Cephalic salt gland evolution in Mesozoic pelagic crocodylomorphs

THOMAS COWGILL[1,*], MARK T. YOUNG FLS[1], JULIA A. SCHWAB[1], STIG WALSH[2], LAWRENCE M. WITMER[3], YANINA HERRERA[4], KATHLEEN N. DOLLMAN[5], ALAN H. TURNER[6] and STEPHEN L. BRUSATTE[1]

[1]*School of GeoSciences, Grant Institute, The King's Buildings, University of Edinburgh, James Hutton Road, Edinburgh, EH9 3FE, UK*
[2]*Department of Natural Sciences, National Museum of Scotland, Edinburgh, EH1 1JF, UK*
[3]*Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Ohio University, Athens, OH 45701, USA*
[4]*Consejo Nacional de Investigaciones Científicas y Técnicas, División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, B1900 La Plata, Buenos Aires, Argentina*
[5]*Evolutionary Studies Institute, University of the Witwatersrand, 2000 Johannesburg, South Africa*
[6]*Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794, USA*

Secondarily marine tetrapod lineages have independently evolved osmoregulatory adaptations for life in salt water but inferring physiological changes in extinct marine tetrapods is difficult. The Mesozoic crocodylomorph clade Thalattosuchia is unique in having both direct evidence from natural endocasts and several proposed osteological correlates for salt exocrine glands. Here, we investigate salt gland evolution in thalattosuchians by creating endocranial reconstructions from CT scans of eight taxa (one basal thalattosuchian, one teleosauroid, two basal metriorhynchoids and four metriorhynchids) and four outgroups (three extant crocodylians and the basal crocodyliform *Protosuchus*) to identify salt gland osteological correlates. All metriorhynchoids show dorsolateral nasal cavity expansions corresponding to the location of nasal salt glands in natural casts, but smaller expansions in teleosauroids correspond more with the cartilaginous nasal capsule. The different sizes of these expansions suggest the following evolutionary sequence: (1) plesiomorphically small glands present in semi-aquatic teleosauroids draining through the nasal vestibule; (2) moderately sized glands in the basalmost metriorhynchoid *Pelagosaurus*; and (3) hypertrophied glands in the clade comprising *Eoneustes* and metriorhynchids, with a pre-orbital fenestra providing a novel exit for salt drainage. The large gland size inferred from basal metriorhynchoids indicates advanced osmoregulation occurred while metriorhynchoids were semi-aquatic. This pattern does not precisely fit into current models of physiological evolution in marine tetrapods and suggests a unique sequence of changes as thalattosuchians transitioned from land to sea.

ADDITIONAL KEYWORDS: Crocodylomorpha – land-sea transition – Metriorhynchidae – salt glands – Teleosauroidea – Thalattosuchia.

INTRODUCTION

Major evolutionary transitions, in which a group of organisms undergoes a radical change in phenotype as they move from one habitat into another, have occurred numerous times in the over 300-million-year history of tetrapods. One prime example is terrestrial tetrapods secondarily returning to a marine habitat (Uhen, 2007; Motani, 2009; Kelley & Pyenson, 2015). During their land-to-sea transitions, various tetrapod lineages—as diverse as modern whales and extinct marine reptiles—converged upon similar morphological, reproductive and physiological adaptations to a pelagic lifestyle. The constraints of swimming in the water column led to a

*Corresponding author. E-mail: thomas231@cowgill.org.uk

common suite of morphological adaptations, including more streamlined bodies, modification of the limbs into paddles and, in groups that use tail propulsion (e.g. cetaceans, ichthyosaurs, mosasaurs), caudal flukes (Motani *et al.*, 1996; Caldwell, 2002; Uhen, 2007; Motani, 2009; Lindgren *et al.*, 2010). Furthermore, changes from oviparity to viviparity in multiple Mesozoic marine reptiles is demonstrated by fossil embryos in ichthyosaurs (Woodward, 1906; Motani *et al.*, 2014), nothosaurs (Cheng *et al.*, 2004), plesiosaurs (O'Keefe & Chiappe, 2011) and mosasaurs (Caldwell & Lee, 2001).

One of the most notable physiological demands experienced by marine tetrapods is the need to maintain the osmoregulation of blood plasma in a saline environment. To meet this demand, sauropsid lineages have independently evolved extrarenal salt exocrine glands by modification of pre-existing cephalic glands (Babonis & Brischoux, 2012). Among these are nasal glands in both birds (Schmidt-Nielsen *et al.*, 1958; Holmes & Phillips, 1985) and lizards (Schmidt-Nielsen & Fange, 1958; Dunson, 1969), lacrimal glands in turtles (Schmidt-Nielsen & Fange, 1958; Hirayama, 1998), sublingual and premaxillary glands in snakes (Dunson *et al.*, 1971; Dunson & Dunson, 1973) and lingual glands in crocodylians (Taplin & Grigg, 1981; Taplin *et al.*, 1982, 1985). Mammals lack salt glands as osmoregulation occurs entirely within the renal system, due to the different structure of the mammalian kidney, enabling greater concentration of solutes in urine (Braun, 1998). Although morphological and reproductive changes are well known among extinct marine tetrapods, osmoregulatory evolution has been more difficult to infer because of the scarcity of direct evidence of salt glands, which requires exceptional preservation in fossils and/or unambiguous osteological correlates.

However, the Mesozoic marine crocodylomorph clade Thalattosuchia provides a unique opportunity to study the evolution of salt glands and osmoregulation in a marine sauropsid clade. Thalattosuchia comprises two subgroups. The first, Teleosauroidea, typically consisted of longirostrine forms (i.e. having a long and narrow snout) that primarily lived in shallow marine and brackish ecosystems (Andrews, 1913; Johnson *et al.*, 2020). The second, Metriorhynchoidea, transitioned from teleosauroid-like forms into highly diverse open-ocean predators (e.g. Young *et al.*, 2010; Wilberg, 2015; Ősi *et al.*, 2018). The metriorhynchoid subclade Metriorhynchidae was obligately pelagic, sharing several convergent adaptations with other marine tetrapods such as paddle-like limbs, a hypocercal tail fin and increased diameter of the pelvic girdle proposed as indirect evidence of viviparity (Andrews, 1913; Young *et al.*, 2010; Herrera *et al.*, 2017). The physiological adaptations of metriorhynchids are exceptionally well known among extinct marine tetrapods because of

multiple metriorhynchid natural endocasts preserving direct evidence of hypertrophied nasal salt glands (Fernández & Gasparini, 2000, 2008; Fernández & Herrera, 2009, 2021; Herrera *et al.*, 2013). The salt glands of metriorhynchids are identified as homologous with the nasal glands in other sauropsids based on their extracapsular morphology (Witmer, 1995, 1997; Fernández & Gasparini, 2000; Fernández & Herrera, 2009). However, these glands are currently only preserved in natural endocasts of the metriorhynchids *Cricosaurus araucanensis* Gasparini & Dellapé, 1976 (Fernández & Gasparini, 2000, 2008; Herrera *et al.*, 2013) and *Dakosaurus andiniensis* Vignaud & Gasparini, 1996 (Fernández & Herrera, 2021).

With limited direct evidence of salt glands in fossil specimens, studying salt gland evolution across Thalattosuchia would require identifying osteological correlates of salt gland presence, size and morphology in fossils lacking exceptional preservation. This would also allow us to determine when salt glands originated in the lineage and how they changed as these crocodylomorphs transitioned from nearshore to fully pelagic environments. Several salt gland osteological correlates have previously been proposed, including the pre-orbital fenestra of Metriorhynchidae, a structure in the position of the antorbital fenestra of archosaurs that does not connect to the antorbital cavity (Fernández & Herrera, 2009; Leardi *et al.*, 2012) and whose homologies are debatable (see Pierce *et al.*, 2017), concave depressions on the internal surface of the prefrontals (Gandola *et al.*, 2006), expansions of the nasal cavity in both three-dimensionally preserved specimens (Buchy *et al.*, 2007) and computed tomography (CT) endocranial reconstructions (Pierce *et al.*, 2017; Wilberg *et al.*, 2021) and the enlarged carotid canals and foramina in teleosauroids, but particularly in metriorhynchoids (Herrera *et al.*, 2013, 2018; Brusatte *et al.*, 2016). However, a broader comparative sample of thalattosuchians and outgroup crocodylomorphs is needed to assess how accurately these correlates represent the presence and morphology of salt glands, and what they infer about changes to the salt gland system as thalattosuchians transitioned into pelagic habitats.

Here, we investigate thalattosuchian salt gland evolution by using CT scans (both micro-CT and medical CT) to reconstruct the internal rostral anatomy of multiple thalattosuchian species, including a semi-aquatic teleosauroid, basal metriorhynchoids and pelagic metriorhynchids, plus three extant semi-aquatic crocodylians and one extinct terrestrial basal crocodylomorph as outgroup comparisons. We use the endocranial reconstructions of the internal rostral anatomy to identify osteological correlates for salt glands, with specific focus on the bony nasal cavity where these nasal glands are located external to the cartilaginous nasal capsule in extant

archosaurs (Witmer, 1995, 1997). Once identified, we use these osteological correlates to investigate broader evolutionary trends and patterns. Both direct (exceptional preservation) and indirect (osteological correlate) evidence for salt glands are discernible for multiple species spanning thalattosuchian evolutionary history. Thus, this clade provides a unique opportunity to both identify evolutionary trends in physiological and osmoregulatory changes, and to test models of osmoregulatory evolution proposed for extant tetrapods during a major land-to-sea transition (Fernández & Gasparini, 2008).

MATERIAL AND METHODS

ABBREVIATIONS

Institutional

BP, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa; MJML, Museum of Jurassic Marine Life, Kimmeridge, Dorset, UK; MLP, Museo de La Plata, La Plata, Argentina; MM, Minden Museum, Minden, Germany; MNB, National Museum of the Bahamas, Nassau, Bahamas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; NHMUK, Natural History Museum, London, UK; TMM, Texas Memorial Museum, University of Texas, Austin, Texas, USA; UF, University of Florida, Gainesville, Florida, USA; USNM, United States National Museum of Natural History, Washington DC, USA.

Anatomical

Antorb, antorbital sinus/cavity; antorb duct, antorbital duct; antorb fen, antorbital fenestra; max, maxillary sinus; max cec, maxillary cecal recess; nc, nasal cavity; npd, nasopharyngeal ducts; olf, olfactory region of nasal cavity; preorb fen, pre-orbital fenestra; post, postvestibular sinus; pss, paranasal sinus system (undifferentiated).

DATA SET

We made rostral endocranial reconstructions of 15 crocodylomorph skulls based on CT scans (see Table 1 for details). Our sample included specimens from 12 species, comprising nine thalattosuchians and four outgroup taxa. Our thalattosuchian sample consisted of: the basal thalattosuchian *Plagiophthalmosuchus gracilirostris* (Westphal, 1961) (NHMUK PV OR 15500); one teleosauroid, *Macrospondylus bollensis* (Jäger, 1828) (NHMUK PV OR 14436 and MCZ VPRA-1063); two basal metriorhynchoid species, *Pelagosaurus typus* Bronn, 1842 (NHMUK PV OR 32599) and *Eoneustes gaudryi* (Collot, 1905) (NHMUK PV R 3263); and four metriorhynchids, *Thalattosuchus superciliosus* (Blainville, 1852) (NHMUK PV R 11999), *Cricosaurus araucanensis* (MLP 72-IV-7-1), *Cricosaurus schroederi* (Kuhn, 1936) (MM unnumbered) and *Torvoneustes coryphaeus* Young *et al.*, 2013 (MJML K1863).

Our sample comes from formations spanning the Toarcian (Early Jurassic) to the Valanginian (Early Cretaceous), covering most of the known thalattosuchian

Table 1. Details of the crocodylomorph specimen data set

Taxon	Number	Age	Scan source
Protosuchus haughtoni	BP/1/4770	Hettangian	University of the Witwatersrand, Johannesburg, South Africa
Gavialis gangeticus	UF-herp-118998	Recent	MorphoSource
Gavialis gangeticus	TMM M-5490	Recent	DigiMorph
Tomistoma schlegelii	USNM 211322	Recent	Ohio University, Athens, Ohio, USA
Tomistoma schlegelii	TMM M-6432	Recent	DigiMorph
Crocodylus rhombifer	MNB AB50.0171	Recent	University of Iowa, Iowa City, Iowa, USA
Plagiophthalmosuchus gracilirostris	NHMUK PV OR 15500	Toarcian	University of Southampton, Southampton, UK
Macrospondylus bollensis	NHMUK PV OR 14436	Toarcian	University of Southampton, Southampton, UK
Macrospondylus bollensis	MCZ VPRA-1063	Toarcian	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
Pelagosaurus typus	NHMUK PV OR 32599	Toarcian	Natural History Museum, London, UK
Eoneustes gaudryi	NHMUK PV R 3263	Bathonian	University of Southampton, Southampton, UK
Thalattosuchus superciliosus	NHMUK PV R 11999	Callovian	University of Southampton, Southampton, UK
Cricosaurus araucanensis	MLP 72-IV-7-1	Tithonian	Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina
Cricosaurus schroederi	MM unnumbered	Valanginian	Minden Museum, Minden, Germany
Torvoneustes coryphaeus	MJML K1863	Kimmeridgian	University of Southampton, Southampton, UK

fossil record. The majority of thalattosuchian skulls included are missing the anterior half of the rostrum (premaxilla and anterior maxilla). *Cricosaurus araucanensis* (MLP 72-IV-7-1) is nearly complete, *Macrospondylus* (NHMUK PV OR 14436) only preserves the posteriormost end of the rostrum, and *Eoneustes* (NHMUK PV R 3263) and *Torvoneustes* (MJML K1863) are also missing the palatines and pterygoids. Only *Cricosaurus schroederi* (MM unnumbered) shows evidence of deformation, with dorsoventral shear deformation on the right side of the skull.

The outgroup sample consists of three extant crocodylian taxa and one early-diverging extinct crocodyliform. The crocodylians capture extant crocodylomorph nasal cavity morphology, and the extinct crocodyliform taxon serves as a proxy for the plesiomorphic nasal cavity morphology in terrestrial crocodylomorphs prior to the thalattosuchian marine transition. The extant crocodylians include *Gavialis gangeticus* (Gmelin, 1789) (UF-herp-118998 and TMM M-5490) and *Tomistoma schlegelii* (Müller, 1838) (USNM 211322 and TMM M-6342), which share a longirostrine skull morphology with thalattosuchians, and *Crocodylus rhombifer* (Cuvier, 1807) (MNB AB50.0171), which has a mesorostrine platyrostral (short, flat snout) morphology typical of many crocodylians. For the longirostrine crocodylians both adult (UF-herp-118998 and USNM 211322) and subadult specimens (TMM M-5490 and TMM M-6342) were sampled. *Protosuchus haughtoni* (Busbey & Gow, 1984) (BP/1/4770) is a basal crocodyliform comprising a near-complete but left-side compressed specimen (Gow, 2000).

