Neurosensory evolution in thalattosuchian crocodylomorphs – Integrating Somatosensory and Visual Adaptations Across Ecological Transitions.

Ashish Soni[1*], Mark T. Young[1,2], Charlotte I. W. Bowman[1], Arthur Erb[1], Julia A. Schwab[3], Yanina Herrera[4], Stephen L. Brusatte[1]

[1] School of GeoSciences, Grant Institute, The King's Buildings, University of Edinburgh, James Hutton Road, Edinburgh, EH9 3FE, United Kingdom

[2] LWL-Museum für Naturkunde, Sentruper Straße 285, 48161 Münster, Germany

[3] Oxford University Museum of Natural History, University of Oxford, Parks Rd, OX1 3PW Oxford, United Kingdom

[4] Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Ohio Center for Ecology and Evolutionary Studies, Ohio University, Athens, Ohio, United States of America

[5] Consejo Nacional de Investigaciones Científicas y Técnicas, División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, UNLP, B1900 La Plata, Buenos Aires, Argentina

[*] Corresponding author: ashish.soni2000@outlook.com.

Author ORCiDs:

Ashish Soni: https://orcid.org/0009-0008-5962-3196

Mark T. Young: https://orcid.org/0000-0002-7263-6505

Charlotte I. W. Bowman: https://orcid.org/0000-0002-9412-798X

Arthur Erb: -

Julia A. Schwab: https://orcid.org/0000-0002-6229-7116

Yanina Herrera: https://orcid.org/0000-0002-2020-1227

Stephen L. Brusatte: https://orcid.org/0000-0001-7525-7319

Abstract

Thalattosuchians, an extinct lineage of Mesozoic crocodylomorphs, underwent a remarkable evolutionary transition from primarily semi-aquatic teleosaurids, through increasingly ocean-adapted metriorhynchoids, to the fully pelagic metriorhynchids. Understanding how such a major habitat shift affected their sensory systems provides valuable perspective on vertebrate adaptations. Here, we present a comparative analysis integrating digital endocranial reconstructions from computed tomography (CT) scans of 22 skulls of crocodylomorph species, including extant crocodylians and a diverse range of thalattosuchians. Focusing on somatosensation and vision, we seek to gain new insights into sensory evolution in the group using statistical comparative methods.

Our findings reveal that thalattosuchians, especially pelagic metriorhynchids, evolved significantly smaller trigeminal ganglia relative to skull size than non-marine crocodylomorphs, suggesting reduced investment in facial mechanoreception. Interestingly, visual structures (orbit and optic nerve canal dimensions) scale proportionally with skull size across thalattosuchians, reflecting proportional scaling rather than enlargement. This pattern suggests that metriorhynchids maintained visual reliance and any functional enhancement was likely achieved through optical or neural optimisation rather than cranial modification. These findings challenge assumptions of uniform sensory trade-off during aquatic transitions and highlight the importance of lineage-specific constraints in shaping evolutionary trajectories.

Keywords: Crocodylomorpha; endocranial anatomy, macroevolution; Metriorhynchidae; Thalattosuchia

Introduction

Major evolutionary transitions can radically transform organisms, reshaping their anatomy, behaviours and habitats. A particularly striking example is the return of tetrapods to aquatic life, which involves extensive modifications to their body plan. Among these transitions, cetaceans are often marked as a prime example in having evolved from terrestrial mammals into fully pelagic swimmers (Gatesy et al., 2013; Kishida et al., 2015; Thewissen et al., 2011). However, they were not the first to make this transition. During the Mesozoic Era, several reptilian groups such as ichthyosaurs, plesiosaurs and mosasaurs transitioned into marine environments, adapting to fill diverse ecological niches (Foffa et al., 2018; Forêt et al., 2025; Motani, 2009).

Among these secondarily aquatic reptiles, thalattosuchians are particularly significant, representing one of five independent transitions into marine habitats within Crocodylomorpha, and the only one that culminated in fully pelagic open-ocean swimmers (Wilberg et al., 2019). While other marine reptiles have been extensively studied, thalattosuchians remain comparatively less investigated. They comprise of two major clades: Teleosauroidea and Metriorhynchoidea (Young et al., 2024b). Teleosauroids were semi-aquatic and superficially resembled extant gharials, with dorsally directed orbits and elongate snouts (Andrews, 1913;

Buffetaut, 1982; Hua, 1999). However, they were also morphologically diverse and inhabited a range of habitats, such as marine, brackish and freshwater environments (Foffa et al., 2019; Johnson et al., 2020; Jouve, 2009; Martin et al., 2019). Metriorhynchoids represent a key stage in this evolutionary transition, exhibiting progressively stronger marine adaptations relative to teleosauroids, culminating in the fully pelagic metriorhynchids. Basal metriorhynchoids, such as *Pelagosaurus typus*, retained some semi-aquatic features while already showing early adaptations to open-marine environments (Pierce et al., 2017; Young et al., 2024b), and it is from within this grade that the fully pelagic metriorhynchids emerged. These derived forms evolved streamlined bodies, paddle-like limbs, hypocercal tails and a strongly reduced or absent osteodermal covering, reflecting a complete ecological shift to open-ocean environments (Andrews, 1913; Fraas, 1902; Young et al., 2010, 2024a; Spindler et al., 2021).

The exceptional fossil record of thalattosuchians, together with extant crocodylians providing a modern baseline, enables detailed investigation of their neurosensory adaptations to marine life. Comparative studies of other secondary aquatic transitions, such as in cetaceans, reveal recurring patterns of sensory trade-offs in which certain systems are enhanced while others are reduced (Berta et al., 2014; Humphries & Ruxton, 2002; Kishida et al., 2007; Thewissen & Williams, 2002). Whether thalattosuchians underwent similar modifications or followed a distinct evolutionary trajectory, however, remains unresolved.

