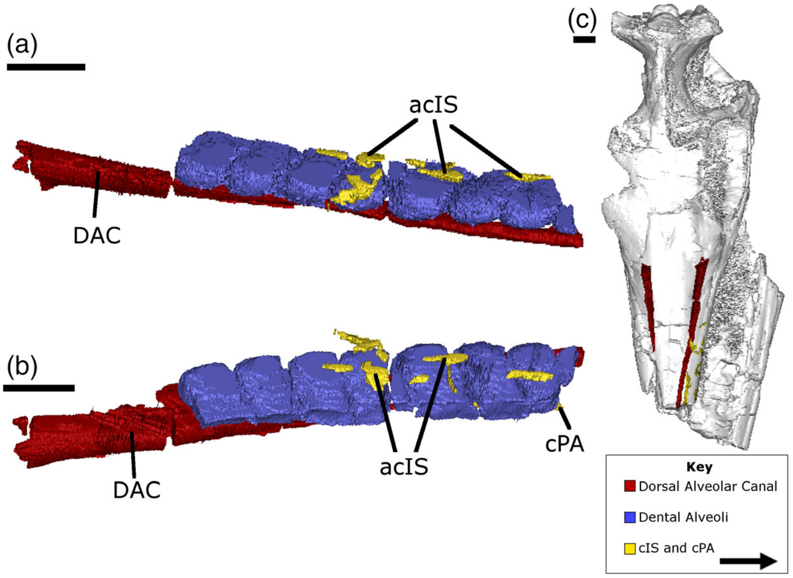

FIGURE 10 Rostral neurovascular canals of the metriorhynchid *Thalattosuchus superciliosus* (NHMUK PV R 11999). (a) Dorsal view of segmented neurovascular canals; (b) lateral view of segmented neurovascular canals on the right; (c) dorsal view of whole specimen. Arrow in key indicates anterior direction for a and b. Scale bars equal 20 mm

metriorhynchids (excluding *Cri. araucanensis*; $p = .8685$, not significant). We found no correlation between body size (using the distance between the vestibular labyrinths as a proxy) and the number of foramina counted on the surface of the maxilla ($R^2 = .0312$, $p = .646$, Figure 13). As our dataset is small (partial snouts of two metriorhynchoids and three metriorhynchids), we cannot confidently test whether snout surface foramina counts were different between basal metriorhynchoids and pelagic metriorhynchids. Future work and datasets are required to properly test this.

Given that extant crocodylians have more foramina on the surface of the maxilla, we tested whether extant crocodylians have larger trigeminal ganglia than metriorhynchoids by measuring the diameter of the trigeminal fossa (following on from the findings of George & Holliday, 2013). We divided the trigeminal fossa diameter by the distance between the vestibular labyrinths (a proxy for body size), and then compared the trigeminal fossa: body size proxy ratios of the crocodylians to those of the metriorhynchoids. We found no significant difference in trigeminal fossa size ($p = .2781$, not significant) between extant crocodylians and metriorhynchoids, but we did find that the trigeminal fossa is larger in larger crocodiles (as estimated by the distance between their vestibular labyrinths; $R^2 = .538$, $p = .016$, Figure 14). Since George and Holliday (2013) suggested that it is differences in trigeminal fossa volume relative to skull size that imply a difference in sensory magnitude, whereas