CT SCANNING AND SEGMENTATION

All skull specimens were subjected to CT scanning prior to analysis in this study at various facilities with different scanning parameters. Three dimensional reconstructions of the internal structures of interest (e.g. paranasal sinus system, nasopharyngeal ducts, nasal cavity, neurovasculature) for all specimens were created by digital segmentation of CT slices in Materialise Mimics 20.0 and 23.0 using the 3D livewire and lasso tools. The CT reconstructions for the nasal cavities and antorbital or pre-orbital fenestrae can be accessed through MorphoSource at the following address: https://www.morphosource.org/projects/000419943?locale=en.

SALT GLAND OSTEOLOGICAL CORRELATES

Some exceptionally preserved metriorhynchid fossils include natural endocasts of hypertrophied nasal glands, which have been interpreted as salt glands (Fernández & Gasparini, 2000, 2008; Fernández & Herrera, 2009, 2021; Herrera *et al.*, 2013). Crucially,

these physical endocasts provide a roadmap for interpreting CT scans. By scrutinizing the internal anatomical regions where physical endocasts have been observed, we assessed whether glands left a signature of their presence on the bony morphology (i.e. an osteological correlate). We then cross-checked these features with previous work to see if such osteological correlates are also preserved in association with known physical endocasts. Of the previously proposed osteological correlates for the hypertrophied cephalic salt glands in thalattosuchians, we focus on those associated with the nasal cavity and rostrum, so the enlarged carotid canals of thalattosuchians (Brusatte *et al.*, 2016) will not be discussed in detail.

Two proposed osteological correlates we focus on herein are:

(1) The dorsolateral expansion of the posterior bony nasal cavity, or the olfactory region, creating concave depressions on the internal surface of the prefrontal and lacrimal. Natural endocasts of metriorhynchid cephalic salt glands show that the extracapsular glands are enlarged in the pre-orbital region of the cranium (Fernández & Gasparini, 2000; Herrera *et al.*, 2013; Fernández & Herrera, 2021). This enlargement corresponds to depressions observed on the internal surface of the prefrontals [Gandola *et al.* (2006); although there is variability in whether these surfaces are smooth or not, see Buchy *et al.* (2007: 396)], and the expansion of the bony nasal cavity (Buchy *et al.*, 2007; Pierce *et al.*, 2017; Wilberg *et al.*, 2021). Thus, we concur with the previous proposal by Pierce *et al.* (2017) that any significant expansions of the olfactory region medial to the prefrontals observed in endocranial reconstructions are likely to be due to the enlargement of the nasal salt glands. The posterior of the nasal cavity where such expansions occur is referred to as the olfactory region because it also includes the olfactory region of the cartilaginous nasal capsule containing the olfactory epithelium (Parsons, 1970). To avoid confusion with the nasal capsule, in this paper the term olfactory region only refers to the posterior region of the bony nasal cavity.

(2) The antorbital fenestrae not being associated with the antorbital sinus cavities. In Archosauria, the rostrum possesses a pair of bony pneumatic cavities, the antorbital cavities, each housing an epithelial paranasal air sinus, the antorbital sinus (Witmer, 1995, 1997; Witmer & Ridgely, 2008). The antorbital cavity of most archosaurs opens laterally through an external antorbital fenestra, but in some archosaurs (such as extant crocodylians) this fenestra is apomorphically closed and the antorbital cavity and sinus are

internalized (Witmer, 1997). Metriorhynchids also have a lateral rostrum opening traditionally called the antorbital fenestra (see Witmer, 1997 and references therein), but its homology has recently come under increasing scrutiny and controversy (Fernández & Herrera, 2009; Leardi *et al.*, 2012).

Fernández & Herrera (2009) proposed that the opening identified as the antorbital fenestrae in metriorhynchids is a novel structure, which they termed the pre-orbital fenestra. They hypothesized that the pre-orbital fenestrae were associated with salt gland drainage, supported by the presence of salt ducts communicating with the salt glands and the fenestrae in natural endocasts of *Cricosaurus araucanensis* (Fernández & Herrera, 2009), and that the 'true' external antorbital fenestrae were apomorphically closed. This followed an earlier hypothesis, where either the naris or pre-orbital fenestrae (called the antorbital fenestrae at the time) were suggested to have been involved in salt excretion (see Fernández & Gasparini, 2000: 274). Furthermore, the pre-orbital fenestra in metriorhynchids is oriented posteromedially and includes an external, elongate, obliquely oriented fossa running anterior to the external fenestra (Witmer, 1997; Fernández & Herrera, 2009), unlike in teleosauroids and the basal metriorhynchoid *Pelagosaurus typus* that exhibit a laterally opening antorbital fenestra where the fossa is either missing or much narrower (Witmer, 1997). Dynamic homology analysis by Leardi *et al.* (2012) supported this hypothesis and found the most parsimonious homology scenario for the metriorhynchid fenestra was as a neomorphic pre-orbital fenestra. The pre-orbital fenestra candidate for salt excretion was supported by Gandola *et al.* (2006), who reported the presence of a channel connecting the imprint of the salt gland on the ventral surface of the prefrontal to the pre-orbital fenestra in *Thalattosuchus superciliosus*. The association between the glands and the pre-orbital fenestra, and the internalization of the antorbital cavity, was confirmed by Herrera *et al.* (2013) through the digital reconstructions of the internal rostral anatomy of *Cricosaurus araucanensis* and the description of several natural snout endocasts.

Therefore we propose that, because the external antorbital fenestra in most archosaurs forms the lateral opening of the antorbital cavity, if we identify an internalized antorbital cavity that is not connected to the external opening on the snout in the classic position of the archosaur antorbital fenestra, then this external opening is most likely a novel pre-orbital fenestra (e.g. Fernández & Herrera, 2009; Leardi *et al.*, 2012). For the reasons outlined above, this pre-orbital fenestra is a strong osteological correlate for a salt gland. However, we do note that homologies

remain controversial, and a supposedly novel pre-orbital fenestra may instead be a highly modified antorbital fenestra, an issue we discuss below. Regardless of terminology, the key fact is that some thalattosuchians have a fenestra on the lateral snout that is not connected to the antorbital cavity, and it is this derived morphology that we posit as a salt gland correlate following previous work, regardless of what name is given to the lateral opening.

We also searched for osteological correlates for the nasal glands homologous with thalattosuchian salt glands in our outgroup sample to compare homologous glands from different crocodyliform clades and ecologies (i.e. terrestrial, semi-aquatic and marine). Extant crocodylids are known to possess lingual salt glands (Taplin & Grigg, 1981; Taplin *et al.*, 1985), but as these are neither homologous with thalattosuchian nasal salt glands nor provide potential osteological correlates, we do not discuss them further.

RESULTS

EXTANT CROCODYLIANS

The nasal cavities in all three extant crocodylian species share a similar morphology (Fig. 1). The nasal cavity comprises the nasal vestibule and the nasal cavity proper. The vestibule opens dorsally through the naris located at the anterior end of the rostrum, bordered solely by the premaxilla in *Gavialis gangeticus* (UF-herp-118998 and TMM M-5490) and *Tomistoma schlegelii* (USNM 211322 and TMM M-6342), and by both the premaxilla and the nasals in *Crocodylus rhombifer* (MNB AB50.0171). Immediately posterior to the vestibule, the nasal cavity proper forms a long tube extending throughout the rostrum to the orbits. The anterior half of the nasal cavity proper is bordered by the maxilla and premaxilla in *Gavialis* and *Tomistoma*, while in *Crocodylus rhombifer* the nasals also form the dorsal wall. Towards its posterior end, the nasal cavity proper exhibits a dorsolateral expansion known as the olfactory region of the nasal cavity (Fig. 1G, H, K). The bones surrounding the olfactory region include the frontal, prefrontals and lacrimals dorsally, the maxilla laterally, the palatines and vomers ventrally and the prefrontal pillars posteriorly. Ventral to the olfactory region, the nasal cavity proper opens ventrally into the nasopharyngeal duct at the primary choana, composed of the maxilla, palatines and vomers. The antorbital cavity (housing the antorbital sinus) opens medially into the nasal cavity through an aperture in the maxilla lateral to the primary choana in *Gavialis* and anterior to the primary choana in *Tomistoma* and *Crocodylus rhombifer*.
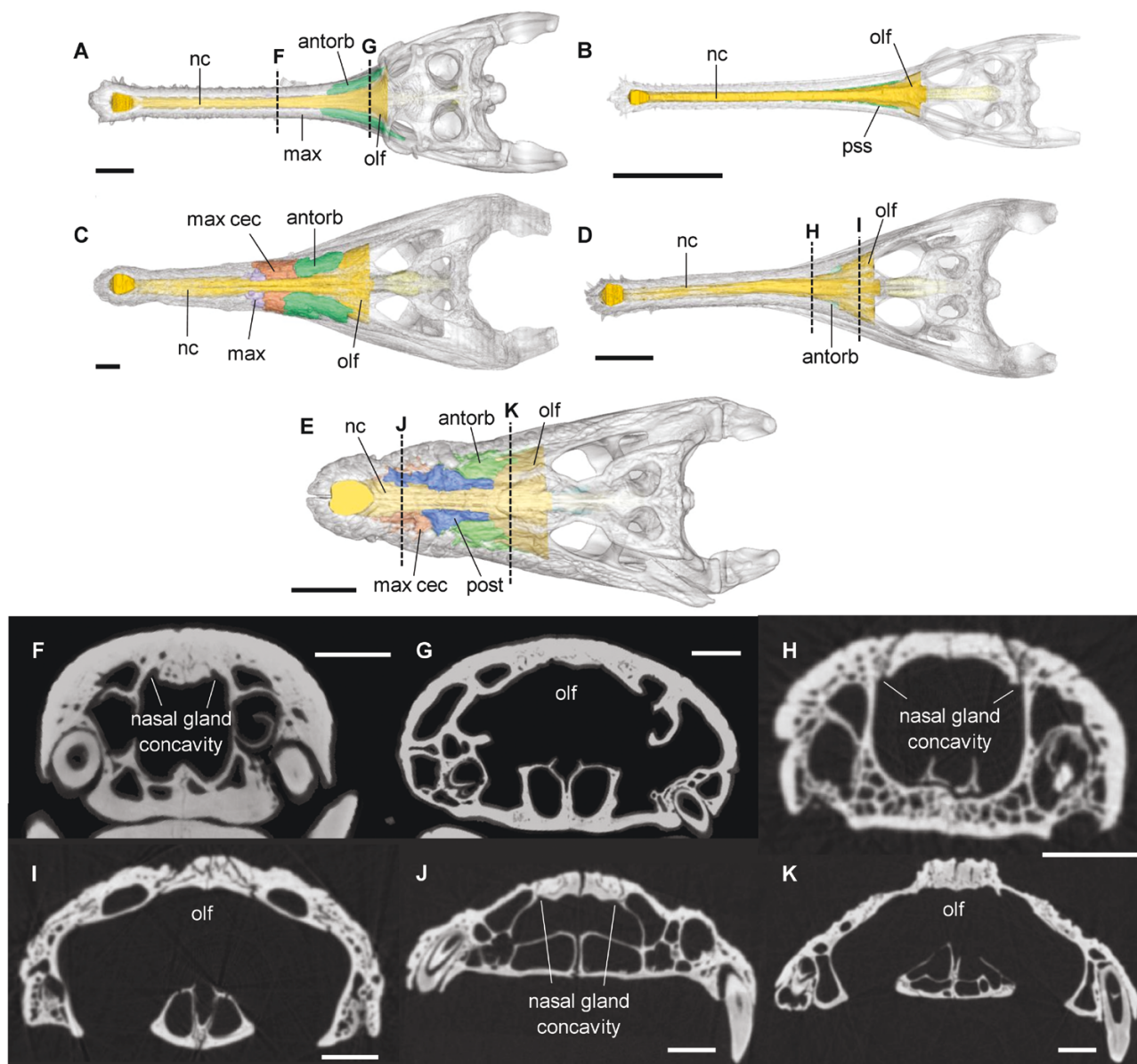
Figure 1. Internal rostral anatomy of extant crocodylians showing the nasal cavity and paranasal sinus system. Abbreviations are provided in the text (see Anatomical Abbreviations). Internal reconstruction colours: nasal cavity, yellow; nasopharyngeal ducts, pale yellow; antorbital cavity/sinus, green; maxillary sinus, violet; maxillary cecal recess, orange; postvestibular sinus, blue. A, B, *Gavialis gangeticus* adult [UF-herp-118998 (A)] and subadult [TMM M-5490 (B)] in dorsal view with skull rendered transparent. C, D, *Tomistoma schlegelii* adult [USNM 211322 (C)] and subadult [TMM M-6342 (D)] in dorsal view with skull rendered transparent. E, *Crocodylus rhombifer* (MNB AB50.0171) in dorsal view with skull rendered transparent. F-K, transverse CT slices of nasal cavities of adult *Gavialis* (F, G), subadult *Tomistoma* (H, I) and *Crocodylus rhombifer* (J, K) showing the concavities where the nasal glands and ophthalmic divisions of the trigeminal nerves are located (F, H, J) and the olfactory region of the nasal cavity (G, I, K). All skulls are rendered transparent. Scale bars equal 50 mm (A-E) and 10 mm (F-K).

In crocodylians, the nasal glands run across the length of the rostrum dorsal to the cartilaginous nasal capsule, from the dorsal margin of the cartilaginous postconcha to the posterior margin of the nasal vestibule (Witmer, 1995). In the nasal cavity, the nasal glands occupy small concavities on the ventral surface of the nasals along the nasomaxillary suture, which they share with the lateral ramus of the ophthalmic division of the trigeminal nerve (Witmer, 1995). These concavities occur in the adult *Gavialis* (UF-herp-118998), subadult *Tomistoma* (TMM M-6342) and *Crocodylus rhombifer*. It was

not possible to identify such concave surfaces in the subadult *Gavialis* (TMM M-5490) or adult *Tomistoma* (USNM 211322) because of the lower scan resolution in these specimens. In both *Tomistoma* (Fig. 1H) and *Crocodylus rhombifer* (Fig. 1J) the concave surfaces are located dorsolaterally along the nasomaxillary suture, although in the former these concavities are restricted to the posterior half of the rostrum. In *Gavialis* (Fig. 1F), the concavities are also pronounced further anteriorly where they occupy a dorsal position lateral to the maxillary suture.