To begin addressing this question, it is necessary to first consider how key sensory systems function in other aquatic amniotes. Vision is a key sensory system shaped by the transition to aquatic life. Vision depends on the eyes and their neural connections, particularly the optic nerve (cranial nerve II), which transmits visual information from the retina to the brain (Herrera et al., 2019). In aquatic environments, light intensity decreases rapidly with depth, imposing strong selective pressures on eye size and retinal sensitivity. Many secondarily aquatic vertebrates evolved enlarged eyes and optic nerves to maximise light capture and visual acuity in dim or turbid conditions (Kröger & Katzir, 2008; Mass & Supin, 2007; Motani, 2009; Churchill & Baltz, 2021). Some cetaceans, for example, possess optic nerves with reduced fiber density but enlarged "giant" axons (up to 15 µm in diameter) that decrease neural transmission time and enhance the rapid detection of prey (Dawson & Perez, 1973; Dawson et al., 1982; Mazzatenta et al., 2001). Similarly, ichthyosaurs developed exceptionally large orbits and scleral rings indicative of acute visual sensitivity, enabling predation under low-light or mesopelagic conditions (Humphries & Ruxton, 2002; Motani et al., 1999; Schmitz & Motani, 2011). Together, these examples show how aquatic adaptation refines the eyes and optic nerves to optimise vision underwater.

Building on the importance of vision, the sense of touch, or somatosensation, forms one of the most direct channels through which vertebrates perceive their surroundings. It is mediated primarily by the trigeminal system, which originates from the brainstem and forms the trigeminal ganglion within the endocranial cavity (George & Holliday, 2013; Lessner & Holliday, 2022). From this centre arise three principal branches of cranial nerve V: the ophthalmic, maxillary, and mandibular nerves, which transmit mechanoreceptive inputs from the integument to the brain (Holliday & Witmer, 2008; Leitch & Catania, 2012). In aquatic environments, where light and chemical cues are often unreliable, this system frequently becomes enhanced to detect water movement and mechanical vibrations. Pinnipeds and sirenians, for example, possess enlarged trigeminal ganglia and highly innervated vibrissae capable of tracking hydrodynamic trails left by prey (Hanke et al., 2013; Jones & Marshall, 2019). Similarly, extant crocodylians also rely heavily on trigeminal input: their integumentary sensory organs (specialised epidermal structures), concentrated around the snout, detect minute changes in surface pressure and vibration (Leitch & Catania, 2012; George & Holliday, 2013). These examples highlight the evolutionary versatility of the trigeminal system and its capacity to compensate for reduced reliability of other sensory cues in aquatic environments.

Within this broader context of sensory evolution, thalattosuchians offer a model for examining how major environmental transitions shape sensory systems. They have shown to possess large orbits, which have been interpreted as indicators of well-developed vision and a reliance on visual cues for hunting in open-marine environments (Massare, 1988; Young et al., 2010). By contrast, previous studies towards their somatosensory abilities have suggested that thalattosuchians exhibited a simplified trigeminal canal with limited branching, implying reduced facial mechanoreception relative to extant crocodylians (Bowman et al., 2022). However, these interpretations remain largely qualitative and derived from limited specimens. Quantitative endocranial analyses are needed to clarify whether thalattosuchians followed broader aquatic trends or developed a distinct sensory pattern.

Here, we investigate the neurosensory evolution of thalattosuchians through the use of computed tomography (CT) scans and phylogenetic comparative analyses of endocranial sensory structures associated with somatosensation and vision. By analysing thalattosuchian crania, alongside those of extant crocodylians, we herein investigate two hypotheses present in the literature:

(1) Thalattosuchians had reduced facial somatosensory capabilities compared to other crocodylomorphs in our sample (Bowman et al., 2022).

(2) Metriorhynchids were vision-based hunters (Massare, 1988; Martill et al., 1994; Young et al., 2010; Bowman et al., 2022).

[Insert Figure 1 here, in double width]

Institutional abbreviations

BP, Bernard Price Institute, Johannesburg, South Africa; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **IGM**, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MJML**, Museum of Jurassic Marine Life – the Steve Etches Collection, Kimmeridge, England, United Kingdom; **MLP-PV**, Museo de La Plata, Paleontología Vertebrados, La Plata, Buenos Aires, Argentina; **MM**, Minden Museum, Minden, Germany; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MNB**, National Museum of the Bahamas, Nassau, The Bahamas; **MPMA**, Museu de Paleontologia "Professor Antônio Celso de Arruda Campos", Monte Alto, São Paulo, Brazil; **NHMUK**, Natural History Museum, London, England, United Kingdom; **NMS**, National Museum Scotland, Edinburgh, Scotland, United Kingdom; **OUVC**, Ohio University Vertebrate Collection, Athens, Ohio, USA; **TMM**, Texas Memorial Museum, University of Texas, Austin, USA; **UF**, University of Florida, Gainesville, Florida, USA; **USNM**, United States National Museum of Natural History, Washington DC, USA.

Materials and methods

Specimens

The dataset comprised CT scans of 22 skulls, including nine species of extant crocodylians, two "protosuchians", two notosuchians, one early diverging neosuchian, two teleosaurids, one metriorhynchoid and five metriorhynchids (Tables 1 and 2; see Fig. 1 for the phylogenetic relationship and age ranges for the dataset).

[Insert Figure 2 here, in double width]

CT Scanning and Segmentation

Each skull was CT-scanned at various facilities, resulting in differences in resolution and voxel size (Supplementary_data_file: Sheet1). Segmentations were performed in Materialize Mimics 25 using the multiple-slice edit tool and a stylus, allowing for the reconstruction of the brain endocast, olfactory system (including olfactory bulb and tract), trigeminal fossa (housing the trigeminal ganglion of the cranial nerve V), and the optic nerve canal (cranial nerve II) (see Fig. 2) (Abel et al., 2012; Lessner & Holliday, 2022; Pérez-Ramos & Figueirido, 2020; Witmer et al., 2008). Segmentation techniques followed established anatomical guidelines (Cerio & Witmer, 2022; Di-Poï & Milinkovitch, 2013; Grigg & Gans, 1993; Kuzmin et al., 2021; Lessner & Holliday, 2022; Pierce et al., 2017; Witmer et al., 2008).

Measurements

Following segmentation, 3D models were generated from the finalized masks using the *Calculate 3D* function in Mimics (All measurements are available in the Supplementary_data_file: Sheet2).