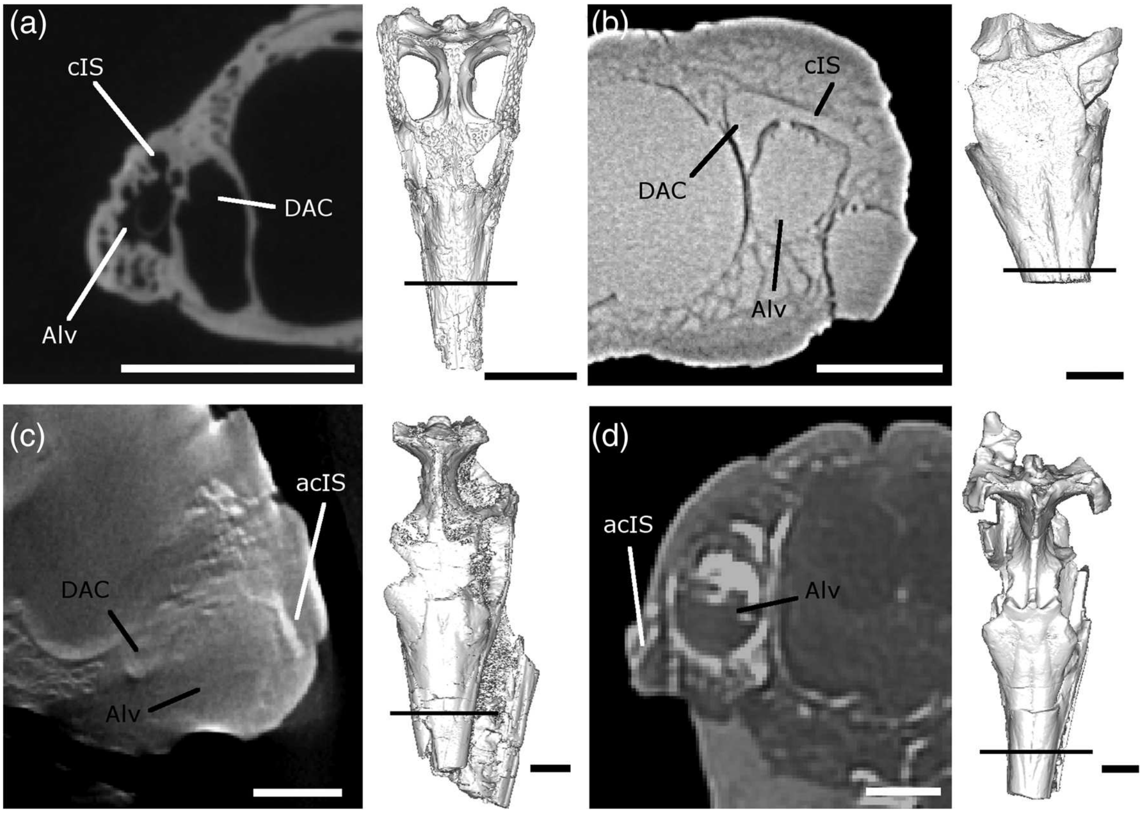

FIGURE 11 Snout coronal views showing the association between the neurovascular canals and the dental alveoli, with the position the image was taken from shown to the right of each coronal view. (a) *Pelagosaurus typus* (NHMUK PV OR 32599); (b) *Eoneustes gaudryi* (NHMUK PV R 3263); (c) *Thalattosuchus superciliosus* (NHMUK PV R 11999); (d) *Cricosaurus schroederi* (MM uncatalogued). In basal metriorhynchoids (a,b) there is a neurovascular which runs dorsal to the alveoli (a), fed directly by the DAC (b), while in the metriorhynchids (c,d) the canals which innervate external of the snout interact directly with the dental alveoli. Scale bars equal 10 mm (a–d), scale bars for the skulls equal 50 mm

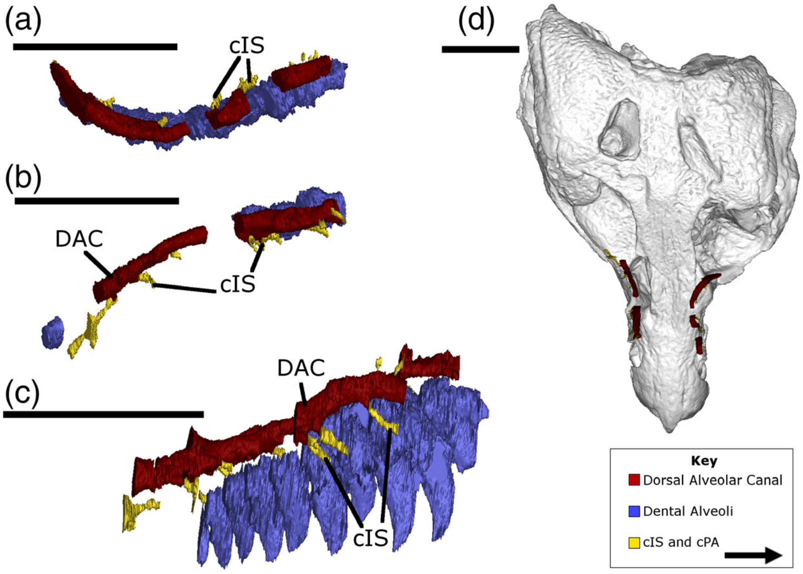

FIGURE 12 Rostral neurovascular canals of the basal crocodyliform *Protosuchus haughtoni* (BP/1/4770). (a) Dorsal view of the segmented neurovascular canals on the right; (b) dorsal view of the segmented neurovascular canals on the left; (c) lateral view of segmented neurovascular canals on the right; (d) dorsal view of whole specimen. Arrow in key indicates anterior direction for a–c. Scale bars equal 10 mm

