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Convergent evolution and possible constraint in the posterodorsal retraction of the external nares in pelagic crocodylomorphs

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Amongst Mesozoic marine reptiles, metriorhynchid crocodylomorphs were unique in evolving into pelagically adapted forms with little-to-no posterodorsal retraction of the external nares. Narial retraction is a common adaptation seen in sustained swimmers, notably occurring during cetacean evolution. Mesosaurids and the basalmost known members of ichthyosauriforms, thalattosaurians, saurosphargids, sauropterygians, pleurosaurids and mosasauroids had the external nares divided by an ossified bar, bound by multiple cranial bones and were positioned back from the tip of the rostrum. However, metriorhynchids evolved from taxa with a single external naris bound solely by the premaxilla, and positioned near the tip of an elongate rostrum. We posit that metriorhynchids were uniquely disadvantaged in evolving into sustained swimmers. Herein we describe three Late Jurassic metriorhynchid cranial rostra that display differing degrees of narial retraction. In our new phylogenetic analyses, the backwards migration of the narial fossa posterior margin occurred independently at least four times in Metriorhynchidae, whereas the backwards migration of the anterior margin only occurred twice. Although Rhacheosaurini share the backwards migration of the anterior and posterior narial margins, posterodorsal retraction occurred differently along three lineages. This culminated in the Early Cretaceous, where a rhacheosaurin evolved nares bound by the premaxilla and maxilla, and significantly posterodorsally retracted.

ADDITIONAL KEYWORDS: Geosaurini – Jurassic – macroevolution – Rhacheosaurini.

INTRODUCTION

Metriorhynchoidea was a group of crocodylomorphs that secondarily returned to a marine lifestyle during the Mesozoic Era. Their body-plan dramatically changed during this macroevolutionary transition, with metriorhynchids sharing a common suite of pelagic adaptations, including flipper-like forelimbs, a highly regionalized caudal vertebral column with a hypocercal tail, loss of osteoderms and preorbital salt exocrine glands (e.g. Fraas, 1902; Andrews, 1913; Fernández & Gasparini, 2000, 2008; Herrera *et al.*, 2013a, b; Sachs *et al.*, 2019a). However, one characteristic pelagic adaptation is not present in basal metriorhynchids:

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the posterodorsal retraction of the external nares. With such an extensive reorganization of their skeleton, the absence of this adaptation is striking, as it evolved in other aquatic and marine dwelling clades, both extant and extinct: from mammals (cetaceans and sirenians) to a range of reptilian clades (mesosaurids, phytosaurians, thalattosaurians, saurosphargids, ichthyosauriforms, sauropterygians, pleurosaurids and mosasauroids) (e.g. see: Nicholls, 1999; Páramo-Fonseca, 2000; Rieppel *et al.*, 2002; Dupret, 2004; Bardet *et al.*, 2005; O'Keefe, 2008; Li *et al.*, 2012, 2014; Piñeiro *et al.*, 2012; Berta *et al.*, 2014; Fischer *et al.*, 2014; Jiang *et al.*, 2016; Díaz-Berenguer *et al.*, 2018). It was not until the Early Cretaceous that at least one metriorhynchid species had significantly retracted their nares (Hua *et al.*, 2000).

Below, we describe three Upper Jurassic cranial rostra from metriorhynchids discovered in Switzerland and the UK. The first specimen can be referred to the subclade Rhacheosaurini based on the position of the narial fossae and the fully ossified internarial bar. The other two rostra are members of a poorly understood clade of geosaurins (the 'E-clade'; Abel *et al.*, 2020). We also present a series of phylogenetic analyses based on two newly revised datasets (one using phenotypic data, the other a combined phenotypic and genotypic dataset), and introduce our new TNT scripts. These analyses suggest that narial retraction repeatedly evolved in Metriorhynchidae, with true posterodorsal retraction occurring twice: once in clade *Metriorhynchus geoffroyii* von Meyer, 1832 + Rhacheosaurini, and also in the Geosaurini 'E-clade'.