Diameters of the orbits, optic nerve canals, and trigeminal fossae were measured using Feret’s diameter, defined as the distance between two parallel tangents on opposite sides of an object. It works well in measuring irregular structures as it captures their true spatial extent without assuming geometric symmetry (Pabst & Gregorová, 2007; Walton, 1948). Both maximum and minimum Feret’s diameters were recorded and averaged to obtain a representative value. Measurements were taken in coronal view from a central point within each segmented structure, with five readings taken anteriorly and five posteriorly. The mean of these ten readings was used for subsequent analysis.

To test the hypotheses, scaling relationships among the above sensory structures and skull size proxies were evaluated. Trigeminal fossa diameter, which closely reflects trigeminal ganglion size and hence somatosensory capabilities (Bowman et al., 2022; George & Holliday, 2013; Lessner et al., 2023), was compared to intervestibular width: defined and measured as the distance between the left and right vestibular chambers of the inner ear. This metric provides a robust proxy for overall skull size because it remains structurally stable through fossilization and is less affected by taphonomic distortion (Higgins et al., 2024; Schwab et al., 2020). Similarly, orbit and optic nerve canal diameter (Hall et al., 2009; Kay & Kirk, 2000; Lautenschlager et al., 2023) were also examined against intervestibular width to assess overall visual investment.

Statistical Methods

We employed a phylogenetic comparative framework to test differences in the relative size of cranial neurosensory structures among crocodyliform clades. Analyses were conducted in R (v4.5.1; R studios IDE) using a time-calibrated strict consensus phylogeny derived from TNT analysis. The TNT scripts for the analyses were taken from Young et al., (2024b). These scripts were run as provided in that study, with the only modification being the addition of *Enalioetes schroederi* based on Sachs et al., (2024). The resulting tree was pruned to match the sampled taxa for each dataset, and branch lengths were assigned using the “equal” method in the strap package (Bell & Lloyd, 2015), which distributes time evenly between dated nodes. All linear measurements were natural log-transformed prior to analysis to linearise allometric relationships and satisfy model assumptions.

We used ANCOVA to test whether thalattosuchians, and specifically metriorhynchids, differ from the rest of the dataset in the relative size of neurosensory structures, fitting models of the form

$$\log(\text{structure size}) \sim \log(\text{body size proxy}) \times \text{Taxa}$$

Where “Taxa” is a binary factor (thalattosuchians vs. non-thalattosuchians and metriorhynchids vs non-metriorhynchids). The interaction term assesses differences in regression slopes, while the main effect of Taxa tests differences in intercepts.

To account for phylogenetic non-independence, we performed PGLS using the *pgls* function from the caper package (Orme et al., 2013). Each PGLS model used the same formula as the ANCOVA and was fitted to a comparative data object linking the pruned, time-scaled phylogeny with the measurement dataset. Pagel’s lambda (λ) was estimated by maximum likelihood in each model to quantify the strength of the phylogenetic signal.

All the results arising from R codes can be found in the Supplementary_data_file: Sheet3 and Sheet4. The TNT scripts, along with the resultant .tre file and R pipeline are available at: https://doi.org/10.6084/m9.figshare.30836687

Exclusions

Due to preservation and reconstruction challenges, certain species were excluded from specific analysis. *Protosuchus haughtoni* (BP/1/4770) was excluded from trigeminal ganglion analysis due to incomplete preservation of the trigeminal region. *Metriorhynchus* cf. ‘*M.*’ *brachyrhynchus* (NHMUK PV OR 32618), *Plagiophthalmosuchus gracilirostris* (NHMUK PV OR 33095) and *Eopneumatosuchus colberti* (MNA V2460), were excluded from vision analyses because of missing and/or deformed orbital structures.

Results

Somatosensation proxy

There is a strong correlation between trigeminal fossa diameter and intervestibular width. This correlation is statistically significant, with an $R^2 = 0.88$ (adjusted $R^2 = 0.86$) across the data (PGLS, $p < 0.001$; Fig. 3). However, the strength and form of this relationship differ among the groups analysed.

In the thalattosuchians versus non-thalattosuchians analysis, a significant interaction term is observed (ANCOVA: $p = 0.012$; PGLS: $\beta = -1.100$, $p = 0.020$), indicating that thalattosuchians exhibit a shallower regression slope (slope = 0.373) than the non-thalattosuchian dataset (slope = 1.474). While the ANCOVA did not detect a difference in intercepts ($p = 0.397$), the PGLS shows a significant taxon effect ($p = 0.008$), suggesting a higher intercept for thalattosuchians when accounting for phylogeny.

A similar pattern is observed for metriorhynchids, with a significant interaction term (ANCOVA: $p = 0.017$; PGLS: $\beta = -0.845$, $p = 0.022$), indicating that metriorhynchids also exhibit a shallower regression slope (0.369) than the non-metriorhynchid dataset (1.215). The main effect of taxa approaches significance (ANCOVA: $p = 0.070$; PGLS: $p = 0.060$), suggesting a possible difference in intercepts.

In both PGLS models, Pagel's λ was near zero ($\lambda < 0.001$ for both thalattosuchians and metriorhynchids), indicating negligible phylogenetic signal in the residuals. Overall, trigeminal fossa diameter scales positively with intervestibular width across all groups; however, thalattosuchians show shallower regression slopes relative to the rest of the dataset.

[Insert Figure 3 here, in double width]

Vision proxies

For vision, three separate analyses were carried out to test for overall visual investment between groups: Optic nerve canal vs orbit, optic nerve canal vs intervestibular width and orbit vs intervestibular width

There is a strong, statistically significant correlation between optic nerve (CN II) canal and orbit diameter across crocodylomorphs ($p < 0.001$ for both thalattosuchian and metriorhynchid datasets; Fig. 4). The models show high explanatory power ($R^2 = 0.93$) and a negligible phylogenetic signal ($\lambda \approx 0$). Neither the taxon effect nor the interaction term is significant ($p > 0.2$), indicating similar scaling between the groups.

In contrast, the correlation between orbit diameter and intervestibular width is inconsistent across groups. Orbit size does not scale significantly with skull size among thalattosuchians ($p = 0.158$), whereas a strong relationship is observed in metriorhynchids ($p < 0.001$). This contrast indicates that visual scaling relationships differ within Thalattosuchia, with metriorhynchids showing more tightly constrained, proportional scaling of orbit size with skull size than thalattosuchians as a whole.