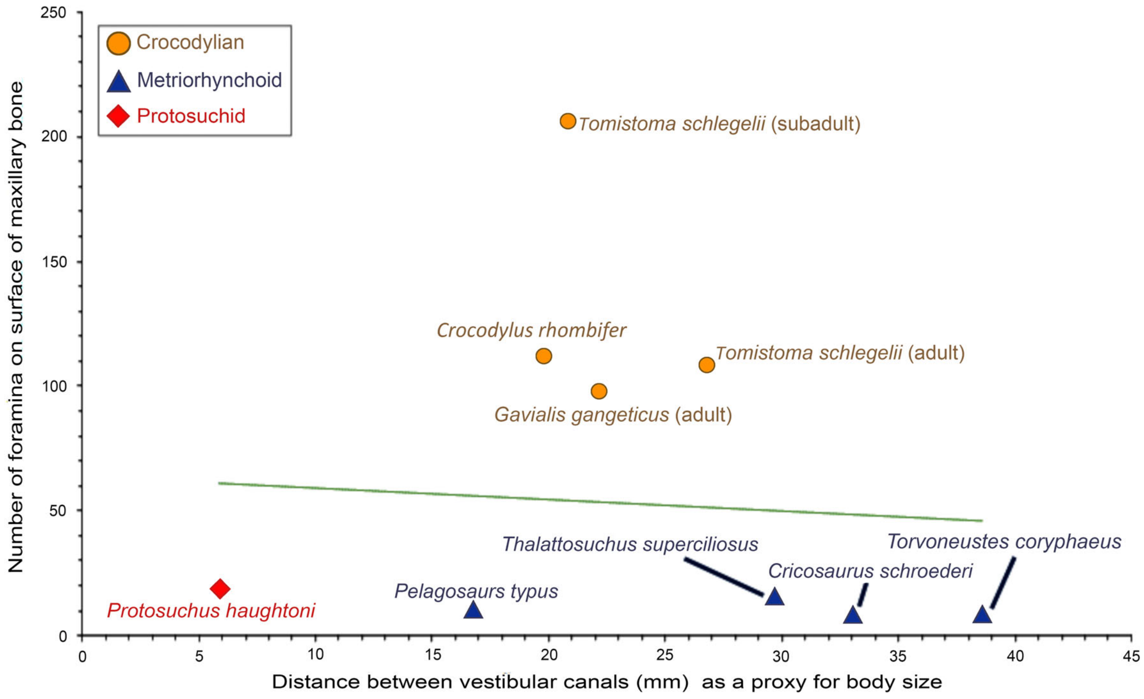

FIGURE 13 Comparing the number of foramina counted on the maxillary bones (lateral to the nasal bones) to the distance between the vestibular labyrinths (a proxy for body size)

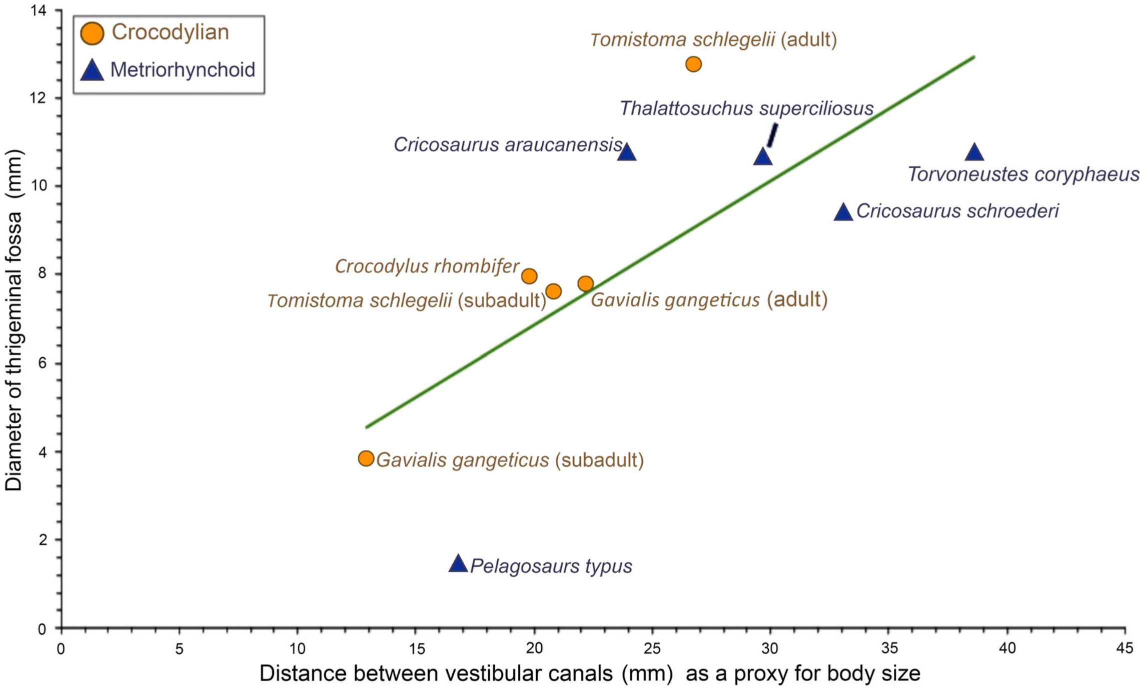

FIGURE 14 Comparing the diameter of the trigeminal fossa to the distance between the vestibular labyrinths (a proxy for body size)

facial foramina may not be the best indicator of the presence or absence of ISOs, our data lead us to hypothesize there is not a significant difference in the sensory magnitude between crocodylians and metriorhynchoids. However, we have a small sample size, so further investigation into the trigeminal fossa volume of metriorhynchoids is warranted.

5 | DISCUSSION

5.1 | Evolution of rostral neurovascular canals within Metriorhynchoidea

The neurovascular canals found in this study would have housed both nerves and vasculature. While discussion of sensory systems focuses on nerves, it is important to remember that changes in the canals that housed the trigeminal nerves may reflect a shift in the rostral vasculature instead, especially as cephalic vasculature is important for thermoregulation of neurosensory tissues in extant crocodylians (Holliday, Porter, Vliet, & Witmer, 2020; Porter et al., 2016; Sedlmayr, 2002).