PROTOSUCHUS HAUGHTONI

The nasal cavity in *Protosuchus haughtoni* (BP/1/4770) is almost complete, with only the right dorsolateral portion missing (Fig. 2). The naris and nasal vestibule are oriented anteriorly, and the nasal cavity proper is relatively short compared to more derived crocodyliforms because of the shorter, dorsoventrally tall rostrum. The olfactory region comprises a relatively larger portion of the nasal cavity and shows greater dorsoventral than mediolateral expansion. Ventral to the olfactory region the nasal cavity opens ventrally into a single choana, homologous with the primary choana in mesoeucrocodylians. Lateral to the choana, the antorbital cavity opens laterally from the nasal cavity to create an external antorbital fenestra surrounded by the maxilla dorsally and ventrally and the lacrimal posteriorly (Fig. 2B). The dorsal surface of the nasal cavity exhibits a shallow depression ventral to a descending process of the nasals that medially separates two shallow dorsal expansions; at the olfactory region these expansions are significantly deeper (Fig. 2C).

Using the Extant Phylogenetic Bracket method, Witmer (1995, 1997) hypothesized that the plesiomorphic archosaur morphology of the nasal gland was positioned dorsally or dorsolaterally within the rostrum and excavated grooved internal surfaces of the bones close to the nasomaxillary suture. A shallow concave internal surface around the nasomaxillary suture is present in *Protosuchus* (Fig. 2D) across the posterior half of the rostrum but is more poorly defined than in the extant crocodylians. The dorsal expansions of the nasal cavity are located dorsomedially to the nasomaxillary suture and are unlikely to be associated with the nasal gland. Instead, they most likely indicate the dorsal surface of the cartilaginous nasal capsule with the descending nasal process inferring the location of the nasal septum.

THALATTOSUCHIA

The nasal cavity reconstructions in the thalattosuchian skulls comprise only the posterior half of the nasal
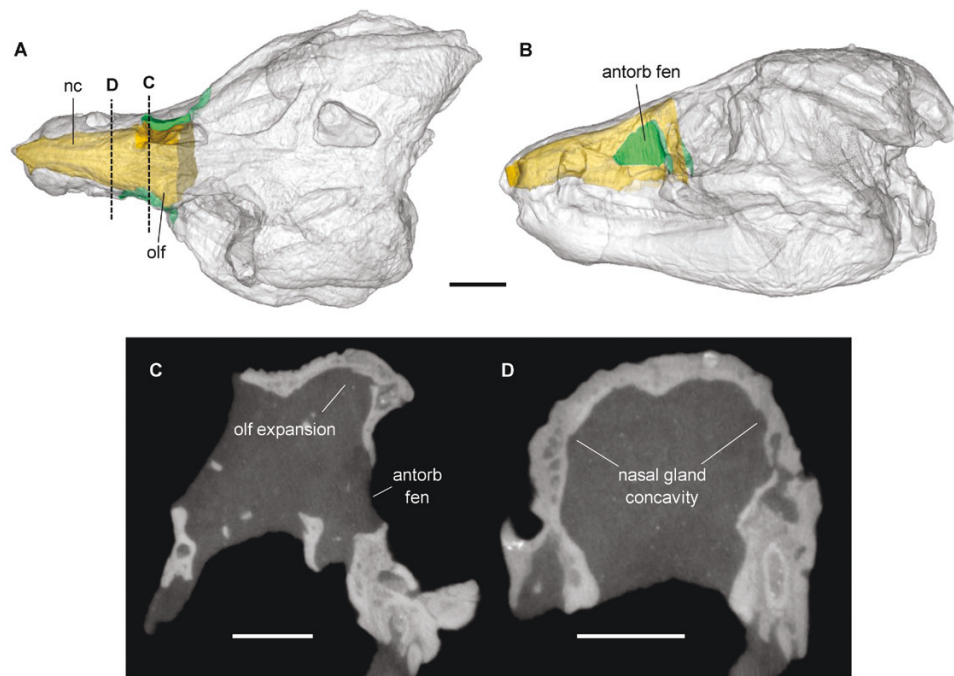

Figure 2. Internal rostral anatomy of *Protosuchus haughtoni* (BP/1/4770) showing the nasal cavity and antorbital fenestra. A, B, dorsal (A) and left lateral (B) views with skull rendered transparent. C, D, transverse CT slices of nasal cavity showing the concavities where the nasal glands are inferred (C) and small dorsal expansions of the olfactory region (D). Internal reconstruction colours: nasal cavity, yellow; antorbital fenestra, green. Scale bars equal 10 mm (A, B) and 5 mm (C, D).

cavity, with the exception of *Cricosaurus araucanensis* (MLP 72-IV-7-1) where the whole rostrum and nasal cavity is preserved.

The basal thalattosuchian *Plagiophthalmosuchus gracilirostris* (NHMUK PV OR 15500) shows a nasal cavity morphology comparable to that of extant crocodylians with a tubular nasal cavity proper with an expanded olfactory region at the posterior end of the rostrum (Fig. 3A, B). The antorbital cavity opens laterally into a reduced external antorbital fenestra (preserved on the right side of the skull) compared to *Protosuchus*, which is bordered by the lacrimal dorsally and maxilla ventrally. The nasals comprising the anterodorsal walls of the nasal cavity are missing and the boundaries between the fossilized bones and sedimentary matrix are poorly defined around the olfactory region (Fig. 3C), particularly on the dorsal surface, so it is not possible to identify any osteological correlates for either nasal glands comparable to crocodylians or enlarged nasal salt glands in metriorhynchids.

The olfactory region of the nasal cavity is better preserved in the teleosauroid skulls (Fig. 3D-I). In *Macrospondylus bollensis* the olfactory region of both NHMUK PV OR 14436 (Fig. 3D-F) and MCZ VPRA-1063 (Fig. 3G-I) exhibits two small dorsal expansions ventral to the nasals and medial to the lacrimals, separated by a shallow midline depression (Fig. 3F, H), concurring with the previous endocranial reconstruction of MCZ VPRA-1063 by Wilberg *et al.* (2021). This morphology is better demonstrated in MCZ VPRA-1063 where the whole olfactory region is preserved, whereas only the posterior portion is present in NHMUK PV OR 14436. Despite their occurrence in the olfactory region, when compared to metriorhynchid natural endocasts these expansions are located further dorsally in the olfactory region than the dorsolaterally positioned salt glands (Fernández &
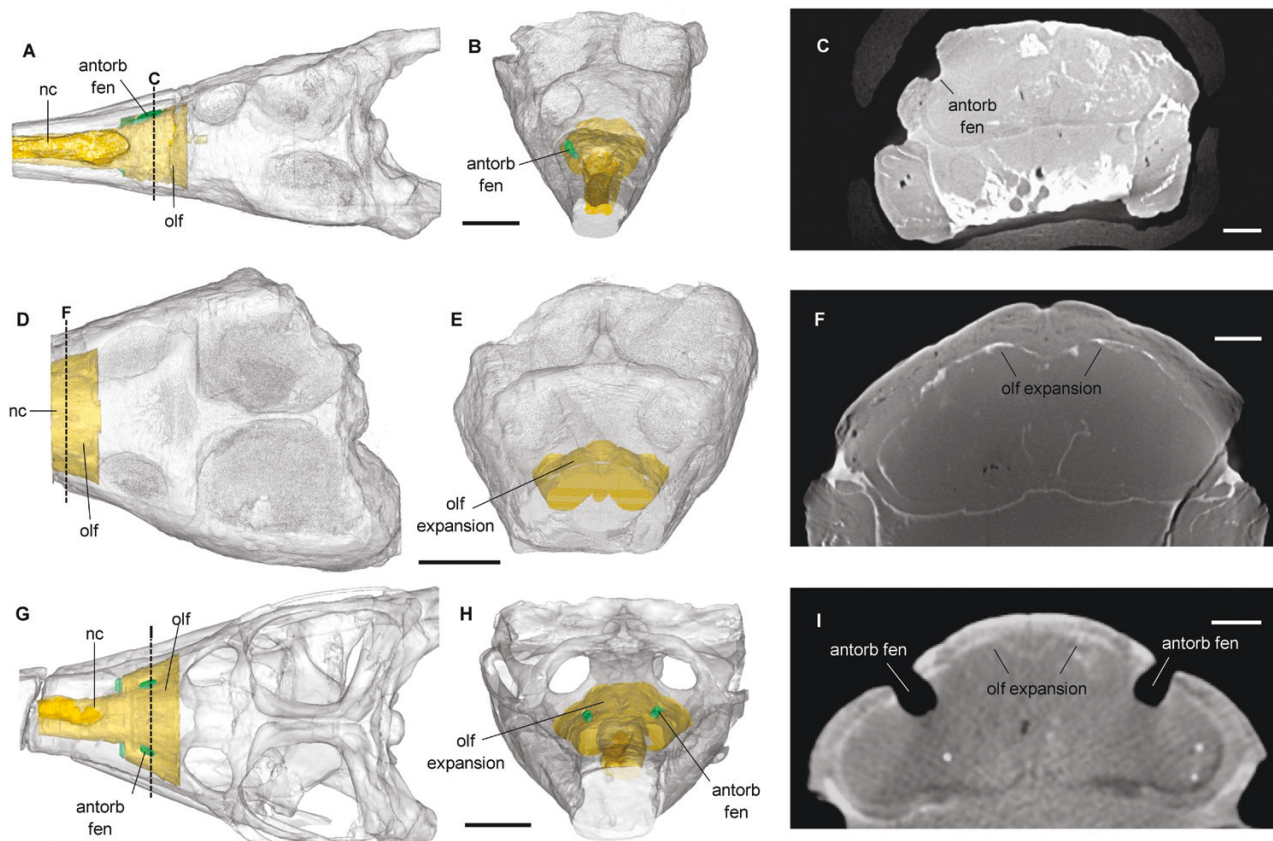

Figure 3. Internal rostral anatomy of basal thalattosuchian *Plagiophthalmosuchus gracilirostris* [NHMUK PV OR 15500 (A-C)] and teleosauroid *Macrospondylus bollensis* [NHMUK PV OR 14436 (D-F) and MCZ VPRA-1063 (G-I)]. A, B, *Plagiophthalmosuchus* in dorsal (A) and anterodorsal views (B). C, transverse CT slice of nasal cavity olfactory region. D, E, NHMUK PV OR 14436 in dorsal (D) and anterodorsal views (E). F, transverse CT slice of nasal cavity olfactory region showing small dorsal expansions where of the olfactory region where the nasal capsule is inferred. G, H, MCZ VPRA-1063 in dorsal (G) and anterodorsal views (H). I, transverse CT slice showing dorsal expansions of the olfactory region. All skulls are rendered transparent. Internal reconstruction colours: nasal cavity, yellow; antorbital fenestra, green. Scale bars equal 50 mm (A, B, D, E, G, H) and 10 mm (C, F, I).

Gasparini, 2000, 2008; Herrera *et al.*, 2013; Fernández & Herrera, 2021). However, their location is comparable to the small olfactory region expansions present in *Protosuchus*. It is also consistent with shallower dorsal convexities of the natural endocasts identified as part of the olfactory region of the cartilaginous nasal capsule (Herrera *et al.*, 2013). Therefore, we cannot confidently infer salt glands were present in *Macrospondylus* from the endocranial reconstructions, and the observed dorsal expansions likely correspond to the nasal capsule instead. The antorbital cavity of *Macrospondylus* is preserved in MCZ VPRA-1063 and, as with *Plagiophthalmosuchus*, opens laterally through a small antorbital fenestra. The antorbital fenestra is bordered by the lacrimal dorsally, the maxilla anteriorly and (unlike *Plagiophthalmosuchus*) the anterior process of the jugal ventrally.

In the basal metriorhynchoid *Pelagosaurus typus* (NHMUK PV OR 32599), the olfactory region differs from crocodylians and teleosauroids by possessing a deep ridge on the ventral surface of the nasals, creating a V-shaped depression on the dorsal surface of the olfactory region that separates the shallow dorsolateral expansions on the internal surface of the prefrontals and lacrimals (Fig. 4A-E). Such nasal cavity expansions have previously been reported in *Pelagosaurus* endocranial reconstructions (Pierce *et al.*, 2017) and, unlike the more dorsally oriented expansions in teleosauroids, the morphology present in *Pelagosaurus* more closely corresponds to the dorsolateral position of salt glands preserved in natural endocasts of metriorhynchids (Fernández & Gasparini, 2000, 2008; Herrera *et al.*, 2013; Fernández & Herrera, 2021). Therefore, we concur with Pierce *et al.* (2017) and can infer that nasal salt glands were present in *Pelagosaurus typus* from such olfactory region expansions, which may have occupied the lateral portion of these expansions while the dorsal portion (as with the teleosauroid expansions), was likely occupied by part of the nasal capsule. The size of the olfactory region expansions suggests the salt glands of *Pelagosaurus* were smaller than those observed in metriorhynchid natural endocasts. The posterior end of the nasal cavity bears a shallow dorsolateral groove ventral to the prefrontal that separates the olfactory region expansions into dorsal and lateral portions (Fig. 4D) similar to the shallow dorsal groove separating the glands and nasal capsule in metriorhynchid natural endocasts (Herrera *et al.*, 2013) and likely indicates the same morphology here, with salt glands occupying the lateral portions of the expansions and the nasal capsule occupying the dorsal portions. The antorbital cavity in *Pelagosaurus* shares with *Plagiophthalmosuchus* and the teleosauroids a lateral opening through a reduced antorbital fenestra bordered by the lacrimal and maxilla. Dorsal to the

antorbital fenestra, a novel antorbital duct is present that opens anteriorly into the nasal cavity through the maxilla anterior to the fenestra (Fig. 4E). It is currently unknown what system occupied this duct, but we do not regard this duct as either an extension of the antorbital cavity, as it does not communicate with the antorbital fenestra or as a rudimentary salt duct to facilitate drainage of the salt glands because no posterior opening into the olfactory region is observed.

In *Eoneustes gaudryi* (NHMUK PV R3263), the expansions of the olfactory region are further enlarged compared to *Pelagosaurus*, with two bulbous dorsolateral concave depressions on the prefrontals and lacrimals (Fig. 4F-H), corresponding to the salt gland location in metriorhynchid natural endocasts (Fernández & Gasparini, 2000, 2008; Herrera *et al.*, 2013) and the prefrontal depressions reported by Gandola *et al.* (2006). Thus, we infer that large, hypertrophied nasal salt glands comparable in size to those reported in metriorhynchids were present in *Eoneustes*. As in *Pelagosaurus*, a deep ridge on the ventral surface of the nasals and the corresponding V-shaped nasal cavity depression medially separates the two dorsolateral expansions of the olfactory region. In *Eoneustes*, there is a fenestra in the typical position for an antorbital fenestra. This region of *Eoneustes* includes a long, obliquely oriented fossa on the external surface of the nasal, maxilla and lacrimal leading to an internal fenestra bordered by the nasal dorsally and lacrimal ventrally. Each fenestra is connected to the nasal cavity by short ducts running posteriorly from the fenestra to the dorsolateral expansions of the olfactory region, comparable to ducts preserved in metriorhynchid natural endocasts (Fernández & Herrera, 2009). As was reported by Cowgill *et al.* (2021), no antorbital cavity could be differentiated from the nasal cavity. However, given that antorbital cavities are present in both basal thalattosuchians and more derived metriorhynchids and the closest homologous location of the antorbital cavity is immediately posterior to the dorsal alveolar canal, ventral to the fenestra, we conclude that it was likely present in *Eoneustes* as well. The ducts connecting the fenestrae to the nasal cavity do not extend to the likely location of the antorbital cavity; thus, there is no evidence that the external fenestra and antorbital cavity are connected, and as such, we refer to it as a pre-orbital fenestra (Fernández & Herrera, 2009; Leardi *et al.*, 2012).