MATERIAL AND METHODS

Abbreviations

Institutional: BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; CAMSM, Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, UK; DORCM, Dorchester County Museum, Dorchester, UK; IRSNB, Institut Royal des Sciences Naturelles de Bruxelles, Belgium; MHNG, Muséum d'histoire Naturelle de la Ville de Genève, Switzerland; MLP, Museo de La Plata, La Plata, Argentina; MNHN.F, fossil collection of the Muséum national d'Histoire naturelle, Paris, France; MOZ, Museo Provincial de Ciencias Naturales 'Prof. Dr Juan A. Olsacher', Zapala, Argentina; MPZ, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain; NHMUK PV, vertebrate palaeontology collection of the Natural History Museum, London, UK (OR, old register; R, reptiles); NMBE, Naturhistorisches Museum der Burgergemeinde Bern, Switzerland; NMO, Naturmuseum Olten, Olten, Switzerland; NMS, National Museums Scotland, Edinburgh, UK; PETMG, Peterborough Museum & Art Gallery, Peterborough, UK; RNGHP, Réserve Naturelle Géologique de Haute Provence, Digne les Bains, France; SMF, Senckenberg Naturmuseum, Frankfurt am Main, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

Anatomical: de, dentary; en, external nares; foi, incisive foramen; mpg, maxillopalatine groove; mx, maxilla; na, nasal; nc, nasal cavity; pmx, premaxilla.

When discussing the tooth count number in the text: P, premaxilla; M, maxilla. Note, tooth count numbering starts from the anteriormost alveolus (e.g. M4 is the fourth maxillary alveolus).

Dataset and analysis

We conducted a series of phylogenetic analyses to test how frequently narial position shifted within Metriorhynchidae. The dataset used herein forms part of the ongoing Crocodylomorph SuperMatrix Project and is continuously being updated. Referred to as the Hastings + Young dataset (or HY dataset), it was first presented in Ristevski *et al.* (2018) and has been subsequently updated (see: Ősi *et al.*, 2018; Foffa *et al.*, 2019; Johnson *et al.*, 2020; Abel *et al.*, 2020; Sachs *et al.*, 2019a, b, In review). It is one of three datasets that form the core of the Crocodylomorph SuperMatrix Project, the other two also being presented in a modified form in Ősi *et al.* (2018). The HY dataset also forms the phylogenetic framework of the Edinburgh-based CrocTransition Project, examining the endocranial evolution of thalattosuchians during the land-to-sea transition.

We first merged the changes made to the HY dataset from the various 2019 and 'in review'/'in press' studies listed above. This yielded a new version that contained the sum of changes those studies made. We also moved the scale character [this was character 379 in dataset two in Ristevski *et al.* (2018)] from the osteoderm section of the dataset into the soft-tissue section.

Once complete, 53 new characters were added into the dataset: one of which is a craniomandibular ornamentation character, five neurosensory anatomy characters, two endocranial vasculature characters, nine craniomandibular pneumaticity characters, one neurovascular foramina character, two cranial rostrum characters, two skull roof characters, three orbit and temporal region characters, five palate characters, three occipital characters, six braincase characters, two hyoid characters, two mandibular characters, one vertebral character, one forelimb character, one pectoral girdle character, three osteoderm characters and four soft-tissue characters. Twenty characters were newly created (those in the neurosensory, vasculature, pneumaticity, neurovascular foramina and osteoderm subsections). Fifteen characters (all of the craniomandibular ornamentation, cranial rostra, palatal, vertebral and pectoral girdle characters; and one of the skull roof characters and one of the mandibular characters) came from the modified Andrade *et al.* (2011) dataset [most recent published version from Ősi *et al.* (2018)]. Two of the braincase characters also came from the modified Andrade dataset, while one braincase character came from the modified Wilberg (2015) dataset [most recent published version from Ősi *et al.* (2018)]. One postorbital bar character came from the modified Andrade dataset in Meunier & Larsson (2017), with the other two coming from the modified Andrade dataset see in Ősi *et al.* (2018). From the Leardi *et al.* (2017) dataset, one skull roof, one occipital, three braincase and one forelimb characters were added. Two soft-tissue characters came from Lee & Yates (2018) (one of which came from an earlier paper). The remaining eight characters (two occipital characters, both hyoid characters, one of the mandibular characters, one of the braincase characters and the two scale soft-tissue characters) were derived from the 'robust' list of characters from Sookias (2020). We also created the new subsection 'hyoid apparatus'. All characters newly added into this dataset are denoted with (NEW) in the Supporting Information, Appendix S1.