In metriorhynchids, some of the neurovascular canals pass from the DAC through the alveoli to the lateral surface of the snout. In basal metriorhynchoids, extant crocodylians, and basal crocodyliforms these neurovascular canals are dorsal to the alveoli. There is no difference in the depth of the alveoli that necessitates this difference in the trigeminal canal arrangement, so there is no obvious reason why the canals passed through the alveoli in metriorhynchids. Other than this minor change, there was no difference between the posterior rostrum trigeminal innervation in basal metriorhynchoids and metriorhynchids. If interpreting these neurovascular canals in the context of the trigeminal nerve, this suggests that the utility of somatosensation is very similar in shallow marine and open ocean environments, and the aspects of the trigeminal system studied here needed very little modification during the metriorhynchoid transition to pelagic life.

5.2 | Evolution of trigeminal innervation

Metriorhynchoids had lower foramina counts than extant crocodylians, suggesting that metriorhynchoids lack the osteological correlates for an extensive system of ISOs similar to that of extant crocodylians. Given that ISOs excel at detecting ripples on the surface of the water (Di-Poï & Milinkovitch, 2013), it is perhaps unsurprising that metriorhynchoids lacked an extensive system of ISOs as they likely hunted prey underwater (see De Andrade, Young, Desojo, & Brusatte, 2010; Pierce, Angielczyk, & Rayfield, 2008). However, ISOs are also used to detect prey underwater, as crocodylian eyes are not suited to focusing underwater (Fleishman, Howland, Howland, Rand, & Davenport, 1988; Grigg & Kirshner, 2015). The ISOs on the gingivae are used to determine prey size for items held in the mouth (Leitch & Catania, 2012) as well as in tactile communication with conspecifics during courtship (Grigg & Kirshner, 2015; Vliet, 2001). In addition to tactile information, ISOs may also be able to detect low frequency sounds and be involved in intraspecific communication (Brazaitis & Watanabe, 2011; Leitch & Catania, 2012), detect pH (Di-Poï & Milinkovitch, 2013), and temperature (Brazaitis & Watanabe, 2011), and there is some evidence that postcranial ISOs can detect salinity (Jackson & Brooks, 2007). As extant crocodylian ISOs are so versatile, the fact that we lack evidence for similar organs on the heads of metriorhynchoids may imply metriorhynchoids used other senses for detecting pH, temperature, or low frequency sounds.

The basal crocodyliform *Pr. haughtoni*, a terrestrial predator, also had a low number of foramina on the maxillae, and it is therefore unlikely to have possessed the enhanced ISO system of extant crocodylians. This suggests that a low foramina count is the ancestral condition for crocodyliforms, and we posit that ISOs and a complexly branched trigeminal system is novel to crocodylians, and is therefore absent in other crocodyliform groups such as metriorhynchoids. Therefore, the hypothesized lack of a complex ISO system in metriorhynchoids is likely related to their basal position in Crocodyliformes rather than an adaptive loss in somatosensory ability.

5.3 | Vision and sensory trade-offs

Within Metriorhynchoidea, the orbits gradually become more laterally oriented, and substantially larger than those seen in modern crocodylians (Frey, Buchy, Stinnesbeck, & López-Oliva, 2002; Pierce et al., 2017; Young et al., 2010; Young & Andrade, 2009). Metriorhynchids were likely vision-based hunters (Martill, Taylor, Duff, Riding, & Bown, 1994; Massare, 1988; Young et al., 2010), and probably relied on sight more than tactile stimuli, especially as they were more likely to be hunting underwater than waiting to ambush prey at the water's surface. Moreover, it is possible that metriorhynchids could hear a narrower range of frequencies than extant crocodylians and basal thalattosuchians, as their inner ears may have had shorter cochlear ducts—although this is equivocal (see Schwab et al., 2020). It appears the physical limitations of living an obligate pelagic existence imposed sensory limitations on metriorhynchoids.

While most pseudosuchians lacked scleral ossicles, they are found in poposauroids, basal crocodylomorphs and in metriorhynchoids, and are thought to have independently re-occurred in each instance (Nesbitt, Turner, & Weinbaum, 2012). Scleral rings improve the acuity of vision, especially in diurnal and crepuscular animals (e.g., Schmitz & Motani, 2011; Walls, 1942) whereas extant crocodylians, which lack scleral rings, have poor visual acuity alongside adaptations for nocturnal vision, such as a large lens and retinal ganglion cell densities comparable to nocturnal squamates (Emerling, 2017; Nagloo, CollinSP, & Hart, 2016). This may mean crocodylian evolution underwent a "nocturnal bottleneck" (Emerling, 2017; Walls, 1942), as these nocturnal adaptations are plesiomorphies indicating that extant crocodylians shared nocturnal ancestors. For these ancestral nocturnal crocodylians, it may have been more efficient to develop rostral somatosensation than increase visual acuity, trading vision for tactile sensitivity.

Moreover, extant crocodylians have poor underwater vision. Fleishman et al. (1988) found that numerous extant species (*Caiman crocodilus*, *Cro. johnstoni*, *Cro. acutus*, *Cro. rhombifer*, *Paleosuchus palpebrosus*, and *G. gangeticus*) have a good ability to focus while in air, but like humans are severely farsighted underwater. There is also no evidence that the nictitating membrane acts as a correcting lens (Fleishman et al., 1988).