Among the metriorhynchids, the reconstructed nasal cavity morphology in *Cricosaurus araucanensis* (MLP 72-IV-7-1) is concordant with the observed internal rostral morphology in natural endocasts from the same species (Fernández & Gasparini, 2000, 2008; Herrera *et al.*, 2013). The olfactory region shows bulbous dorsolateral expansions expressed
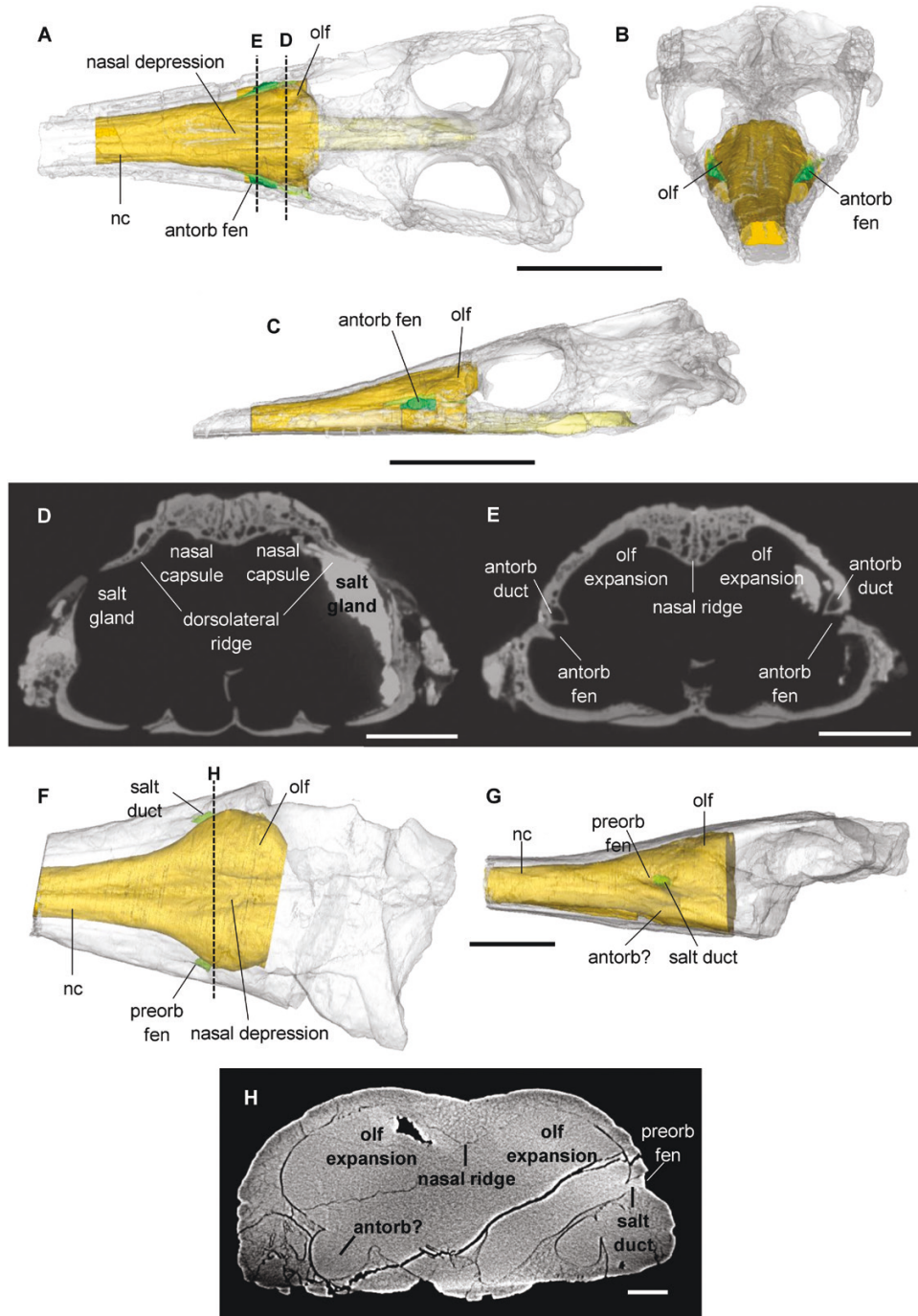
Figure 4. Internal rostral anatomy of basal metriorhynchoids *Pelagosaurus typus* [NHMUK PV OR 32599 (A-E)] and *Eoneustes gaudryi* [NHMUK PV R 3263 (F-H)]. A-C, *Pelagosaurus* in dorsal (A), anterodorsal (B) and left lateral views (C) with the skull rendered transparent. D, E, transverse CT slices of nasal cavity olfactory region showing dorsal expansions where salt glands are inferred, the dorsolateral groove separating the inferred positions of salt glands and the nasal capsule (D) and the nasal ridge creating a V-shaped depression of the olfactory region ventral to the nasals (E). F-G, *Eoneustes* in dorsal (F) and left lateral views (G) with the skull rendered transparent. H, transverse CT slice of nasal cavity olfactory region showing the left salt duct, larger dorsolateral expansions where salt glands are inferred and ridge on the ventral surface of the nasals. Internal reconstruction colours: nasal cavity, yellow; nasopharyngeal ducts, pale yellow; antorbital fenestra, green; preobrital fenestra, light green. Scale bars equal 50 mm (A-C, F, G) and 10 mm (D, E, H).

as broad depressions on the internal surfaces of the prefrontals with partial extension onto the lacrimals (Fig. 5A, B, G) and a shallow dorsolateral ridge separating the inferred location of salt glands from the nasal capsule (Fig. 5H). Identical nasal cavity morphologies are present in both *Thalattosuchus*
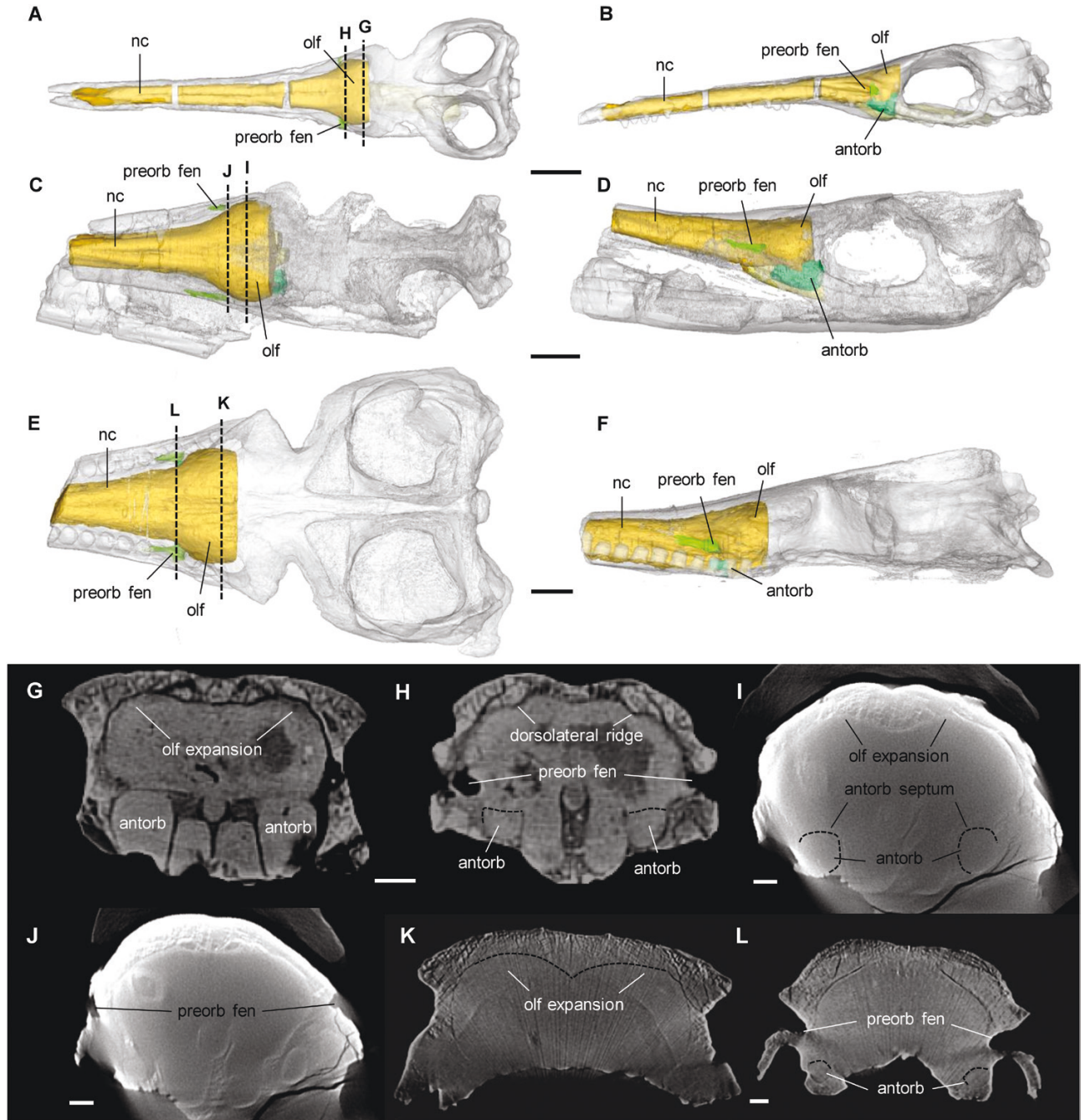

Figure 5. Internal rostral anatomy of metriorhynchids *Cricosaurus araucanensis* [MLP 72-IV-7-1 (A, B, G, H)], *Thalattosuchus superciliosus* [NHMUK PV R 11999 (C, D, I, J)] and *Torvoneustes coryphaeus* [MJML K1863 (E, F, K, L)]. A, B, *Cricosaurus araucanensis* in dorsal (A) and left lateral view (B). C, D, *Thalattosuchus* in dorsal (C) and left lateral view (D). E, F, *Torvoneustes* in dorsal (E) and left lateral view (F). G-L, transverse CT slices of nasal cavity olfactory region of *Cricosaurus araucanensis* (G, H), *Thalattosuchus* (I, J) and *Torvoneustes* (K, L) showing the pre-orbital fenestra external opening (G, I, K) and dorsolateral expansions of olfactory region where salt glands are inferred (H, J, L). All skulls are rendered transparent. Internal reconstruction colours: nasal cavity, yellow; nasopharyngeal ducts, pale yellow; antorbital cavity/sinus, green; preobrital fenestra, light green. Scale bars equal 50 mm (A-F). and 10 mm (G-L).

superciliosus (NHMUK PV R11999) (Fig. 5C, D, I, J) and *Torvoneustes coryphaeus* (MJML K1863) (Fig. 5E, F, K, L). However, in *Cricosaurus schroederi* (MM unnumbered) no bulbous expansions of the olfactory region are present. The olfactory region itself is dorsoventrally narrow and the nasopharyngeal ducts and antorbital cavities located ventral to this region are larger compared to the other metriorhynchids (Fig. 6). The lack of any dorsoventral compression in the rest of the skull demonstrates this was not a deformation artefact. However, two small lateral expansions of the olfactory region are present medial to the prefrontals in *Cricosaurus schroederi* and correspond to the salt gland locations in natural casts.

Unlike *Pelagosaurus* and *Eoneustes*, no medial V-shaped depression of the nasal cavity occurs in the metriorhynchids, and the olfactory region expansions are instead separated by a smaller ridge on the ventral surface of the nasals creating a shallower depression. The depth and breadth of this depression varies among the sample; in *Cricosaurus araucanensis* and *Thalattosuchus* this depression extends across the medial third of the dorsal surface of the olfactory region, but in *Cricosaurus schroederi* and *Torvoneustes* it is limited to a small medial ridge marking the dorsal surface of the cartilaginous nasal septum. The metriorhynchids all have a fenestra in the classic antorbital fenestra position of archosaurs

sharing a near identical morphology with each other and *Eoneustes*, including an oblique external antorbital fossa leading to the internal fenestra. The inferred antorbital cavities of all the metriorhynchids are internalized and do not connect to the fenestrae; at their closest point, the anterior of the antorbital cavity is ventromedial to the fenestra. In *Cricosaurus schroederi*, short ducts located dorsal to the antorbital cavity connect the fenestra to the lateral expansions of the olfactory region (Fig. 6C). Thus, as with *Eoneustes*, we consider the fenestra in these metriorhynchids to be a pre-orbital fenestra.