Additionally, the optic nerve canal diameter scales positively with intervestibular width in both comparisons ($p < 0.001$), with low phylogenetic signal ($\lambda < 0.001$). However, thalattosuchians exhibit a significant negative taxon effect ($\beta = -1.010$, $p = 0.008$), implying relatively smaller CN II canals for their skull size compared with other crocodylomorphs.

Interestingly, removal of the teleosaurid *Macrospondylus bollensis* produces a significant positive correlation between orbit size and intervestibular width ($p < 0.001$) and the negative taxon effect observed in CN II versus intervestibular width disappears when the metriorhynchoid

Pelagosaurus typus was excluded. Given the small thalattosuchian sample (n = 6), these shifts most likely reflect statistical noise and sampling limitations rather than genuine functional divergence. Nevertheless, these results indicate that orbit and optic nerve scale proportionally across crocodylomorphs, with negligible variation among groups. Once phylogeny is accounted for, neither thalattosuchians nor metriorhynchids show clear deviation from the general trend, suggesting proportional scaling of visual structures.

[Insert Figure 4 here, in double width]

Discussion

Somatosensation

The trigeminal neurovascular canals, which support facial mechanoreception via structures like integumentary sensory organs (specialised epidermal structures that detect external stimuli), show complex branching patterns in extant crocodylians (Lessner et al., 2023). These canals enhance environmental sensitivity in semi-aquatic habitats. However, in thalattosuchians, especially metriorhynchids, this branching is reduced, with only two major canals running in parallel (Bowman et al., 2022; Leitch & Catania, 2012), whereas extant crocodylians typically have numerous branches diverging from the trigeminal canal, forming a more complex network (Lessner et al., 2023).

Previously, Bowman et al., (2022) reported no significant difference in trigeminal ganglion size between extant crocodylians and metriorhynchoids. Our results, however, show that the trigeminal ganglia of metriorhynchids exhibit a reduced allometric scaling relative to skull size proxy (intervestibular width). This reduced scaling suggests a lower relative investment in trigeminal structures compared to other crocodylomorphs. When paired with the lack of extensive trigeminal innervation of the rostral bones in thalattosuchians (see Bowman et al., 2022), these findings support the hypothesis that this clade ancestrally lacked the sophisticated rostral somatosensory abilities seen in modern crocodylians (George & Holliday, 2013; Lessner et al., 2023) and retained this limited sensory system throughout its evolution.

It remains uncertain whether this apparent reduction represents a true sensory regression or a reflection of phylogenetic placement. From our dataset, it remains difficult to determine whether thalattosuchians had reduced trigeminal ganglia, or if their relative size simply reflects their basal position within the crocodylomorph tree. However, previous studies help address this uncertainty, suggesting that highly elaborated facial mechanoreception may be a derived trait of Neosuchia or crown Crocodylia rather than the ancestral crocodylomorph condition. Bowman et al. (2022) proposed that the complex ISO network evolved within Neosuchia following a nocturnal bottleneck (Emerling, 2017) as sensory compensation for reduced visual acuity, and Lessner et al. (2023) identified a stepwise increase in trigeminal canal complexity along the lineage leading to extant crocodylians. Under this framework, thalattosuchians may have retained an ancestrally limited trigeminal system rather than secondarily reducing it. Broader sampling, including more sphenosuchians, protosuchians, and diverse metriorhynchids, is needed to clarify these evolutionary trends.

Taken together, these results suggest that metriorhynchids exhibit a distinct somatosensory pathway, characterised by limited trigeminal investment and less complex neurovascular branching compared to extant crocodylians.

Vision

Complementing the patterns seen in somatosensation, the visual system of metriorhynchids appears conserved. In many secondarily aquatic tetrapods (e.g., ichthyosaurs, plesiosaurs and pinnipeds) the shift to marine environments is often accompanied by prominent visual adaptations, including enlarged orbits and modified ocular structures to accommodate underwater vision (Churchill & Baltz, 2021; Kröger & Katzir, 2008; Motani et al., 1999; Schmitz & Motani, 2011). In contrast, our analyses show a consistent relationship between orbit size, optic nerve canal size, and skull size across crocodylomorphs, indicating that metriorhynchids followed the same proportional scaling pattern as their non-marine relatives. Even when phylogeny was accounted for, we found no significant differences in slope or intercept for either orbit or optic nerve canal sizes between groups, supporting the interpretation that visual structures scaled proportionally despite ecological and morphological divergence. These results indicate conservation over enlargement of visual features, although they do not preclude the possibility that metriorhynchids relied on vision for hunting, as subtle optical or neural adaptations could have enhanced their visual capabilities.

The pattern observed here is consistent with broader evidence that secondarily aquatic vertebrates often retain the fundamental geometry of the eye while modifying only its optical components to function underwater. Kröger and Katzir (2008) showed that in many lineages (from marine reptiles to pinnipeds) adaptation to an aquatic environment typically involves changes to the cornea and lens rather than to orbital structure. Additionally, quantitative analyses across archosaurs further demonstrate that orbit dimensions scale predictably with skull size, following general allometric trends that persist despite ecological and morphological diversification (Lautenschlager et al., 2023). Together, these studies suggest that visual structures can remain relatively stable even amid ecological transitions.

Interestingly, previous studies have noted potential orbital changes linked to the marine transition in thalattosuchians. Endocranial reconstructions of the basal metriorhynchoid *Pelagosaurus typus* show relatively large, laterally positioned orbits interpreted as early adaptations to open-marine predation (Pierce et al., 2017). Similarly, geometric-morphometric analyses by Young et al. (2010) found that some derived metriorhynchids developed more streamlined skulls with proportionally larger orbits. Our results, however, indicate that these features fit within the broader crocodylomorph trend, suggesting variation among species rather than a major shift in visual structures.

Other marine reptiles display more radical visual transformations: for instance, *Ophthalmosaurus* and other ichthyosaurs evolved massive eyes to increase sensitivity and acuity at depth (Humphries & Ruxton, 2002; Motani et al., 1999), while cetaceans show a spectrum of orbit and eye modifications ranging from enlargement in deep-divers to reduction in murky freshwater forms (Churchill & Baltz, 2021). For metriorhynchids, however, evidence for routine deep or mesopelagic foraging remains limited (Young et al., 2010; Massare, 1988; Motani, 2009). Considered together, these examples and our findings highlight the diversity of visual evolution in aquatic amniotes, demonstrating how different lineages variously modify, conserve or reduce visual structures in response to their sensory demands.