As extant crocodylians have such poor underwater vision, it is therefore perhaps unsurprising crocodylians would use a sophisticated somatosensory system to aid in prey detection and capture. Moreover, given the lack of evidence for such an extensive trigeminally innerved rostral sensory system in metriorhynchids, and their large orbits occupied by a large scleral ring, we concur with previous studies (Martill et al., 1994; Massare, 1988; Young et al., 2010) that metriorhynchids were likely vision-based hunters.

5.4 | Thalattosuchian rostral vasculature

Thalattosuchians have numerous hypertrophied endocranial vasculature canals, including the carotid and orbital canals, hypertrophy of the pituitary fossa (which could be linked to hypertrophy of the cavernous sinus), the transverse sinus and stapedial canals (Brusatte et al., 2016; Fernández et al., 2011; Herrera et al., 2013, 2018; Pierce et al., 2017; Schwab et al., 2021). Thus, ancestrally, thalattosuchians had increased cephalic blood-flow, and we therefore expect that the internal craniofacial vascular canals of thalattosuchians will follow a similar pattern.

Due to the hypothesized increase of cephalic vasculature in thalattosuchians, some of the rostral changes found herein are perhaps relevant to discussions on vasculature rather than neurology. For example, in metriorhynchids, the canals that likely supplied vasculature to the epidermis (cIS) travelled from the DAC through the alveoli rather than dorsal or lateral to the dental alveoli (as seen in metriorhynchoids, extant crocodylians and *Protosuchus*). Metriorhynchids lack the longitudinal cIS that in extant species primarily transmits vasculature to the anastomosis of palatine and maxillary vessels at the anterior of the rostrum (Porter et al., 2016). The significance of this difference between basal metriorhynchoids and metriorhynchids is unknown.

There is no significant difference between the size of the trigeminal ganglion in metriorhynchoids and crocodylians, which may mean that the differences in the trigeminal canals may be caused by differences in vasculature and hence differences in thermoregulatory strategies, as suggested for dinosaurs (Porter & Witmer, 2020). However, we do not know how the neurovascular canals of fossil taxa were occupied, whether neuronal, vasculature, or support tissues dominated.

5.5 | Foramina on the maxillae used in discussions about lips

Neurovascular foramina counts on the maxillae have been used in previous studies to examine the possibility of extra-oral tissues, such as lips (Morhardt, 2009). Modern crocodylians have numerous foramina on the maxillae and do not have lips. Animals with lips have smoother premaxillae, maxillae, and dentaries in comparison to animals without lips. The movement of soft tissues such as those associated with the movement of lips would be impeded by a rugose texture like that seen on these bones in crocodylians (Ford, 2015; Morhardt, 2009).

When high foramina counts are observed on the maxillary bones of dinosaurs, it is often assumed that, they had dermal specializations similar to crocodylians (ISOs) and therefore lacked lips (Barker et al., 2017; Carr et al., 2017). Both *Protosuchus* and the metriorhynchoids had low foramina counts; however, there is no further evidence for the presence or absence of lips.

Many marine animals, such as odontocete whales and pinnipeds have lips to aid in suction feeding, as a means to guide prey toward their mouth before striking (Bloodworth & Marshall, 2005; Jones, Ruff, & Goswami, 2013; Loch, Kieser, & Fordyce, 2015; Werth, 2000, 2006). However, members of Physteroidea (sperm whale and relatives), which lack lips on their lower jaws, utilize suction in prey capture by depressing their hyoid and tongue (Bloodworth & Marshall, 2005; Werth, 2006). Depressing the hyoid to expand the buccal cavity is an important part of suction feeding in fish and amphibians (Heiss, Natchev, Gumpenberger, Weissenbacher, & Van Wassenbergh, 2013; Svanbäck, Wainwright, & Ferry-Graham, 2002; Wainwright, McGee, Longo, & Patricia, 2015; Westneat, 2005). As such, even if metriorhynchoids used suction as a way to manipulate prey closer to striking range (as has been hypothesized for the genus *Dakosaurus*, Young et al., 2012), this could have been accomplished without lips.

6 | CONCLUSION

Herein we show a dramatic difference of snout trigeminal canal distribution between extant crocodylians and fossil relatives. Given that the maxillary ramus of the trigeminal system innervates the sophisticated rostral sensory systems of crocodylians, it implies that their fossil relatives may have primarily hunted using other senses. As metriorhynchoids lack complex trigeminal innervation, this possibly indicates they also lacked the specialized ISOs unique to Crocodylia (and possibly Neosuchia). Metriorhynchoids have a facial neurovasculature system that is more comparatively complex than protosuchids (basal crocodyliformes), which do not have concurrent canals of neurovasculature running through the snout but branches all radiate from one canal, the DAC. Given the lack of a well-developed secondary palate in protosuchids, it is unclear if some trigeminal rami and vasculature travelled through soft tissues instead. Regardless, using such features as proxies for trigeminal-innervated somatosensation, metriorhynchoids would have lacked the sophisticated somatosensory abilities seen in extant crocodylians, which when coupled with their increasingly larger orbits, hint that metriorhynchoids (and metriorhynchids in particular) were vision-based hunters.