DISCUSSION

SALT GLAND DISTRIBUTION AND STRUCTURE ACROSS THALATTOSUCHIA

Our CT reconstructions reveal that osteological correlates of salt glands are clearly demonstrated across metriorhynchoids. All sampled metriorhynchoids exhibit significant dorsolateral expansions of the olfactory region of the nasal cavity, corresponding to the known location of salt glands in metriorhynchid natural endocasts (Fernández & Gasparini, 2000, 2008; Fernández & Herrera, 2009, 2021; Herrera *et al.*, 2013). In *Eoneustes* and metriorhynchids, the fenestrae (in the traditional antorbital fenestra
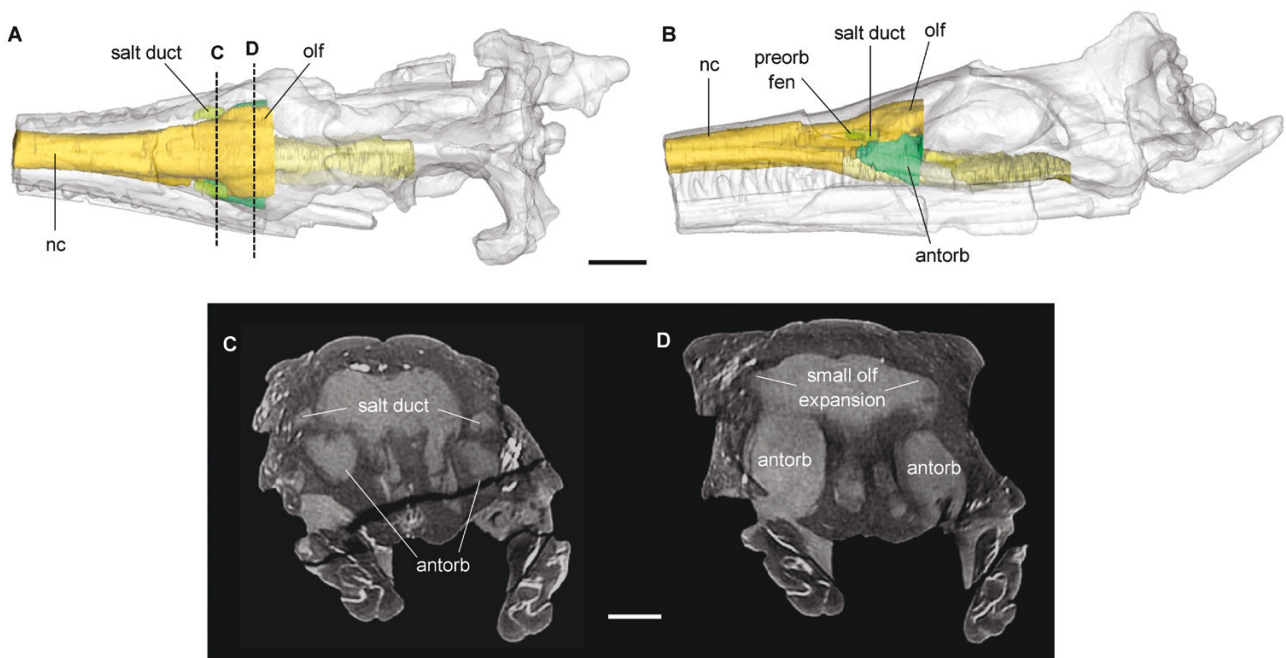

Figure 6. Internal rostral anatomy of *Cricosaurus schroederi* (MM unnumbered). A, B, dorsal (A) and left lateral views (B) with the skull rendered transparent. C, D, transverse CT slices of the nasal cavity olfactory region showing salt ducts (C) and small lateral olfactory region expansions where salt glands are inferred (D). Internal reconstruction colours: nasal cavity, yellow; nasopharyngeal ducts, pale yellow; antorbital cavity/sinus, green; preobrital fenestra, light green. Scale bars equal 50 mm (A, B) and 10 mm (C, D).

position) do not connect to the antorbital cavity and in some species (*Eoneustes* and *Cricosaurus schroederi*) show evidence of salt ducts connecting the fenestrae to the nasal cavity, again consistent with morphology observed in natural endocasts (Fernández & Herrera, 2009) and previous CT reconstructions (Herrera *et al.*, 2013). However, in teleosauroids, while dorsal olfactory region expansions occur in *Macrospondylus*, they do not correspond to the salt gland morphology in metriorhynchid natural endocasts, thus teleosauroid salt glands cannot be confidently inferred from our CT reconstructions.

Inferring the presence of enlarged nasal glands in the olfactory region of the nasal cavity in thalattosuchians from CT reconstructions is difficult, because without exceptionally preserved direct evidence it not possible to precisely identify details of the gland structure or differentiate it from other soft tissues present in the olfactory region, notably the cartilaginous nasal capsule. Despite these limitations, our endocranial reconstructions demonstrate both the presence of salt gland osteological correlates and the broad morphology of the glands in the olfactory region across most of the sampled thalattosuchians.

Aside from *Plagiophthalmosuchus* (NHMUK PV OR 15500), where the olfactory region is poorly preserved, all thalattosuchian reconstructions exhibit significant nasal cavity expansions in comparison to extant crocodylians and the basal crocodyliform *Protosuchus*. Comparisons to the nasal glands are more limited with extant crocodylians than *Protosuchus* because they instead show a derived structure and position of the glands, running along the nasomaxillary suture. This deviates from the plesiomorphic location of the main gland body in the olfactory region inferred in *Protosuchus* and other basal crocodyliforms (Witmer, 1997). Regardless, the olfactory region expansions at least in metriorhynchoids, compared to both terrestrial and semi-aquatic crocodylomorph taxa, remain consistent with the hypothesis that these were a marine adaptation to accommodate hypertrophied extracapsular salt exocrine glands.

Comparisons of the nasal cavity reconstructions with metriorhynchid natural endocasts strongly support the reliability of the olfactory region expansions as salt gland osteological correlates. The bulbous dorsolateral olfactory region expansions in *Eoneustes*, *Cricosaurus araucanensis*, *Thalattosuchus* and *Torvoneustes* (Figs 4F-H, 5) correspond precisely to the location of the enlarged extracapsular nasal glands preserved in metriorhynchid natural endocasts, including multiple *Cricosaurus araucanensis* specimens (Fernández & Gasparini, 2000, 2008; Herrera *et al.*, 2013) and *Dakosaurus andiniensis* (Fernández & Herrera, 2021). These expansions also correspond to previously reported internal prefrontal depressions

in *Thalattosuchus* (Gandola *et al.*, 2006) and on both the prefrontals and lacrimals in '*Metriorhynchus*' *westermanni* Gasparini, 1980 (Gasparini *et al.*, 2008). Thus, not only do the nasal cavity reconstructions provide further evidence that salt glands were common across Metriorhynchidae, but the olfactory region expansions in *Eoneustes* suggest hypertrophied salt glands appeared prior to the evolution of the obligate pelagic metriorhynchids. Further evidence for the presence of large salt glands prior to Metriorhynchidae comes from the basal metriorhynchoid *Zoneait nargorum* Wilberg, 2015, where a large nasal cavity expansion ventral to the prefrontal has also been reported (Wilberg, 2015).

Metriorhynchids and *Eoneustes* share a fenestra in the position of the antorbital fenestra ancestral for archosaurs but lacking a connection with the antorbital cavity. Given this, we concur with the hypothesis that the fenestra was an apomorphic pre-orbital fenestra that likely enabled drainage of the glands via a salt duct (see Fernández & Herrera, 2009, 2021). Conduits running from the pre-orbital fenestra to the olfactory region that likely housed salt ducts are clearly identified in *Eoneustes* and *Cricosaurus schroederi* and concur with the ducts inferred from natural endocasts of *Cricosaurus araucanensis* (Fernández & Herrera, 2009; Herrera *et al.*, 2013) and grooves on the ventral surface of the prefrontals in *Thalattosuchus* connecting salt gland imprints to the pre-orbital fenestra (Gandola *et al.*, 2006). Not only does this support using the fenestra as a salt gland osteological correlate, but it further demonstrates salt glands were widespread across Metriorhynchoidea.

We do note here that the homology of the opening called the pre-orbital fenestra remains the subject of uncertainty and debate. Although traditionally interpreted as homologous with the antorbital fenestrae of other archosaurs (e.g. Witmer, 1997), Fernández & Herrera (2009) proposed that this fenestra of metriorhynchids was a neomorphic structure, a pre-orbital fenestra, and the true external antorbital fenestra was closed. This was supported by dynamic homology analysis by Leardi *et al.* (2012). However, Pierce *et al.* (2017) suggested that there was no evidence against the antorbital fenestra of more basal thalattosuchians (e.g. *Pelagosaurus*) facilitating drainage of salt glands as well as connecting to the antorbital cavity. In this hypothesis, the fenestra present in metriorhynchids cannot be considered an apomorphic pre-orbital fenestra. Furthermore, no known basal metriorhynchoids show any intermediate stage between the closure of the antorbital fenestra and the opening of the pre-orbital fenestra, i.e. lacking any external fenestra in the antorbital region. It has previously been reported that *Teleidosaurus calvadosii* (Eudes-Deslongchamps, 1866) lacked

an antorbital fenestra (Young *et al.*, 2010), but this was based on the plastoholotype (NHMUK PV OR 32612) where the reconstructed antorbital region is unclear; new material has since shown *Teleidosaurus* does possess a small fenestra (Hua, 2020), but it is unclear if an anterior fossa was present. The more basal metriorhynchoid *Opisuchus meieri* Aiglstorfer *et al.* (2020) does exhibit a clearer pre-orbital fenestra with an elongated anterior fossa similar to *Eoneustes*.

The fully internalized antorbital cavity of *Eoneustes* and metriorhynchids observed in both our and previous reconstructions (Herrera *et al.*, 2013; Cowgill *et al.*, 2021), as opposed to *Pelagosaurus* and teleosauroids where the antorbital fenestra creates a small lateral opening in the cavity, support the hypothesis that derived metriorhynchoids underwent apomorphic changes to the antorbital fenestra and cavity region. We here follow Fernández & Herrera (2009) and Leardi *et al.* (2012) in referring to the fenestrae of these crocodylomorphs as a 'pre-orbital fenestra'. However, for the sake of the current study, we are agnostic on the alternate hypotheses regarding the development of this fenestra and our reconstructions are insufficient to distinguish between them. As a result, we are confident that a lateral fenestra lacking any connection to the internalized antorbital cavity is a robust osteological correlate for a hypertrophied nasal salt gland, but the uncertainty around its homology means we cannot be certain that specimens lacking this morphology did not possess a salt gland that was drained through a traditional antorbital fenestra.

Evidence for salt glands among teleosauroids is less clear. Not only have no natural rostrum endocasts of teleosauroids been discovered so far that could directly preserve salt glands, but endocranial reconstructions cannot identify unambiguous osteological correlates of such glands. Dorsal expansions of the olfactory region do occur in both our reconstructions of *Macrospondylus* and a previous reconstruction of MCZ VPRA-1063 by Wilberg *et al.* (2021), who inferred that such expansions contained both glandular tissue and olfactory epithelium. However, when compared to metriorhynchid natural endocasts, the olfactory region expansions of *Macrospondylus* more closely correspond to the dorsal convexities medial to the nasal salt glands, identified as the olfactory region of the cartilaginous nasal capsule (Herrera *et al.*, 2013; Fernández & Herrera, 2021). Given that any potential nasal glands cannot confidently be differentiated from the expansions housing the posterior of the nasal capsule from the *Macrospondylus* reconstructions, olfactory region expansions cannot be used as reliable osteological correlates for salt glands in teleosauroids.

More compelling evidence for teleosauroid salt glands has previously been reported by Brusatte *et al.* (2016), who identified enlarged carotid arteries and foramina in *Plagiophthalmosuchus*, which are known across Thalattosuchia (Pol & Gasparini, 2009; Fernández *et al.*, 2011; Wilberg, 2015; Pierce *et al.*, 2017; Herrera *et al.*, 2018) and proposed that they enabled increased blood flow to large salt glands. Enlarged carotid arteries and foramina are known across Thalattosuchia (Pol & Gasparini, 2009; Fernández *et al.*, 2011; Wilberg, 2015; Pierce *et al.*, 2017; Herrera *et al.*, 2018) and blood vessels preserved on the surface of salt glands in *Cricosaurus araucanensis* endocasts (Fernández & Gasparini, 2000; Herrera *et al.*, 2013) indicate that such glands were highly vascularized and would require increased blood flow. If enlarged carotid arteries were coupled with the development of nasal salt glands, this would support the presence of salt glands in teleosauroids homologous with those of metriorhynchoids. If salt glands were present, then the lack of major olfactory region expansions across teleosauroids compared to metriorhynchoids suggests that such glands were smaller and likely less efficient than the hypertrophied glands of derived metriorhynchoids. Furthermore, the lateral fenestrae of the rostrum of teleosauroids do connect to the antorbital cavities and sinuses, as observed in *Pelagosaurus* but unlike in metriorhynchids. Not only can we confidently state that these fenestrae in teleosauroids are true antorbital fenestrae, but the lack of a novel conduit for gland drainage indicates that the salt gland ducts of teleosauroids retain the plesiomorphic exit at the nasal vestibule with the nasal gland ducts of other archosaurs (Witmer, 1995, 1997).

The dorsolateral expansions of the olfactory region of *Pelagosaurus* represent an intermediate morphology between teleosauroids and more derived metriorhynchoids. Whereas olfactory region expansions have previously been reported in *Pelagosaurus* endocranial reconstructions (Pierce *et al.*, 2017), our reconstruction shows such expansions (and thus the glands) were still smaller than the bulbous expansions present in *Eoneustes* and metriorhynchids. Thus, while salt glands can be inferred across Metriorhynchoidea, we propose that metriorhynchoid salt glands were plesiomorphically small or moderately sized and preceded the appearance of larger hypertrophied glands in more derived taxa. The presence of a true antorbital fenestra in *Pelagosaurus* (as opposed to what we refer to as the pre-orbital fenestrae in more derived metriorhynchoids, separated from the antorbital cavity) would seem to indicate a different structure of the nasal salt glands present in the basalmost thalattosuchians. In these taxa, the nasal ducts possibly exited at the nasal vestibule instead, sharing a plesiomorphic structure inferred across Archosauria (Witmer, 1997). A narrow groove anterior to the antorbital fenestra, occurring in a similar

location to the fossa of the pre-orbital fenestra in metriorhynchids, is known in *Pelagosaurus* (Witmer, 1997) and could support the alternate hypothesis that salt glands could have exited via the antorbital fenestra in basal thalattosuchians, which was later modified into the pre-orbital fenestra of metriorhynchids. This possibility is ambiguous because *Pelagosaurus* lacks a clear conduit connecting the fenestra to the dorsolateral nasal cavity expansions as opposed to the ducts observed in *Eoneustes* and metriorhynchids. A possible alternative nasal duct in *Pelagosaurus* could be the antorbital duct dorsal to the antorbital fenestra, but its incomplete preservation and lack of a posterior opening into the olfactory region makes this hypothesis unlikely.

The basal metriorhynchoids *Pelagosaurus* and *Eoneustes* share a deep dorsomedial depression of the nasal cavity ventral to a corresponding ridge on the surface of the nasals separating the olfactory region expansions (Fig. 4E, H). A similar depression is also known in *Zoneait* formed by a ventral extension of the anterior process of the frontals (Wilberg, 2015). In metriorhynchids this dorsomedial nasal cavity depression is much shallower. When compared to natural endocasts, the shallow depression in metriorhynchids corresponds to the dorsal margin of the cartilaginous nasal septum and medially separates two elongate convexities, which are interpreted as the olfactory region of the cartilaginous nasal capsule (Herrera *et al.*, 2013; Fernández & Herrera, 2021). If the salt glands of the basal metriorhynchoids *Eoneustes* and *Zoneait* occupied the same relative volume of the bony nasal cavity as metriorhynchids, then the change in depth of both the nasal ridge and dorsal nasal cavity depression between basal metriorhynchoids and metriorhynchids could indicate a restructuring of the cartilaginous nasal capsule and septum in Metriorhynchidae.