These findings, however, are subject to a few limitations. The number of thalattosuchian specimens available for comparison is limited, and the instability of results when individual taxa are removed (*Macrospondylus bollensis* and *Pelagosaurus typus*) demonstrates the leverage individual specimens can exert on regression parameters. It is also important to note that these inferences are based on orbit dimensions, which are an imprecise proxy for actual eyeball size. While orbit and eyeball size generally correspond in many taxa, cranial soft tissue, scleral rings, and evolutionary cranial modifications can cause significant deviations (Schmitz & Motani, 2011). Furthermore, methodological limitations must be considered. Orbit and optic nerve measurements may not fully reflect sensory capability, and taphonomic distortion or segmentation variability can introduce measurement uncertainty. These factors underscore the need for cautious interpretation and highlight the importance of future studies using additional proxies such as the aperture of the scleral ring.

Ontogeny also constitutes a limitation. For instance, *Montealtosuchus arrudacampo*si is regarded as a subadult, which could influence the dimensions of its endocranial structures. However, given the restricted notosuchian sample size (n = 2), together with the ontogentic patterns documented in the vestibular system (see Schwab et al., 2022) and brain morphology (see Jirak and Janack, 2017) of extant crocodylians, the impact of this single subadult is unlikely to substantially alter our results. Nevertheless, future work incorporating broader ontogenetic series of extant crocodylians could help clarify how growth stages can affect neurosensory structures such as the trigeminal ganglion and the optic nerve. In summary, while metriorhynchids demonstrate morphological and ecological divergence from other crocodylomorphs, their visual system appears to have remained relatively conserved. While absolute orbit sizes may have increased in some species to enhance visual capabilities in marine environments, the relative scaling of these visual structures remained consistent with that of their terrestrial and semi-aquatic relatives. Taken together, these findings neither confirm nor contradict the idea that metriorhynchids were vision-based hunters and suggest that any enhancement in visual capacity likely occurred within conserved cranial proportions.

Implications

Our findings demonstrate that thalattosuchian sensory evolution was neither uniform nor strictly directional, but rather a modular rebalancing of modalities driven by ecological pressures and phylogenetic constraints.

The comparative simple branching of the trigeminal system in Metriorhynchidae (and amongst thalattosuchians more broadly; Bowman et al., 2022) suggests that facial somatosensation foraging was not important for prey detection. This diverges from the rich facial mechanoreception and complex branching seen in extant crocodylians (Leitch & Catania, 2012; George & Holliday, 2013) and should caution against uncritical comparisons with modern analogues, emphasizing the need to interpret sensory systems in their specific functional and ecological contexts.

Conversely, the hypotheses that metriorhynchids were vision-based hunters (Massare, 1988; Martill et al., 1994; Young et al., 2010; Bowman et al., 2022) remain plausible although unconfirmed based on our data. Our findings show that visual structures (orbits and optic nerve canals) are relatively consistent across Crocodylomorpha, while some species exhibit relatively large orbits (Pierce et al., 2017; Young et al., 2010), these deviations fall within the expected variation and do not indicate a clade-wide enlargement. This highlights the limitations of using orbit and optic nerve canal dimensions as proxies for visual capability and highlights the need for cautious interpretation, as any enhancement in visual performance in metriorhynchids likely occurred within conserved cranial proportions.

The pattern observed in thalattosuchians gains broader significance when placed in the context of other secondarily aquatic tetrapod lineages. A simple sensory trade-off model would predict that reduction of one modality is compensated by enlargement of another, yet evidence from other secondarily aquatic vertebrates increasingly supports a more complex picture. In ichthyosaurs, endocranial reconstructions reveal concurrent enlargement of the optic lobes, olfactory region and cerebellum (Marek et al., 2015), indicating simultaneous enhancement of multiple systems. Among marine mammals, cetaceans show dramatic enhancement of auditory processing alongside olfactory reduction, pinnipeds retain well-developed vision alongside vibrissal mechanoreception and sirenians elaborated their trigeminal system independently of either solution (Berta et al., 2014). The common thread across these lineages is not a universal sensory hierarchy but lineage-specific rebalancing driven by ecological context and phylogenetic history (Motani, 2009). Thalattosuchians fit this broader pattern, showing reduced mechanosensory investment alongside conserved visual proportions, reflecting the specific demands of open-ocean predation rather than any generalised aquatic sensory template.

Taken together, the sensory evolution of thalattosuchians appears modular: facial somatosensation shows reduction, and vision remains consistent with potential species-level variation. This pattern underscores that secondarily aquatic transitions can produce a mix of retained, reduced or subtly modified modalities rather than a uniform sensory shift.

Conclusion

This study sheds new light on the sensory evolution of thalattosuchians, revealing a mosaic pattern of adaptation shaped by ecological pressures and phylogenetic constraints. In metriorhynchids, appear reduced compared with other crocodylomorphs and the visual structures maintain relative consistency with crocodylomorphs overall. These divergent trends suggest that sensory systems evolved modularly rather than through uniform enhancement or reduction.

Taken together with the dramatic changes in the metriorhynchid vestibular system (see Schwab et al., 2020), these patterns support a model of modular sensory evolution, wherein different modalities respond independently to environmental pressures. This flexible reorganisation, rather than strict functional trade-offs, aligns with broader trends observed in other secondarily aquatic vertebrates (Berta et al., 2014; Marek et al., 2015; Motani, 2009). Together, these results demonstrate how combining neuroanatomical, ecological, and phylogenetic perspectives can reveal the diverse evolutionary pathways of vertebrate sensory systems and establish a comparative framework for interpreting sensory evolution during major habitat shifts.

Acknowledgements

We are grateful to the numerous museum curators and staff who facilitated access to specimens and CT data, including those from the Natural History Museum (London), Museo de La Plata, Texas Memorial Museum, Ohio University Vertebrate Collection, and others listed in our Institutional Abbreviations. We thank the staff at the University of Edinburgh for institutional support and computing access. We are also indebted to the imaging specialists and technicians at various CT facilities who enabled the scanning and reconstruction of the fossil and extant specimens used in this study.