It is also noted that metriorhynchids are missing a longitudinal canal compared to the basal metriorhynchoids and crocodylians—as this canal likely permitted the passage of mostly vasculature, this difference between metriorhynchoids and metriorhynchids may be important in future discussions of thalattosuchians craniofacial vasculature and thermal physiology.

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AUTHOR CONTRIBUTIONS

Charlotte Bowman: Investigation; writing - original draft; writing-review & editing. **Mark Young:** Data curation; supervision; writing-review & editing. **Julia Schwab:** Resources; writing-review & editing. **Stig Walsh:** Resources. **Lawrence Witmer:** Resources; writing-review & editing. **Yanina Herrera:** Resources; writing-review & editing. **Jonah Choiniere:** Resources; writing-review & editing. **Kathleen Dollman:** Resources; writing-review & editing. **Stephen Brusatte:** Supervision; Resources; writing-review & editing.

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REFERENCES

Andrade, M. B., Young, M. T., Desojo, J. B., & Brusatte, S. L. (2010). The evolution of extreme hypercarnivory in Metriorhynchidae (Mesoeucrocodylia: Thalattosuchia) based on evidence from microscopic denticle morphology. *Journal of Vertebrate Paleontology*, *30*, 1451–1465.

Andrews, C. W. (1913). *A descriptive catalogue of the marine reptiles of the Oxford clay*. London: British Museum of Natural History.

Barker, C. T., Naish, D., Newham, E., Katsamenis, O. L., & Dyke, G. (2017). Complex neuroanatomy in the rostrum of the Isle of Wight therapod *Neovenator salerii*. *Scientific Reports*, *7*, 1–8.

Bloodworth, B., & Marshall, C. D. (2005). Feeding kinematics of *Kogia* and *Tursiops* (Odontoceti: Cetacea): Characterization of suction and ram feeding. *Journal of Experimental Biology*, *208*, 3721–3730.

Brazaitis, P., & Watanabe, M. E. (2011). Crocodilian behaviour: A window to dinosaur behaviour? *Historical Biology*, *23*, 73–90.

Brusatte, S. L., Muir, A., Young, M. T., Walsh, S., Steel, L., & Witmer, L. M. (2016). The braincase and neurosensory anatomy of an Early Jurassic marine crocodylomorph: Implications for crocodylian sinus evolution and sensory transitions. *The Anatomical Record*, *299*, 1511–1530.

Carr, T. D., Varricchio, D. J., Sedlmayr, J. C., Roberts, E. M., & Moore, J. R. (2017). A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. *Scientific Reports*, *7*, 44842.

Di-Poï, N., & Milinkovitch, M. C. (2013). Crocodylians evolved scattered multi-sensory micro-organs. *EvoDevo*, *4*, 19.

Emerling, C. A. (2017). Archelosaurian color vision, parietal eye loss, and the crocodylian nocturnal bottleneck. *Molecular Biology and Evolution*, *34*, 666–676.

Fernández, M., & Gasparini, Z. (2000). Salt glands in a Tithonian metriorhynchid crocodyliform and their physiological significance. *Lethaia*, *33*, 269–276.

Fernández, M., & Gasparini, Z. (2008). Salt glands in the Jurassic metriorhynchid *Geosaurus*: Implications for the evolution of osmoregulation in Mesozoic marine crocodyliforms. *Naturwissenschaften*, *95*, 79–84.

Fernández, M. S., Carabajal, A. P., Gasparini, Z., & Chong, D. G. (2011). A metriorhynchid crocodyliform braincase from northern Chile. *Journal of Vertebrate Paleontology*, *31*, 369–377.

Fernández, M. S., & Herrera, Y. (2009). Paranasal sinus system of *Geosaurus araucanensis* and the homology of the antorbital fenestra of metriorhynchids (Thalattosuchia: Crocodylomorpha). *Journal of Vertebrate Paleontology*, *29*, 702–714.

Fleishman, L. J., Howland, H. C., Howland, M. J., Rand, A. S., & Davenport, M. L. (1988). Crocodiles don't focus underwater. *Journal of Comparative Physiology A*, *163*, 441–443.

Ford TL. 2015. *Tactile faced therapods*. Symposium of Vertebrate Paleontology 75th Annual Meeting, Meeting Program and Abstracts, p. 47.

Fraas, E. (1902). Die Meer-Krocodilier (Thalattosuchia) des oberen Jura unter specieller Berücksichtigung von *Dacosaurus* und *Geosaurus*. *Palaeontographica*, *49*, 1–72.

Frey, E., Buchy, M. C., Stinnesbeck, W., & López-Oliva, J. G. (2002). *Geosaurus vignaudi* n. sp. (Crocodyliformes: Thalattosuchia), first evidence of metriorhynchid crocodilians in the Late Jurassic (Tithonian) of central-east Mexico (State of Puebla). *Canadian Journal of Earth Sciences*, *39*, 1467–1483.

Gandola, R., Buffetaut, E., Monaghan, N., & Dyke, G. (2006). Salt glands in the fossil crocodile *Metriorhynchus*. *Journal of Vertebrate Palaeontology*, *26*, 1009–1010.