In *Cricosaurus schroederi* salt glands are inferred by the presence of a pre-orbital fenestra separate from the paranasal sinus system but the lack of bulbous olfactory region expansions like those present in other metriorhynchids is surprising. Instead, only small lateral expansions medial to the prefrontals may infer the location of the salt glands (Fig. 6) and their size could indicate a unique nasal gland morphology within Metriorhynchidae. The dorsoventrally narrow olfactory region further supports a derived nasal cavity morphology present in *Cricosaurus schroederi* (Fig. 7). The exceptionally large antorbital cavities and nasopharyngeal ducts in *Cricosaurus schroederi* among metriorhynchids suggests that the narrower olfactory region was a consequence of restructuring of the nasal cavity to accommodate larger ducts and paranasal sinuses. This would result in less space available for hypertrophied salt exocrine glands in the dorsolateral portion of the olfactory region, so instead they are repositioned in a lateral location. Alternatively, nasal cavity restructuring could have repositioned hypertrophied salt glands away from the medial surfaces of the bones, which would make any osteological correlates unreliable, but it would still be uncertain if there was enough space within the olfactory region to accommodate such large glands further interiorly. It is worth noting that *Cricosaurus schroederi* is the youngest thalattosuchian in our sample, from the Early Cretaceous, whereas all other thalattosuchians included are from the Jurassic. Thus, our observation that it had a derived morphology compared to other metriorhynchids is perhaps not surprising, as it was separated from them by a long stretch of time.

SALT GLAND EVOLUTION ACROSS THALATTOSUCHIA AND MARINE TETRAPODS

Based on our endocranial reconstructions and previous reconstructions and observations (Fernández & Gasparini, 2000, 2008; Gandola *et al.*, 2006;
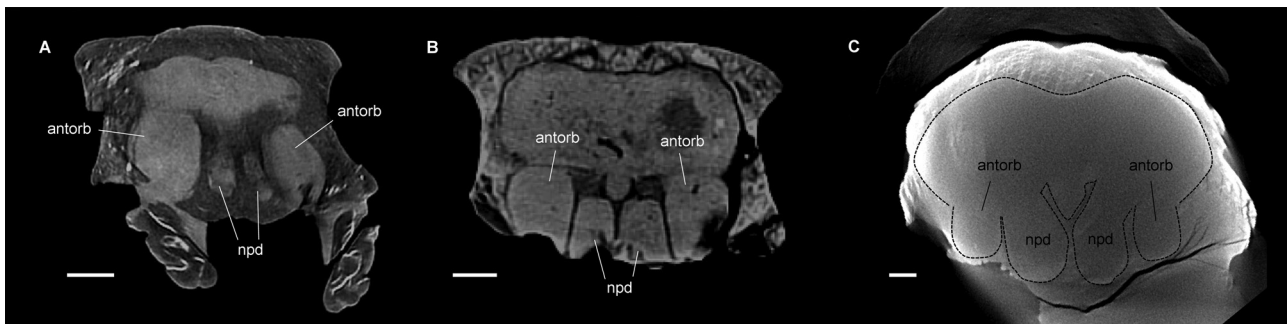

Figure 7. Transverse CT slices of the nasal cavity olfactory region of *Cricosaurus schroederi* (A), *Cricosaurus araucanensis* (B) and *Thalattosuchus superciliosus* (C). In comparison to other metriorhynchids, *Cricosaurus schroederi* exhibits a dorsoventrally narrow olfactory region, exceptionally large antorbital cavities and dorsoventrally taller nasopharyngeal ducts.

Buchy *et al*., 2007; Fernández & Herrera, 2009; Herrera *et al*., 2013; Brusatte *et al*., 2016; Pierce *et al*., 2017; Wilberg *et al*., 2021), we propose the following stepwise sequence of changes in the evolution of nasal salt glands across the thalattosuchian transition from semi-aquatic to pelagic forms (Fig. 8):

(1) Plesiomorphically, thalattosuchians possessed small salt glands with a low secretory capacity and with salt ducts exiting through the nasal vestibule. This morphology was present in semi-aquatic teleosauroids.

(2) In the basalmost metriorhynchoid *Pelagosaurus*, larger salt glands, with a higher excretion rate, located in the dorsolateral portion of the olfactory region of the nasal cavity were present, but these still likely drained through the nasal vestibule.

(3) In the metriorhynchoid clade comprising *Eoneustes* and obligately pelagic metriorhynchids, the salt glands were hypertrophied and occupied the dorsolateral portions of the olfactory region. The fenestra in the traditional location of the archosaur antorbital fenestra (an apomorphic structure called the pre-orbital fenestra) did not communicate with the antorbital cavity and instead provided a novel exit for salt drainage.

The timing of osmoregulatory changes appears to predate the appearance of many skeletal adaptations present in pelagic metriorhynchids, but comparing the timing of soft tissue and skeletal changes across the thalattosuchian marine transition is extremely difficult, especially among basal metriorhynchoids. Some skeletal elements clearly show a stepwise evolutionary trend, such as the progressive reorientation of the orbits from a slight lateral orientation position in basal teleosauroids and metriorhynchoids (e.g. *Plagiophthalmosuchus* and *Pelagosaurus*; Johnson *et al*., 2020) to a fully lateral position in the clade *Zoneait* + Metriorhynchidae (Wilberg, 2015).

Postcranial adaptations are harder to map across the transition, as the only basal metriorhynchoid known to have a completely preserved postcranial skeleton is *Pelagosaurus typus*. For example, no basal metriorhynchoid is currently known to possess the deep hypocercal tail characteristic of metriorhynchids, but a shallow tail bend has been inferred in *Magyarosuchus fitosi* (Ősi *et al*., 2018). It is also unclear when osteoderms were lost. Both *Pelagosaurus* and *Magyarosuchus* had extensive osteodermal armour, but its presence or absence is unknown in *Opisuchus*, *Teleidosaurus*, *Eoneustes* and *Zoneait* (Young *et al*., 2010; Wilberg, 2015; Ősi *et al*., 2018;
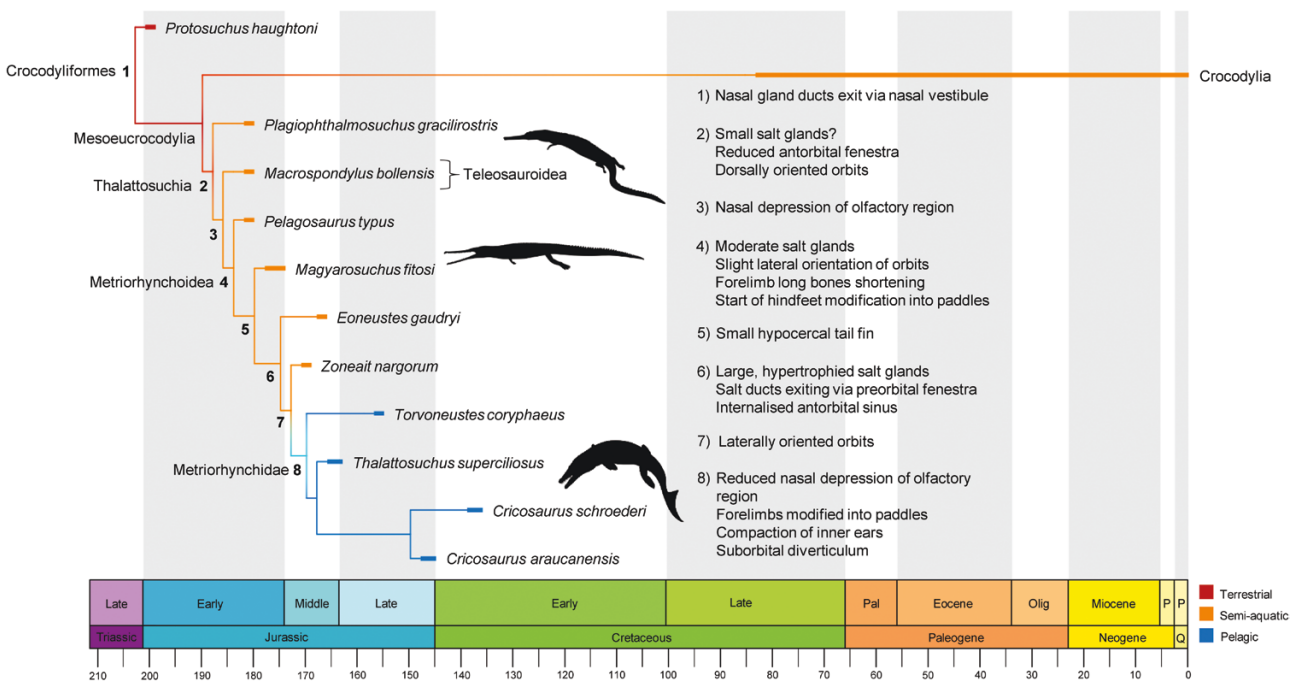

Figure 8. Simplified time-scaled crocodylomorph phylogeny showing the sequence of both known marine adaptations and nasal salt gland evolution in thalattosuchians. Numbers indicate the nodes where the first appearance of adaptations are known, from most basal (1) to most derived (8). Phylogeny based on the Crocodylomorph SuperMatrix data set (Young *et al*., 2021). Silhouettes from http://phylopic.org/.

Aiglstorfer et al., 2020). However, in *Zoneait*, which is recovered as the sister taxon to Metriorhynchidae in phylogenetic analyses (Wilberg, 2015; Young et al., 2021), the humerus and ulna were not modified into 'plate-like' elements observed in the flippers of metriorhynchids (Wilberg, 2015). The ulna of *Zoneait* (Wilberg, 2015) does have two characteristics showing the forelimb had undergone some modification: (1) the ulna is proportionally shortened relative to the humerus (much like in metriorhynchids); and (2) the ulnar diaphysis has a flattened cross-section (but still not modified into a 'plate-like' rounded element seen in metriorhynchids). This means that all metriorhynchoids outside Metriorhynchidae were likely still capable of terrestrial locomotion, possibly in a manner similar to extant *Gavialis gangeticus* [where terrestrial locomotion in larger individuals is primarily a 'sprawling belly slide' with the limbs working in synchrony, see Bustard & Singh (1977)]. This is in contrast with the obligately pelagic metriorhynchids, which had the forelimbs modified into flippers, straightened humeral epiphyses creating a planar humerus-antebrachium joint surface, femora with incompletely ossified distal condyles that are poorly developed, and a highly regionalized caudal vertebral column including a deep hypocercal tail. Therefore, we hypothesize that hypertrophy of the salt glands occurred while metriorhynchoids were still semi-aquatic.

Other endocranial or internal rostral adaptations also demonstrate a stepwise pattern across the thalattosuchian marine transition, with many occurring while basal metriorhynchoids were likely still semi-aquatic. The endosseous labyrinths of the inner ears of metriorhynchids were more compact and had thicker, semicircular canals than the semi-aquatic *Pelagosaurus*, comparable to other pelagic marine reptiles and cetaceans (Schwab et al., 2020). Additionally, the paranasal sinus system exhibited a progressive reduction and internalization of the antorbital sinus across teleosauroids and basal metriorhynchoids prior to the appearance of pelagic metriorhynchids (Cowgill et al., 2021). Natural endocasts of both *Cricosaurus araucanensis* and *Dakosaurus andiniensis* also preserve an accessory suborbital diverticulum extending through the postnasal fenestra and into the orbit (Fernández & Herrera, 2009, 2021). These accessory diverticula are analogous to those present in birds (Witmer, 1995), which interleave between the jaw adductor muscles so that during mandibular adduction and abduction they create positive and negative air pressures within the diverticulum (Witmer & Ridgely, 2008), enabling active ventilation of the paranasal sinus system. Fernández & Herrera (2021) proposed that inflation of the antorbital sinus as the jaw muscles contract would

compress the salt glands directly above and force salt secretions through the pre-orbital fenestra to prevent salt encrustations from blocking the ducts. There is currently no direct evidence for suborbital diverticula in basal metriorhynchoids, but their presence could be hypothesized in *Zoneait* based on a significantly expanded antorbital cavity contiguous with the orbit (Wilberg, 2015). We can more confidently infer that metriorhynchoids basal to *Zoneait* lacked suborbital diverticula and actively ventilated paranasal sinuses, because *Eoneustes* exhibits no such expanded antorbital cavity communicating with the orbit (Cowgill et al., 2021).

Our proposed sequence for osmoregulatory adaptations in thalattosuchians provides an opportunity to test hypothesized models for physiological evolution of marine tetrapods in a fossil group. Dunson & Mazzotti (1989) proposed the following model for physiological evolution in marine reptiles based on extant estuarine species, which comprises four major transitional stages. Firstly, behavioural osmoregulation (i.e. avoiding water with high salinity), the plesiomorphic condition present in freshwater species. Secondly, physiological adaptations such as reduced net salt uptake, water loss or incidental drinking of salt water that occur in estuarine species or coastal populations of freshwater species. Thirdly, appearance of morphological adaptations through rudimentary salt glands with a low excretion rate. Finally, development of hypertrophied salt glands with a high excretion rate allowing ingestion of seawater and osmoconforming prey, which primarily occurs in pelagic species.

Fernández & Gasparini (2008) stated that metriorhynchids represent the fourth stage of osmoregulation evolution in Dunson & Mazzotti's (1989) model based on the large salt glands in natural endocasts of *Cricosaurus araucanensis* and suggested that semi-aquatic thalattosuchians, including teleosauroids and *Pelagosaurus*, represented stage three. Our endocranial reconstructions corroborate that metriorhynchids achieved stage four. The likely inference of small salt glands in teleosauroids from enlarged carotid arteries (Brusatte et al., 2016) supports teleosauroids likely representing stage three, although teleosauroid species known from freshwater deposits (see Martin et al., 2016, 2019; Johnson et al., 2020) could also represent stage two. However, the placement of basal metriorhynchoids within this model is uncertain. The moderately sized salt glands of *Pelagosaurus* suggest that, despite sharing a similar ecology with basal teleosauroids and that its status as stage three remains plausible, this species could instead occupy an intermediate step between stages three and four. The placement of *Eoneustes* and *Zoneait* within this model depends on how the criteria

for the derived fourth stage are defined. If the fourth stage is restricted to obligately pelagic taxa, then both *Eoneustes* and *Zoneait* represent an intermediate step between stages three and four, because we infer that both genera were at least capable of some terrestrial locomotion. Thus, we would have semi-aquatic forms possessing large salt glands. If stage four can include any aquatic taxon with hypertrophied salt glands, then both species would fall in stage four. Regardless, both possibilities indicate that metriorhynchoids were capable of drinking salt water and were primarily or exclusively consuming osmoconforming prey before completing the transition into the marine realm through their postcranial modifications to an obligate pelagic lifestyle.

An alternative model was proposed by Motani & Vermeij (2021) that can apply to all extant marine and estuarine tetrapods (except for birds and snakes). They created a sequential series for aquatic adaptations, haline adaptations, and also for marine adaptations (which combined aquatic and haline steps; see Table 2). Motani & Vermeij (2021) considered metriorhynchids to be one of four extinct clades that achieved the final step of their marine adaptation series (step five), based on the loss of terrestrial locomotion through a lack of pronation and supination of the forelimb, whereas semi-aquatic thalattosuchians were placed in steps two to three.