Special thanks to colleagues who provided valuable feedback and discussions during the early stages of this research. We also acknowledge the support of the Leverhulme Trust (RPG-2017-167), which funded this project, and SLB acknowledge Swedish Research Council grant 2021-02973 for funding their work on cognition and sensory evolution in deep time. J.A.S is supported by a Leverhulme Trust Early Career Fellowship (ECF-2023-365)

Data Availability Statement

All the codes are available at https://doi.org/10.6084/m9.figshare.30836687 and data in the Supplementary_data_file.

Disclosure Statement

One of the co-authors (MTY) is Editor-in-Chief of the journal.

Funding

This project was supported by a Leverhulme Trust Research Project grant (RPG-2017-167) and Swedish Research Council grant 2021-02973. MTY receives an honorarium from Taylor & Francis (journal publisher) as part of his contract as Editor-in-Chief for *Historical Biology*. JAS is supported by a Leverhulme Trust Early Career Fellowship (ECF-2023-365).

References

Abel, R. L., Laurini, C. R., Richter, M. (2012). A palaeobiologist's guide to 'virtual' micro-CT preparation. *Palaeontologia Electronica, 15(2)*, 15.2.6T. https://palaeo-electronica.org/content/issue-2-2012-technical-articles/233-micro-ct-workflow

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

Bell, M. A., & Lloyd, G. T. (2015). strap: An R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology, 58(2)*, 379–389. https://doi.org/10.1111/pala.12142

Berta, A., Ekdale, E. G., & Cranford, T. W. (2014). Review of the cetacean nose: form, function, and evolution. *The Anatomical Record, 297(11)*, 2205-2215. https://doi.org/10.1002/ar.23034

Bowman, C. I. W., Young, M. T., Schwab, J. A., Walsh, S., Witmer, L. M., Herrera, Y., Choiniere, J., Dollman, K. N., & Brusatte, S. L. (2022). Rostral neurovasculature indicates sensory trade-offs in Mesozoic pelagic crocodylomorphs. *The Anatomical Record, 305(10)*, 2654-2669. https://doi.org/10.1002/ar.24733

Buffetaut, E. (1982). Radiation évolutive, paléoécologie et biogéographie des crocodiliens mésosuchiens. *Mémoires de la Société Géologique de France 60,* 1-88.

Cerio, D. G., & Witmer, L. M. (2022). Orbital soft tissues, bones, and allometry: implications for the size and position of crocodylian eyes. *The Anatomical Record, 306(10)*, 2537-2561. https://doi.org/10.1002/ar.25133

Churchill, M., & Baltz, C. (2021). Evolution of orbit size in toothed whales (Artiodactyla: Odontoceti). *Journal of Anatomy, 239(6)*, 1419-1437. doi: 10.1111/joa.13522

Dawson, W. W., Hawthorne, M. N., Jenkins, R. L., & Goldston, R. T. (1982). Giant neural systems in the inner retina and optic nerve of small whales. *The Journal of Comparative Neurology, 205(1),* 1–7. https://doi.org/10.1002/cne.902050102

Dawson, W. W., & Perez, J. M. (1973). Unusual retinal cells in the dolphin eye. *Science, 181(4101),* 747–749. https://doi.org/10.1126/science.181.4101.747

Di-Poï, N., & Milinkovitch, M. C. (2013). Crocodylians evolved scattered multi-sensory micro-organs. *EvoDevo, 4(1),* 19. https://doi.org/10.1186/2041-9139-4-19

Christopher A. Emerling, Archelosaurian Color Vision, Parietal Eye Loss, and the Crocodylian Nocturnal Bottleneck, *Molecular Biology and Evolution*, Volume 34, Issue 3, March 2017, Pages 666–676, https://doi.org/10.1093/molbev/msw265

Foffa, D., Johnson, M. M., Young, M. T., Steel, L., & Brusatte, S. L. (2019). A revision of the deep-water teleosauroid crocodylomorph *Teleosaurus megarhinus* Hulke, 1871 from the Kimmeridge Clay Formation (Late Jurassic) of England, UK. *PeerJ 7,* e6646. https://doi.org/10.7717/peerj.6646

Foffa, D., Young, M. T., Stubbs, T. L., Dexter, K. G., & Brusatte, S. L. (2018). The long-term ecology and evolution of marine reptiles in a Jurassic seaway. *Nature Ecology & Evolution, 2(10)*, 1548-1555. https://doi.org/10.1038/s41559-018-0656-6

Forêt, T., Aubier, P., Jouve, S., & Cubo, J. (2025). Analysing Thalattosuchia palaeobiodiversity through the prism of phylogenetic comparative methods. *Palaeontology, 68(1)*, e70000. https://doi.org/10.1111/pala.70000

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

Gatesy, J., Geisler, J. H., Chang, J., Buell, C., Berta, A., Meredith, R. W., Springer, M. S., & McGowen, M. R. (2013). A phylogenetic blueprint for a modern whale. *Molecular Phylogenetics and Evolution, 66(2)*, 479-506. https://doi.org/10.1016/j.ympev.2012.10.012

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(4)*, 670-680. https://doi.org/10.1002/ar. 22666

Grigg, G., & Gans, C. (1993). Morphology and physiology of the Crocodylia. In C. J. Glasby, G. J. B. Ross, & P. L. Beesley (Eds.), Fauna of Australia: Vol. 2A. *Amphibia and Reptilia* (pp. 326–336). Australian Government Publishing Service.