George, I. D., & Holliday, C. M. (2013). Trigeminal nerve morphology in *Alligator mississippiensis* and its significance for Crocodyliform facial sensation and evolution. *The Anatomical Record*, *296*, 670–680.

Gow, C. E. (2000). The skull of *Protosuchus haughtoni*, an early Jurassic crocodyliform from southern Africa. *Journal of Vertebrate Paleontology*, *20*, 49–56.

Grigg, G., & Kirshner, D. (2015). Sense organs of the skin. In *Biology and evolution of crocodylians* (pp. 198–199). Victoria: CSIRO Publishing.

Heiss, E., Natchev, N., Gumpenberger, M., Weissenbacher, A., & Van Wassenbergh, S. (2013). Biomechanics and hydrodynamics of prey capture in the Chinese giant salamander reveal a high-performance jaw-powered suction feeding mechanism. *Journal of the Royal Society Interface*, *10*, 20121028.

Herrera, Y., Fernández, M. S., & Gasparini, Z. (2013). The snout of *Cricosaurus araucanensis*: A case study in novel anatomy of the nasal region of metriorhynchids. *Lethaia*, *46*, 331–340.

Herrera, Y., Fernández, M. S., Lamas, S. G., Campos, L., Talevi, M., & Gasparini, Z. (2017). Morphology of the sacral region and reproductive strategies of Metriorhynchidae: A counter-intuitive approach. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *106*, 247–255.

Herrera, Y., Leardi, J. M., & Fernández, M. S. (2018). Braincase and endocranial anatomy of two thalattosuchian crocodylomorphs and their relevance in understanding their adaptations to the marine environment. *PeerJ*, *6*, e5686.

Holliday, C. M., Porter, W. R., Vliet, K. A., & Witmer, L. M. (2020). The frontoparietal fossa and dorsotemporal fenestra of archosaurs and their significance for interpretations of vascular and muscular anatomy in dinosaurs. *The Anatomical Record*, *303*, 1060–1074.

Hua, S., & De Buffrénil, V. (1996). Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate Paleontology*, *16*, 703–717.

Jackson, K., & Brooks, D. (2007). Do crocodiles co-opt their sense of "touch" to "taste"? A possible new type of vertebrate sensory organ. *Amphibia-Reptilia*, *28*, 277–285.

Johnson, M. M., Young, M. T., & Brusatte, S. L. (2020). The phylogenetics of Teleosauroidea (Crocodylomorpha, Thalattosuchia) and implications for their ecology and evolution. *PeerJ*, *8*, e9808.

Jones, K. E., Ruff, C. B., & Goswami, A. (2013). Morphology and biometrics of the pinniped jaw: Mandibular evolution without mastication. *The Anatomical Record*, *296*, 1049–1063.

Leitch, D. B., & Catania, C. K. (2012). Structure, innervation and response properties of integumentary sensory organs in crocodilians. *Journal of Experimental Biology*, *215*, 4217–4230.

Lessner, E. J. (2020). Quantifying neurovascular canal branching patterns reveals a shared crocodylian arrangement. *Journal of Morphology*, *282*, 1–20.

Lessner, E. J., & Holliday, C. M. (2020a). A 3D Ontogenetic atlas of *Alligator mississippiensis* Cranial nerves and their significance for comparative neurology of reptiles. *The Anatomical Record*, *2020*, 1–29.

Lessner, E. J. & Holliday, C. M.. (2020b). Trigeminal nerve branching patterns reveal diversity and evolution of facial sensitivity among archosaurs. *Journal of Vertebrate Paleontology Program and Abstracts*, pp. 219–220.

Loch, C., Kieser, J. A., & Fordyce, R. E. (2015). Enamel ultrastructure in fossil cetaceans (Cetacea: Archaeoceti and Odontocete). *PLoS One*, *10*, e0116557.

Martill, D. M., Taylor, M. A., Duff, K. L., Riding, J. B., & Bown, P. R. (1994). The trophic structure of the biota of the Peterborough Member, Oxford Clay Formation (Jurassic), UK. *Journal of the Geological Society*, *151*, 173–194.

Massare, J. A. (1988). Swimming capabilities of Mesozoic marine reptiles: Implications for method of predation. *Paleobiology*, *14*, 187–205.

Morhardt, A. C. (2009). *Dinosaur smiles: Do the texture and morphology of the Premaxilla, Maxilla and Dentary bones of Sauropsids provide osteologyical correlates for inferring extra-oral structures reliably in dinosaurs?* (Masters' Thesis submitted to Western Illinois University).

Nagloo, N., CollinSP, H. J. M., & Hart, N. S. (2016). Spatial resolving power and spectral sensitivity of the saltwater crocodile, *Crocodylus porosus*, and the freshwater crocodile, *Crocodylus johnstoni*. *Journal of Experimental Biology*, *219*, 1394–1404.

Nesbitt, S. J., Turner, A. H., & Weinbaum, J. C. (2012). A survey of skeletal elements in the orbit of Pseudosuchia and the origin of the crocodylian palpebral. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *103*, 365–381.

Pierce, S. E., Angielczyk, K. D., & Rayfield, E. J. (2008). Patterns of morphospace occupation and mechanical performance in extant crocodilian skulls: A combined geometric morphometric and finite element modelling approach. *Journal of Morphology*, *269*, 840–864.