Contra Motani & Vermeij (2021), who placed the American alligator (*Alligator mississippiensis*) in their M1c category (see Table 2), we consider this species as M1-to-M2. This is due to adult individuals living in coastal ecosystems directly feeding in saline waters, particularly on benthic crustaceans and small-bodied fish [although this species is also known to scavenge or prey upon sea turtles, stingrays and smaller-bodied sharks, see Nifong *et al.* (2017), and the references therein]. American alligator populations that live far from coastal ecosystems would fulfil step M1, but not any of the substeps M1a-c, see Table 2. This highlights that extant crocodylians can range from steps M1-to-M1c-to-M2 (possibly also M3, see below), with different populations of the same species being able to fall within different marine step categories. Moreover, it shows that crocodylians are capable of falling within step M2 even if they lack salt glands [such as alligatorids; see Taplin *et al.* (1982)].

We concur with Motani & Vermeij (2021) that metriorhynchids achieved step M5, not only because of their extensive osteological adaptations for pelagic locomotion (see Supporting Information, Tables S1–S5) and their large salt glands, but also due to the smooth body integument lacking osteoderms and scales (Spindler *et al.*, 2021). Likewise, oxygen isotope analyses of thalattosuchian tooth enamel suggest that metriorhynchids were non-homeothermic endotherms [whereas teleosauroids were likely ectothermic; Séon *et al.* (2020)]. Motani & Vermeij (2021) placed 'basal thalattosuchians' in steps M2-M3, which we broadly concur with, although with some exceptions. For example, there are teleosaurids known from exclusively freshwater deposits (Martin *et al.*, 2016, 2019; Johnson *et al.*, 2020), and some machimosaurids are thought to be present in both freshwater and brackish environments (Johnson *et al.*, 2020).

The presence of clear osteological correlates for salt glands across metriorhynchoids and possible osteological correlates in teleosauroids could suggest that all thalattosuchians reached M3, where they can maintain osmoregulation without necessarily drinking fresh water. However, it is unclear if the presence of salt glands means a taxon must have reached M3, because Motani & Vermeij (2021) also categorized two extant saltwater crocodylians in M2, *Crocodylus porosus* Schneider, 1801 and *Crocodylus acutus* Cuvier, 1807, both of which possess lingual salt glands (Taplin & Grigg, 1981; Taplin *et al.*, 1982). However, it is possible that some extant crocodylians could also be placed in step M3. Hatchlings of *Crocodylus porosus*, *Crocodylus acutus* and even *Crocodylus niloticus* can osmoregulate in saltwater, while individuals of all three species will avoid drinking saltwater and instead gain water from food (e.g. see Taplin & Loveridge, 1988; Leslie & Spotila, 2000). Populations of *Crocodylus acutus* that live off the coast of Belize range from hatchlings to adults, with hatchlings and small juveniles feeding on a diet primarily of insects and crustaceans, while larger individuals have a crustacean dominated diet (Platt *et al.*, 2013). Interestingly, all size classes can grow in saltwater, and there is no evidence that this population had access to fresh water during the dry season (Platt *et al.*, 2013). The water balance, salt glands and renal/cloacal complex of *Crocodylus porosus* have been well studied. All size classes can osmoregulate in brackish and saltwater, will avoid drinking in saltwater and have a crab and shrimp dominated diet, which is selective in hatchlings/small juveniles for crustaceans with a lower salt content [see Griggs (2015) for a summation of the field and the references therein].

Thus, were teleosauroids and basal metriorhynchoids such as *Pelagosaurus* ecologically similar to salt-tolerant extant crocodiles? While the salt glands of *Pelagosaurus* (at least) are small compared to metriorhynchids, they distinctly alter the shape of the posterior nasal cavity and are clearly enlarged. If so, were they able to survive dry periods without drinking fresh water, even as hatchlings? We tentatively include teleosauroids and *Pelagosaurus* in M3, but clearer criteria for categories M2 and M3 are required to confirm this. The basal metriorhynchoids *Eoneustes* and *Zoneait* can confidently be placed in step M3 as both share

Table 2. The sequential series of aquatic (A), haline (H) and marine (M) adaptations proposed by Motani & Vermeij (2021)

Steps	Aquatic adaptations	Haline adaptations	Marine adaptations
0	A0: completely terrestrial lifestyle (plesiomorphy)	H0: fully terrestrial diet (plesiomorphy)	-
1	A1: at least occasional locomotion in water	H1: diet of at least some food originating in brackish or saline marine water, including beached food	M1: incipient use of marine resources (i.e. A1, H1 or both) M1a: ocean swimmer without marine diet M1b: intertidal feeders M1c: brackish swimmers and feeders
2	A2: absence of terrestrial travel (may bask onshore regularly)	H2: diet of at least some food collected directly in sea water. This involves consumption of salty food and incidental ingestion of sea water through prey capture in water	M2: direct feeding in the saline sea (i.e. H2 and A1 if absent at first)
3	A3: fully aquatic lifestyle except for reproduction	H3A: water balance maintenance without terrestrial fresh water H3B: completely marine diet without any terrestrial food	M3: water balance maintenance without terrestrial fresh water (i.e. H3A)
4	A4: fully aquatic across all aspects of life history	-	M4: minimized terrestrial locomotion and loss of terrestrial feeding (i.e. A2 and H3B)
5	-	-	M5: loss of terrestrial thermoregulation and fur/plumage (i.e. A3)

hypertrophied salt glands with metriorhynchids, while the forelimb morphology of *Zoneait* (Wilberg, 2015) suggests both this taxon and the more basal *Eoneustes* were still capable of terrestrial locomotion (thus ruling out being in M5).

No metriorhynchoid can confidently be placed in step M4. This is due to Motani & Vermeij (2021) suggesting only one osteological correlate for this step: the humerus being longer than the femur. However, only one known highly aquatic or marine-adapted crocodylomorph is known to share this feature (Salih *et al.*, 2021). In fact, all highly aquatic crocodylomorphs reduce both the forelimbs and the hind limbs relative to the trunk, reduce the humerus relative to the femur, and reduce the ulna relative to the humerus [e.g. Buscalioni *et al.* (2011); Iijima *et al.* (2018); Foffa *et al.* (2021); see phylogenetic characters from Young *et al.* (2021)]. Amongst extant crocodylians, this trend is most evident amongst longirostrine taxa, especially *Gavialis gangeticus* (Iijima *et al.*, 2018)—the most aquatic of all living species, and the one species where terrestrial locomotion in larger individuals is restricted to the 'sprawling belly slide' (Bustard & Singh, 1977). However, amongst all crocodylomorphs, thalattosuchians and metriorhynchids in particular represent the most extreme example of this appendicular trend. In fact, not only do metriorhynchids have the proportionally smallest forelimbs of any crocodylomorph, but they

are the only known crocodylomorph clade with the hind limbs being less than 40% the length of the trunk (Foffa *et al.*, 2021; Sachs *et al.*, 2021). Thus, we disagree with Motani & Vermeij's (2021) assessment that metriorhynchids had a 'normal hind limb' or 'large hind limbs' (see Supporting Information, Table S4, for some of the changes in metriorhynchid hind limbs).

Therefore, at least in part, Motani & Vermeij's (2021) model does not apply to thalattosuchians or even crocodylomorphs. A different sequence of marine adaptations was identified in snakes by Motani & Vermeij (2021) where osmoregulation without fresh water occurs after loss of terrestrial feeding and thermoregulation, so alternative sequences across marine transitions are possible among tetrapods. We suggest that thalattosuchians may have had their own unique sequence of morphological changes across their land-to-shallows-to-sea transition.

CONCLUSION

In this study we describe CT endocranial reconstructions of the internal rostral anatomy from multiple thalattosuchian skulls in order to identify osteological correlates for nasal salt exocrine glands and assess evolutionary trends within Thalattosuchia. Compared to the nasal cavities of both the basal

crocodyliform *Protosuchus* and extant crocodylians, all metriorhynchoids exhibit significant dorsolateral expansions of the olfactory region corresponding precisely to the location of hypertrophied salt glands preserved in metriorhynchid natural endocasts. No olfactory region expansions were identified in the basal thalattosuchian *Plagiophthalmosuchus* because of poor preservation of the olfactory region. Despite small dorsal expansions ventral to the nasals present in multiple specimens of the teleosauroid *Macrospondylus*, these do not correspond with the salt gland location in metriorhynchid natural endocasts and thus teleosauroid salt glands could not be inferred from our reconstructions. However, this does not necessarily refute the presence of plesiomorphically small salt glands with a low excretion rate in teleosauroids given that they share enlarged carotid arteries with metriorhynchoids that potentially provided increased blood flow to salt glands. The moderately sized dorsal olfactory region expansions in the basalmost metriorhynchoid *Pelagosaurus* indicates an intermediate salt gland size and osmoregulatory capability between teleosauroids and metriorhynchoids, but this gland may have drained via the nasal vestibule, as the antorbital fenestra is still connected to the internal antorbital cavity. The basal metriorhynchoid *Eoneustes* exhibits a near-identical nasal cavity morphology to metriorhynchids, with dorsolateral olfactory region expansions ventromedial to the prefrontals and connected to an external fenestra that is not confluent with the antorbital cavity (what we consider the pre-orbital fenestra), demonstrating that both enlarged salt glands were present before the appearance of pelagic metriorhynchids and derived osmoregulation evolved while metriorhynchoids were still semi-aquatic.

The observed sequence of osmoregulatory adaptations in thalattosuchians does not precisely fit with current models for physiological evolution in marine tetrapods, especially concerning basal metriorhynchoids. In the models proposed by Dunson & Mazzotti (1989) and Montani & Vermeij (2021), depending on how the stages of both models are defined, basal metriorhynchoids can either share the same stage as semi-aquatic teleosauroids based on a similar ecology, the same stage as pelagic metriorhynchids based on comparable osmoregulation or an intermediate stage between the two. Furthermore, given that only one known marine crocodylomorph possesses a humerus longer than the femur, we find that Montani & Vermeij's (2021) model (at least the advanced aquatic stages proposed) does not fully apply to thalattosuchians or crocodylomorphs. Placement of basal metriorhynchoids into such models is limited primarily by the currently poorly known timing of postcranial adaptations across the thalattosuchian marine transition.

Corroborating the results and hypotheses proposed in this study requires further endocranial reconstructions identifying nasal salt gland osteological correlates across a larger diversity of thalattosuchian taxa. This is particularly important among teleosauroids, where there are few current nasal cavity reconstructions and limited reliable osteological correlates, and more basal metriorhynchoids, which will provide further details on the sequence of osmoregulatory adaptations across the thalattosuchian marine transition. Future discoveries of postcranial fossils from basal metriorhynchoid taxa will enable both more accurate placements of the timing of postcranial and osmoregulatory adaptations in metriorhynchoids and better placement of basal metriorhynchoids into current models of evolution of marine tetrapods. Such models may also require refinement of how different steps in a marine evolutionary transition are defined to allow more accurate placement of certain species or new steps to account for intermediate morphologies across evolutionary grades of semi-aquatic and marine tetrapods.

DATA AVAILABILITY

Endocranial CT reconstructions can be accessed through MorphoSource at the following address: https://www.morphosource.org/projects/000419943?locale=en.

REFERENCES

Aiglstorfer M, **Havlik P**, **Herrera Y. 2020.** The first metriorhynchoid crocodyliform from the Aalenian (Middle Jurassic) of Germany, with implications for the evolution of Metriorhynchoidea. *Zoological Journal of the Linnean Society* **188:** 522–551.

Andrews CW. 1913. *A descriptive catalogue of the marine reptiles of the Oxford Clay, part two*. London: British Museum (Natural History).

Babonis LS, **Brischoux F. 2012.** Perspectives on the convergent evolution of tetrapod salt glands. *Integrative and Comparative Biology* **52:** 245–256.

de Blainville HD. 1852. Letter by HD de Blainville. 109–120. In: Eudes-Deslongchamps JA ed. Lettres sur les crocodiles vivants et fossiles. *Bulletin de la Société Linnéenne de Normandie (Années 1849–1853)* **9:** 103–138.

Braun EJ. 1998. Comparative renal functions in reptiles, birds and mammals. *Seminars in Avian and Exotic Pet Medicine* **7:** 62–71.

Bronn HG. 1842. Untersuchung zweier Gavial-Skelette und der Gaumen zweier anderer aus den Boller Lias-Schiefern, Rücksicht auf Geoffroy´s Genus *Teleosaurus*. In: Bronn HG, Kaupp JJ, eds. *Abhandlungen über die gavialartigen Reptilien der Lias-Formation*. Stuttgart: Schweizerbart-Verlag, 5–30.

Brusatte SL, **Muir A**, **Young MT**, **Walsh S**, **Steel L**, **Witmer LM. 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.

Buchy M-C, **Stinnesbeck W**, **Frey E**, **González AHG. 2007.** Première mention du genre *Dakosaurus* (Crocodyliformes, Thalattosuchia) dans le Jurassique supérieur du Mexique. *Bulletin Société Géologique de France* **178:** 63–69.

Busbey AB, **Gow CE. 1984.** A new protosuchian crocodile from the Upper Elliot Formation of South Africa. *Palaeontologia Africana* **25:** 127–149.

Buscalioni AD, **Piras P**, **Vullo R**, **Signore M**, **Barbera C. 2011.** Early Eusuchia Crocodylomorpha from the vertebrate-rich Plattenkalk of Pietraroia (Lower Albian, southern Apennines, Italy). *Zoological Journal of the Linnean Society* **163:** S199–S227.

Bustard HR, **Singh LAK. 1977.** Studies on the Indian gharial *Gavialis gangeticus* (Gmelin) (Reptilia, Crocodilia). Change in terrestrial locomotory pattern with age. *Journal of Bombay Natural History Society* **74:** 534–536.

Caldwell MW. 2002. From fins to limbs to fins: limb evolution in fossil marine reptiles. *American Journal of Medical Genetics* **112:** 236–249.

Caldwell MW, **Lee MSY. 2001.** Live birth in Cretaceous marine lizards (mosasauroids). *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268:** 2397–2401.

Cheng Y, **Wu X**, **Ji Q. 2004.** Triassic marine reptiles gave birth to live young. *Nature* **432:** 383–386.

Collot L. 1905. Reptile Jurassique (*Teleidosaurus gaudryi*) trouvé à Saint-Seine l'Abbaye (Côte-d'or). *Mémoire Academy de Sciences, Arts et Belles Lettres Dijon (4th series)* **10:** 41–45.

Cowgill T, **Young MT**, **Schwab JA**, **Walsh S**, **Witmer LM**, **Herrera Y**, **Dollman KN**, **Choiniere JN**, **Brusatte SL. 2021.** Paranasal sinus system and upper respiratory tract evolution in Mesozoic pelagic crocodylomorphs. *The Anatomical Record* [early view] doi: 10.1002/ar.24727.

Cuvier F. 1807. Sur les différentes espèces de crocodiles vivants et sur leurs caractères distinctifs. *Annales du Muséum National d'Histoire Naturelle* **10:** 8–66.