Hall, M. I., Iwaniuk, A. N., & Gutiérrez-Ibáñez, C. (2009). Optic foramen morphology and activity pattern in birds. *The Anatomical Record, 292(11)*, 1827–1845. https://doi.org/10.1002/ar.21007

Hanke, W., Wieskotten, S., Marshall, C., & Dehnhardt, G. (2013). Hydrodynamic perception in true seals (Phocidae) and eared seals (Otariidae). *Journal of comparative physiology. A, Neuroethology, sensory, neural, and behavioral physiology, 199(6)*, 421–440. https://doi.org/10.1007/s00359-012-0778-2

Herrera, E., Agudo-Barriuso, M., & Murcia-Belmonte, V. (2019). Cranial pair II: the optic nerves. *The Anatomical Record*, *302*(3), 428-445. https://doi.org/10.1002/ar.23922

Higgins, R. R., Cowgill, T., Young, M. T., Schwab, J. A., Herrera, Y., Witmer, L. M., & Brusatte, S. L. (2024). The internal braincase anatomy of *Thalattosuchus superciliosus* – with implications for the endocranial evolution of metriorhynchid crocodylomorphs. *Historical Biology*, 1–12. https://doi.org/10.1080/08912963.2024.2427096

Holliday, C. M., & Witmer, L. M. (2009). The epipterygoid of crocodyliforms and its significance for the evolution of the orbitotemporal region of eusuchians. *Journal of Vertebrate Paleontology*, *29*(3), 715–733. https://doi.org/10.1671/039.029.0330

Hua S. (1999). Le crocodilien *Machimosaurus mosae* (Thalattosuchia, Teleosauridae) du Kimmeridgien du Boulonnais (Pas de Calais, France). *Palaeontographica A 252*, 141-170

Humphries, S., & Ruxton, G. (2002). Why did some ichthyosaurs have such large eyes? The *Journal of Experimental Biology*, *205(4)*, 439-441. https://doi.org/10.1242/JEB.205.4.439

Jirak, D., & Janacek, J. (2017). Volume of the crocodilian brain and endocast during ontogeny. *PLoS ONE, 12*(6), e0178491. https://doi.org/10.1371/journal.pone.0178491

Johnson, M., Young, M., & Brusatte, S. (2020). The phylogenetics of Teleosauroidea (Crocodylomorpha, Thalattosuchia) and implications for their ecology and evolution. *PeerJ, 8,* e9808. https://doi.org/10.7717/peerj.9808

Jones, A., & Marshall, C. D. (2019). Does Vibrissal Innervation Patterns and Investment Predict Hydrodynamic Trail Following Behavior of Harbor Seals (Phoca vitulina)? *The Anatomical record, 302(10),* 1837–1845. https://doi.org/10.1002/ar.24134

Jouve, S. (2009). The skull of *Teleosaurus cadomensis* (Crocodylomorpha; Thalattosuchia), and phylogenetic analysis of Thalattosuchia. *Journal of Vertebrate Paleontology, 29(1)*, 88-102. https://doi.org/10.1080/02724634.2009.10010364

Kay, R. F., & Kirk, E. C. (2000). Osteological evidence for the evolution of activity pattern and visual acuity in primates. American Journal of Physical Anthropology: *The Official Publication of the American Association of Physical Anthropologists*, 113(2), 235-262.

Kishida, T., Kubota, S., Shirayama, Y., & Fukami, H. (2007). The olfactory receptor gene repertoires in secondary-adapted marine vertebrates: evidence for reduction of the functional proportions in cetaceans. *Biology Letters*, *3(4)*, 428-430. https://doi.org/10.1098/rsbl.2007.0191

Kishida, T., Thewissen, J., Hayakawa, T., Imai, H., & Agata, K. (2015). Aquatic adaptation and the evolution of smell and taste in whales. *Zoological Letters*, *1(1)*, 9. https://doi.org/10.1186/s40851-014-0002-z

Kröger, R. H. H., & Katzir, G. (2008). Comparative anatomy and physiology of vision in aquatic tetrapods. In J. G. M. Thewissen & S. Nummela (Eds.), Sensory evolution on the threshold: *Adaptations in secondarily aquatic vertebrates* (pp. 121–148). University of California Press. https://doi.org/10.1525/9780520934122-010

Kuzmin, I. T., Boitsova, E. A., Gombolevskiy, V. A., Mazur, E. V., Morozov, S. P., Sennikov, A. G., Skutschas, P. P., & Sues, H.-D. (2021). Braincase anatomy of extant Crocodylia, with new insights into the development and evolution of the neurocranium in crocodylomorphs. *Journal of Anatomy, 239(5),* 983-1038. https://doi.org/10.1111/joa.13490

Lautenschlager, S., Aston, R. F., Baron, J. L., Boyd, J. R., Bridger, H. W. L., Carmona, V. E. T., Ducrey, T., Eccles, O., Gall, M., Jones, S. A., Laker-Mchugh, H., Lawrenson, D. J., Mascarenhas, K. J., Mcschnutz, E., Quinn, J. D., Robson, T. E., Stöhr, P. W., Strahl, E. J., Tokeley, R. R., ... Dunne, E. M. (2023). Orbit size and estimated eye size in dinosaurs and other archosaurs and their implications for the evolution of visual capabilities. *Journal of Vertebrate Paleontology*, *43(3)*, Article e2295518. https://doi.org/10.1080/02724634.2023.2295518

Leitch, D. B., & Catania, K. C. (2012). Structure, innervation and response properties of integumentary sensory organs in crocodilians. *The Journal of experimental biology, 215* (Pt 23), 4217-4230. https://doi.org/10.1242/jeb.076836

Lessner, E. J., Dollman, K. N., Clark, J. M., Xu, X., & Holliday, C. M. (2023). Ecomorphological patterns in trigeminal canal branching among sauropsids reveal sensory shift in suchians. *Journal of Anatomy, 242(5),* 927-952. https://doi.org/10.1111/joa. 13826

Lessner, E. J., & Holliday, C. M. (2022). A 3D ontogenetic atlas of *Alligator mississippiensis* cranial nerves and their significance for comparative neurology of reptiles. *The Anatomical Record, 305(10),* 2854-2882. https://doi.org/10.1002/ar.24550

Marek, R. D., Moon, B. C., Williams, M., & Benton, M. J. (2015). The skull and endocranium of a Lower Jurassic ichthyosaur based on digital reconstructions. *Palaeontology, 58(4),* 723-742. https://doi.org/10.1111/pala.12174

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

Martin, J. E., Suteethorn, S., Lauprasert, K., Tong, H., Buffetaut, E., Liard, R., Salaviale, C., Deesri, U., Suteethorn, V., & Claude, J. (2019). A new freshwater teleosaurid from the Jurassic of northeastern Thailand. *Journal of Vertebrate Paleontology 38*, e1549059. https://doi.org/10.1080/02724634.2018.1549059