Pierce, S. E., Williams, M., & Benson, R. B. J. (2017). Virtual reconstruction of the endocranial anatomy of the early Jurassic marine crocodylomorph *Pelagosaurus typus* (Thalattosuchia). *PeerJ*, *5*, e3225.

Porter, W. R., Sedlmayr, J. C., & Witmer, L. M. (2016). Vascular patterns in the heads of crocodylians: Blood vessels and sites of thermal exchange. *Journal of Anatomy*, *229*, 800–824.

Porter, W. R., & Witmer, L. M. (2020). Vascular patterns in the heads of dinosaurs: Evidence for blood vessels, sites of thermal exchange, and their role in physiological thermoregulatory strategies. *The Anatomical Record*, *303*, 1075–1103.

Schmitz, L., & Motani, R. (2011). Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. *Science*, *332*, 705–708.

Schwab, J. A., Young, M. T., Herrera, Y., Witmer, L. M., Walsh, S., Katsamenis, O. L., & Brusatte, S. L. (2021). The braincase and inner ear of '*Metriorhynchus*' cf. *brachyrhynchus*—Implications for aquatic sensory adaptations in crocodylomorphs. *Journal of Vertebrate Paleontology*, e1912062. https://doi.org/10.1080/02724634.2021.1912062

Schwab, J. A., Young, M. T., Neenan, J. M., Walsh, S. A., Witmer, L. M., Herrera, Y., … Brusatte, S. L. (2020). Inner ear sensory system changes as extinct crocodylomorphs transitioned from land to water. *Proceedings of the National Academy of Sciences*, *117*, 10422–10428.

Sedlmayr JC. 2002. *Anatomy*, *evolution*, *and functional significance of cephalic vasculature in Archosauria*. OhioLINK Electronic Thesis and Dissertation Centre, Ohio University.

Séon, N., Amiot, R., Martin, J. E., Young, M. T., Middleton, H., Fourel, F., … Lécuyer, C. (2020). Thermophysiologies of Jurassic marine crocodylomorphs inferred from the oxygen isotope composition of their tooth apatite. *Philosophical Transactions of the Royal Society B*, *375*, 2019–2039.

Soares, D. (2002). An ancient sensory organ in crocodilians. *Nature*, *417*, 241–242.

Svanbäck, R., Wainwright, P. C., & Ferry-Graham, L. A. (2002). Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. *Physiological and Biochemical Zoology*, *75*, 532–543.

Vliet, K. A. (2001). Courtship behaviour of American alligators *Alligator mississippiensis*. In G. C. Grigg, F. Seebacher, & C. E. Franklin (Eds.), *Crocodilian Biology and Evolution* (pp. 383–408). Chipping Norton: Surrey Beatty and Sons.

Wainwright, P. C., McGee, M. D., Longo, S. J., & Patricia, H. L. (2015). Origins, innovations, and diversification of suction feeding in vertebrates. *Integrative and Comparative Biology*, *55*, 134–145.

Walls, G. (1942). *The vertebrate eye and its adaptive radiation*. Bloomfield Hills, MI: Cranbrook Press 785 pp.

Werth, A. J. (2000). Feeding in marine mammals. In K. Schwenk (Ed.), *Feeding: Form, function and evolution in tetrapod vertebrates* (pp. 475–514). San Diego: Academic Press.

Werth, A. J. (2006). Mandibular and dental variation and the evolution of suction feeding in Odontoceti. *Journal of Mammalogy*, *87*, 579–588.

Westneat, M. W. (2005). Skull biomechanics and suction feeding in fishes. *Fish Physiology*, *23*, 29–75.

Wilberg, E. W. (2015). A new metriorhynchoid (Crocodylomorpha, Thalattosuchia) from the Middle Jurassic of Oregon and the evolutionary timing of marine adaptations in thalattosuchian crocodylomorphs. *Journal of Vertebrate Paleontology*, *35*, e902846.

Young, M. T., & Andrade, M. B. (2009). What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. *Zoological Journal of the Linnean Society*, *157*, 551–585.

Young, M. T., Brignon, A., Sachs, S., Hornung, J. J., Foffa, D., Kitson, J. J. N., … Steel, L. (2021). Cutting the Gordian knot: a historical and taxonomic revision of the Jurassic crocodylomorph Metriorhynchus. *Zoological Journal of the Linnean Society*, *192*, 510–553.

Young, M. T., Brusatte, S. L., Andrade, M. B., Desojo, J. B., Beatty, B. L., Steel, L., … Schoch, R. R. (2012). The cranial osteology and feeding ecology of the metriorhynchid crocodylomorph genera *Dakosaurus* and *Plesiosuchus* from the Late Jurassic of Europe. *PLoS One*, *7*, e44985.

Young, M. T., Brusatte, S. L., Ruta, M., & Andrade, M. B. (2010). The evolution of Metriorhynchoidea (Mesoeucrocodylia, Thalattosuchia): An integrated approach using geometrics morphometrics, analysis of disparity and biomechanics. *Zoological Journal of the Linnean Society*, *158*, 801–859.

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