Dunson WA. 1969. Electrolyte excretion by the salt gland of the Galápagos marine iguana. *The American Journal of Physiology* **216:** 995–1002.

Dunson WA, **Dunson MK. 1973.** Convergent evolution of sublingual salt glands in the marine file snake and true sea snakes. *Journal of Comparative Physiology* **86:** 193–208.

Dunson WA, **Mazzotti FJ. 1989.** Salinity as a limiting factor in the distribution of reptiles in Florida Bay—a theory for the estuarine origin of marine snakes and turtles. *Bulletin of Marine Science* **44:** 229–244.

Dunson WA, **Packer RK**, **Dunson MK. 1971.** Sea snakes: an unusual salt gland under the tongue. *Science* **173:** 437–441.

Eudes-Deslongchamps JA. 1866. Description d'une espèce inédite de Téléosaure des environs de Caen. *Bulletin de la Société Linnéenne de Normandie (Années 1864–1865)* **10:** 193–223.

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 MS, **Carabajal AP**, **Gasparini Z**, **Chong DG. 2011.** A metriorhynchid crocodyliform braincase from northern Chile. *Journal of Vertebrate Paleontology* **31:** 369–377.

Fernández MS, **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.

Fernández MS, **Herrera Y. 2021.** Active airflow of the paranasal sinuses in extinct crocodyliforms: evidence from a natural cast of the thalattosuchian *Dakosaurus andiniensis*. *The Anatomical Record* [early view]. doi: 10.1002/ar.24678.

Foffa D, **Johnson MM**, **Schwab JA**, **Formoso K**, **Young MT. 2021.** Changes in limb and body proportions linked with major habitat shifts in Crocodylomorpha. In: Carolina Loch, Ana Valenzuela Toro, Judith M. Pardo-Pérez , Mónica R. Buono, Carolina S. Gutstein, eds. *9th International Meeting on the Secondary Adaptation of Tetrapods to Life in Water*. Virtual Meeting, Chile.

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

Gasparini Z, **Paulina-Carabajal A**, **Chong G. 2008.** Un nuevo especimen de cocodrilo marino del Jurásico Medio del norte de Chile: revalidación de *Metriorhynchus westermanni* (Crocodyliformes: Metriorhynchidae). *Revista Geológica de Chile* **35:** 335–346.

Gasparini ZB. 1980. Un nuevo cocodrilo marino (Crocodylia, Metriorhynchidae) del Caloviano del norte de Chile. *Ameghiniana* **17:** 97–103.

Gasparini ZB, **Dellapé D. 1976.** Un nuevo cocodrilo marino (Thalattosuchia, Metriorhynchidae) de la Formación Vaca Muerta (Jurasico, Tithoniano) de la Provincia de Neuquén (República Argentina). *Congreso Geológico Chileno* **1:** c1–c21.

Gmelin JF. 1789. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymies, locis. (Caroli a Linne systema naturae)*, *13th edn*, *Vol. I., Pars III*. Leipzig: G.E. Beer, 1033–1516.

Gow CE. 2000. The skull of *Protosuchus haughtoni*, an Early Jurassic crocodyliform from southern Africa. *Journal of Vertebrate Paleontology* **20:** 49–56.

Griggs G. 2015. 11. Salt and water balance. In: Griggs GC, Kirshner D, eds. *Biology and evolution of crocodylians*. Ithaca: Cornell University Press, 391–430.

Herrera Y, **Fernández MS**, **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 MS**, **Lamas SG**, **Campos L**, **Talevi M**, **Gasparini Z. 2017.** Morphology of the sacral region and reproductive strategies of Metriorhynchidae: a counter-inductive approach. *Earth and Environment Science Transactions of the Royal Society of Edinburgh* **106:** 247–255.

Herrera Y, **Leardi JM**, **Fernández MS. 2018.** Braincase and endocranial anatomy of two thalattosuchian crocodylomorphs and their relevance in understanding their adaptations to the marine environment. *PeerJ* **6:** e5686.

Hirayama R. 1998. The oldest known sea turtle. *Nature* **392:** 705–708.

Holmes WN, **Phillips JG. 1985.** The avian salt gland. *Biological Reviews* **60:** 213–256.

Hua S. 2020. A new specimen of *Teleidosaurus calvadosii* (Eudes-Deslongchamps, 1866) (Crocodylia, Thalattosuchia) from the Middle Jurassic of France. *Annales de Paléontologie* **106:** 102423.

Iijima M, **Kubo T**, **Kobayashi Y. 2018.** Comparative limb proportions reveal differential locomotor morphofunctions of alligatoroids and crocodyloids. *Royal Society Open Science* **5:** 171774.

Jäger CF. 1828. *Über die fossile Reptilien, welche in Württemberg aufgefunden worden sind*. Stuttgart: J.B. Metzler.

Johnson MM, **Young MT**, **Brusatte SL. 2019.** Re-description of two contemporaneous mesorostrine teleosauroids (Crocodylomorpha, Thalattosuchia) from the Bathonian of England, and insights into the early evolution of Machimosaurini. *Zoological Journal of the Linnean Society* **189:** 449–482.

Johnson MM, **Young MT**, **Brusatte SL. 2020.** The phylogenetics of Teleosauroidea (Crocodylomorpha, Thalattosuchia) and implications for their ecology and evolution. *PeerJ* **8:** e9808.

Kelley NP, **Pyenson ND. 2015.** Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* **348:** aaa3716.

Kuhn O. 1936. *Crocodilia. Fossilium Catalogus I: Animalia* 75. The Hague: W. Junk, 1–114.

Leardi JM, **Pol D**, **Fernández MS. 2012.** The antorbital fenestra of Metriorhynchidae (Crocodyliformes, Thalattosuchia): testing its homology within a phylogenetic framework. *Journal of Vertebrate Paleontology* **32:** 490–494.

Leslie AJ, **Spotila JR. 2000.** Osmoregulation of the Nile crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu/Natal, South Africa. *Comparative Biochemistry and Physiology A* **126:** 351–365.

Lindgren J, Caldwell MW, **Konishi T**, **Chiappe LM. 2010.** Convergent evolution in aquatic tetrapods: insights from an exceptional mosasaur fossil. *PLoS One* **5:** e11998.

Martin JE, **Deesri U**, **Liard R**, **Wattanapituksakul A**, **Suteethorn S**, **Lauprasert K**, **Telouk P. 2016.** Strontium isotopes and the long-term residency of thalattosuchians in the freshwater environment. *Paleobiology* **42:** 143–156

Martin JE, **Suteethorn S**, **Lauprasert K**, **Tong H**, **Buffetauti 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.

Motani R. 2009. The evolution of marine reptiles. *Evolution: Education and Outreach* **2:** 224–235.

Motani R, **Jiang DY**, **Tintori A**, **Rieppel O**, **Chen GB. 2014.** Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by Early Triassic embryonic fossils. *PLoS One* **9:** e88640.

Motani R, **Vermeij GJ. 2021.** Ecophysiological steps of marine adaptation in extant and extinct non-avian tetrapods. *Biological Reviews* **96:** 1769–1798.

Motani R, **You H**, **McGowan C. 1996.** Eel-like swimming in the earliest ichthyosaurs. *Nature* **382:** 347–348.

Müller S. 1838. Waarnemingen over de Indische krokodillen en beschrijving van eene nieuwe soort. *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie* **5:** 61–87.

Nifong JC, **Lowers RH. 2017.** Reciprocal intraguild predation between *Alligator mississippiensis* (American alligator) and Elasmobranchii in the southeastern United States. *Southern Naturalist* **16:** 383–396.

O'Keefe FR, **Chiappe LM. 2011.** Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). *Science* **333:** 870–873.

Ősi A, **Young MT**, **Galácz A**, **Rabi M. 2018.** A new large-bodied thalattosuchian crocodyliform from the Lower Jurassic (Toarcian) of Hungary, with further evidence of the mosaic acquisition of marine adaptations in Metriorhynchoidea. *PeerJ* **6:** e4668.

Parsons TS. 1970. The nose and Jacobson's organ. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*. New York: Academic Press, 99–191.

Pierce SE, **Williams M**, **Benton MJ. 2017.** Virtual reconstruction of the endocranial anatomy of the Early Jurassic marine crocodylomorph *Pelagosaurus typus* (Thalattosuchia). *PeerJ* **5:** e3225.

Platt SG, **Thorbjarnarson JB**, **Rainwater TR**, **Martin DR. 2013.** Diet of the American crocodile (*Crocodylus acutus*) in marine environments of coastal Belize. *Journal of Herpetology* **47:** 1–10.

Pol D, **Gasparini Z. 2009.** Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Palaeontology* **7:** 163–197.

Sachs S, **Young MT**, **Abel P**, **Mallison H. 2021.** A new species of *Cricosaurus* (Thalattosuchia, Metriorhynchidae) based a remarkably well-preserved skeleton from the Upper Jurassic of Germany. *Palaeontologia Electronica* **24:** a24.

Salih KO, **Evans DC**, **Bussert R**, **Klein N**, **Mueller J. 2021.** *Brachiosuchus kababishensis*, a new long-snouted dyrosaurid (Mesoeucrocodylia) from the Late Cretaceous of north central Sudan. *Historical Biology*, 1–20.

Schmidt-Nielsen K, **Fange R. 1958.** Salt glands in marine reptiles. *Nature* **182:** 783–785.

Schmidt-Nielsen K, **Jorgensen CB**, **Osaki H. 1958.** Extrarenal salt excretion in birds. *American Journal of Physiology* **193:** 101–107.

Schneider JG. 1801. *Historiae amphibiorum naturalis et literariae. Fasciculus secundus continens crocodilos, scincos, chamaesauras, boas, pseudoboas, elapes, angues, amphisbaenas et caecilias.* Jena: F. Fromann.

Schwab JA, **Young MT**, **Neenan AM**, **Walsh SA**, **Witmer LM**, **Herrera Y**, **Allain R**, **Brochu CA**, **Choiniere JN**, **Clark JM**, **Dollman KN**, **Etsches S**, **Fritsch G**, **Ruebenstahl A**, **Sachs S**, **Turner JH**, **Vignuad P**, **Wilberg E**, **Xu X**, **Zanno LE**, **Brusatte SL. 2020.** Inner ear sensory system changes as extinct crocodylomorphs transitioned from land to water. *Proceedings of the National Academy of Sciences of the USA* **117:** 10422–10428.

Séon N, **Amiot R**, **Martin JE**, **Young MT**, **Middleton H**, **Fourel F**, **Picot L**, **Valentin X**, **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:** 20190139.

Spindler F, **Lauer R**, **Tischlinger H**, **Mäuser M. 2021.** The integument of pelagic crocodylomorphs (Thalattosuchia: Metriorhynchidae). *Palaeontologia Electronica* **24:** a25.

Taplin LE, **Grigg GC. 1981.** Salt glands in the tongue of the estuarine crocodile *Crocodylus porosus*. *Science* **212:** 1045–1047.

Taplin LE, **Grigg GC**, **Beard L. 1985.** Salt gland function in fresh water crocodiles: evidence for a marine phase in eusuchian evolution? In: Grigg G, Shine R, Ehmann H, eds. *Biology of Australasian frogs and reptiles*. Chipping Norton: Royal Zoological Society of New South Wales/Surrey Beatty, 403–410.

Taplin LE, **Grigg GC**, **Harlow P**, **Ellis TM**, **Dunson WA. 1982.** Lingual salt glands in *Crocodylus acutus* and *C. johnstoni* and their absence from *Alligator mississippiensis* and *Caiman crocodilus*. *Journal of Comparative Physiology B* **149:** 43–47.

Taplin LE, **Loveridge JP. 1988.** Nile crocodiles, *Crocodylus niloticus*, and estuarine crocodiles, *Crocodylus porosus*, show similar osmoregulatory responses to seawater. *Comparative Biochemistry and Physiology A* **89:** 443–448.

Uhen MD. 2007. Evolution of marine mammals: back to the sea after 300 million years. *The Anatomical Record* **290:** 514–522.

Vignaud P, **Gasparini ZB. 1996.** New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) from the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences, Paris* **2:** 245–250.

Westphal F. 1961. Zur Systematik der deutschen und englischen Lias-Krokodilier. *Neues Jahrbuch für Geologie und Paläontologie* **113:** 207–218.

Wilberg EW. 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.

Wilberg EW, **Beyl AR**, **Pierce SE**, **Turner AH. 2021.** Cranial and endocranial anatomy of a three-dimensionally preserved teleosauroid thalattosuchian skull. *The Anatomical Record* [early view]. doi: 10.1002/ar.24704.

Witmer LM, **Ridgely RC. 2008.** The paranasal air sinuses of predatory and armored dinosaurs (Archosauria: Theropoda and Ankylosauria) and their contribution to cephalic structure. *The Anatomical Record* **291:** 1362–1388.

Witmer LM. 1995. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. *Journal of Morphology* **225:** 269–327.

Witmer LM. 1997. The evolution of the antorbital cavity in archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Journal of Vertebrate Palaeontology* **17:** 1–76.

Woodward AS. 1906. On two specimens of *Ichthyosaurus* showing contained embryos. *Geological Magazine* **3:** 443–444.

Young MT, **Andrade MB**, **Etches S**, **Beatty BL. 2013.** A new metriorhynchid crocodylomorph from the Lower Kimmeridge Clay Formation (Late Jurassic) of England, with implications for the evolution of dermatocranium ornamentation in Geosaurini. *Zoological Journal of the Linnean Society* **169:** 820–848.

Young MT, **Brignaud A**, **Sachs S**, **Hornung JJ**, **Foffa D**, **Kitson JJN**, **Johnson MM**, **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 MT, **Brusatte SL**, **Rutta M**, **Andrade MB. 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:** 801–859.

Young MT, **Steel L. 2019.** Chapter 19: Reptiles – Crocodylomorphs. In: Lord AR, ed. *Fossils from the Lias of the Yorkshire Coast. Palaeontological Association field guide 15.* London: Palaeontological Association, 301–316.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Ecological, mandibular and cranial features used for inferring the extent of marine specialization in various thalattosuchian groups, and successively derived basal metriorhynchoids that can be scored for these features.

Table S2. Endocranial and internal craniofacial features used for inferring the extent of marine specialization in various thalattosuchian groups, and successively derived basal metriorhynchoids that can be scored for these features.

Table S3. Forelimb features used for inferring the extent of marine specialization in various thalattosuchian groups, and successively derived basal metriorhynchoids that can be scored for these features.

Table S4. Hind limb features used for inferring the extent of marine specialization in various thalattosuchian groups, and successively derived basal metriorhynchoids that can be scored for these features.

Table S5. Vertebral and osteoderm features used for inferring the extent of marine specialization in various thalattosuchian groups, and successively derived basal metriorhynchoids that can be scored for these features.