Mass, A. M., & Supin, A. Y. (2007). Adaptive features of aquatic mammals' eye. *The Anatomical Record, 290(6)*, 701-715. https://doi.org/10.1002/ar.20529

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

Mazzatenta, A., Caleo, M., Baldaccini, N. E., & Maffei, L. (2001). A comparative morphometric analysis of the optic nerve in two cetacean species, the striped dolphin (*Stenella coeruleoalba*) and fin whale (*Balaenoptera physalus*). *Visual Neuroscience, 18(2)*, 319–325. https://doi.org/10.1017/s0952523801182155

Motani, R., Rothschild, B. M., & Wahl Jr, W. (1999). Large eyeballs in diving ichthyosaurs. *Nature*, *402*(6763), 747-747. https://doi.org/10.1038/45435

Motani, R. (2009). The evolution of marine reptiles. *Evolution: Education and Outreach*, 2(supplement 2), 224-235. https://doi.org/10.1007/s12052-009-0139-y

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2013). caper: *Comparative analysis of phylogenetics and evolution in R (Version 1.0.1)* [R package]. https://cran.r-project.org/package=caper

Pabst, W., & Gregorova, E. (2007). Characterization of particles and particle systems. *ICT Prague*, *122*, 122 pp.

Pérez-Ramos, A., & Figueirido, B. (2020). Toward an "ancient" virtual world: improvement methods on X-ray CT data processing and virtual reconstruction of fossil skulls. *Frontiers in Earth Science, 8,* 345. https://doi.org/10.3389/feart.2020.00345

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. https://doi.org/10.7717/peerj.3225

Sachs, S., Young, M. T., Hornung, J. J., Cowgill, T., Schwab, J. A., & Brusatte, S. L. (2024). A new genus of metriorhynchid crocodylomorph from the Lower Cretaceous of Germany. *Journal of Systematic Palaeontology, 22*(1). https://doi.org/10.1080/14772019.2024.2359946

Schmitz, L., & Motani, R. (2011). Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. *Science, 332(6030),* 705–708. https://doi.org/10.1126/science.1200043

Schwab, J. A., Young, M. T., Neenan, J. M., Walsh, S. A., Witmer, L. M., Herrera, Y., Allain, R., Brochu, C. A., Choiniere, J. N., Clark, J. M., Dollman, K. N., Etches, S., Fritsch, G., Gignac, P. M., Ruebenstahl, A., Sachs, S., Turner, A. H., Vignaud, P., Wilberg, E. W., Xu, X., Zanno, L. E., & Brusatte, S. L. (2020). Inner ear sensory system changes as extinct crocodylomorphs transitioned from land to water. *Proceedings of the National Academy of Sciences of the United States of America, 117(19)*, 10422-10428. https://doi.org/10.1073/pnas.2002146117

Schwab, J. A., Young, M. T., Walsh, S. A., Witmer, L. M., Herrera, Y., Brochu, C. A., Butler, I. B., & Brusatte, S. L. (2022). Ontogenetic variation in the crocodylian vestibular system. *Journal of Anatomy, 240*(5), 821–832. https://doi.org/10.1111/joa.13601

Spindler, F., Lauer, R., Tischlinger, H., Mäuser, M., & Bayerns, S. N. S. (2021). The integument of pelagic crocodylomorphs (Thalattosuchia: Metriorhynchidae). *Palaeontologia Electronica, 24*(2), a22. https://doi.org/10.26879/1099

Thewissen, J. G. M., George, J., Rosa, C., & Kishida, T. (2011). Olfaction and brain size in the bowhead whale (*Balaena mysticetus*). *Marine Mammal Science, 27(2)*, 282-294. https://doi.org/10.1111/j.1748-7692.2010.00406.x

Thewissen, J. G. M., & Williams, E. M. (2002). The early radiations of Cetacea (Mammalia): evolutionary pattern and developmental correlations. Annual Review of Ecology, Evolution, and *Systematics*, *33(1)*, 73-90. https://doi.org/10.1146/annurev.ecolsys.33.020602.095426

Walton, W. (1948). Feret's statistical diameter as a measure of particle size. *Nature*, *162,* 329–330. https://doi.org/10.1038/162329b0

Wilberg, E. W., Turner, A. H., & Brochu, C. A. (2019). Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. *Scientific Reports, 9(1)*, 514. https://doi.org/10.1038/s41598-018-36795-1

Witmer, L. M., Ridgely, R. C., Dufeau, D. L., & Semones, M. C. (2008). Using CT to peer into the past: 3D visualization of the brain and ear regions of birds, crocodiles, and nonavian dinosaurs. In: Endo, H., & Frey, R. (eds). *Anatomical Imaging: towards a new morpohology*. *Springer Tokyo, Tokyo*. 67–87. https://doi.org/10.1007/978-4-431-76933-0_6

Young, Mark T., Brusatte, S. L., Ruta, M., & Andrade, M. B. (2010). The evolution of Metriorhynchoidea (Mesoeucrocodylia, Thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. *Zoological Journal of the Linnean Society, 158(4)*, 801-859. https://doi.org/10.1111/j.1096-3642.2009.00571.x

Young, M. T., Schwab, J. A., Dufeau, D., Racicot, R. A., Cowgill, T., Bowman, C. I. W., Witmer, L. M., Herrera, Y., Higgins, R., Zanno, L., Xing, X., Clark, J., & Brusatte, S. L. (2024a). Skull sinuses precluded extinct crocodile relatives from cetacean-style deep diving as they transitioned from land to sea. *Royal Society Open Science, 11(10)*, 241272. https://doi.org/10.1098/rsos.241272

Young, M. T., Wilberg, E. W., Johnson, M. M., Herrera, Y., Brandalise de Andrade, M., Brignon, A., Sachs, S., Abel, P., Foffa, D., Fernández, M. S., Vignaud, P., Cowgill, T., & Brusatte, S. L. (2024b). The history, systematics, and nomenclature of Thalattosuchia

(Archosauria: Crocodylomorpha). *Zoological Journal of the Linnean Society*, *200(2)*, 547–617. https://doi.org/10.1093/zoolinnean/zlad165