We also revised or replaced some characters. The cerebral carotid canal foramina size character was replaced by the multistate version from the modified Wilberg dataset. The tympanic membrane fossa character was changed from a multistate character to a binary one. We replaced the quadrate dorsal head articulation character with the modified quadrate–laterosphenoid contact character from the Leardi *et al.* (2017) dataset. The parietal fusion character from Nesbitt (2011) was replaced with the ordered multistate from Leardi *et al.* (2017). We also replaced the coracoid postglenoid process character from Nesbitt (2011) with the coracoid character from Leardi *et al.* (2017). The frontoparietal fossa character was revised following Holliday *et al.* (2020). The metriorhynchid premaxillary internarial bar was changed from a binary character to a multistate one. We merged two binary characters relating to the positions of the first and second dentary alveoli into a single multistate character. The two limb-bone proportion characters were revised, with new character states and new state delineations. This was based on the data in Iijima *et al.* (2018). A new state was added to the external nares' shape character, to accommodate the shape seen in Rhacheosaurini. A new state was added to the proportion of the premaxilla posterior to the external nares' character. The character describing the distance between the premaxilla and the nasals was altered into an ordered multistate (to accommodate the extreme elongation seen in teleosauroids and basal metriorhynchoids). The multistate character reflecting the two different ways the longirostrine condition can develop (maxilla-only elongation, or maxilla and nasal elongation) was split into two separate ordered multistate characters: one scoring for the elongation of the maxilla, and the other scoring for the elongation of the maxilla and nasal. Finally, the posterodorsal narial retraction character was split into two characters: one scoring for the backwards migration of the narial anterior margin, and the second scoring for the backwards migration of the narial posterior margin. All data are summarized in the Supporting Information, Appendix S1.

Thirty-two new operational taxonomic units (OTUs) were added into the HY dataset. Taxa scored from the literature were *Carnufex carolinensis* Zanno *et al.*, 2015, *Coloradisuchus abelini* Martínez *et al.*, 2019, *Cassissuchus sanziuami* Buscalioni, 2017, *Mecistops leptorhynchus* (Bennett, 1835) and *Osteolaemus osborni* (Schmidt, 1919). *Batrachotomus kurpferzellensis* Gower, 1999 was scored based on the literature and photographs of the SMNS material provided by Stephen Brusatte. An 'in press' sphenosuchian was scored based on photographs of the holotype provided by Lindsay Zanno. *Shamosuchus djadochtaensis* Mook, 1924 was added based on the literature and CT data (see Supporting Information, Appendix S1). Based on first-hand examination, the following fossil taxa (scored for NHMUK specimens) were added: *Hylaeochampsa vectiana* Owen, 1874, *Brochuchus pigotti* (Tchernov & Van Couvering, 1978) and *Voay robustus* (Grandidier & Vaillant, 1872). We also added extant taxa (based on first-hand examination of NHMUK and NMS specimens, observations of living individuals and CT datasets): *Tomistoma schlegelii* (Müller, 1838), *Crocodylus acutus* (Cuvier, 1807), *Crocodylus halli* Murray *et al.*, 2019, *Crocodylus intermedius* (Graves, 1819), *Crocodylus johnstoni* (Krefft, 1873), *Crocodylus moreletii* (Duméril & Bibron, 1851), *Crocodylus palustris* (Lesson, 1831), *Crocodylus rhombifer* (Cuvier, 1807), *Crocodylus siamensis* (Schneider, 1801), *Mec. cataphractus* (Cuvier, 1824), *Osteolaemus tetraspis* (Cope, 1860), *Alligator sinensis* Fauvel, 1879, *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1801), *Caiman yacare* (Daudin, 1801), *Melanosuchus niger* (Spix, 1825) and *Paleosuchus trigonatus* (Schneider, 1801). *Pelagosaurus typus* Bronn, 1842 was split into two OTUs due to the presence of two distinct cranial morphs. Two Aalenian metriorhynchoids, *Pelagosaurus tomarensis* Ferreira, 1959 and *Opisuchus meieri* Aiglstorfer *et al.*, 2020, were added, based on first-hand examination of their holotypes. The addition of these OTUs forms part of the ongoing CrocTransition Project. Finally, the Swiss rhacheosaurin cranial rostrum described herein was added as an OTU. Scoring sources are summarized in the Supporting Information, Appendix S1.

Osteoderm characters were scored for *Montealtosuchus arrudacamposi* Carvalho *et al.* (2007) based on data in Tavares *et al.* (2015). Some scores for *Bernissartia fagesii* Dollo, 1883 were updated based on first-hand examination of the lectotype (IRSNB R46), although this was limited as the specimen was being exhibited in the public gallery within a glass container. We also revised the character scoring for the four extant taxa already in the HY dataset (using NHMUK and NMS specimens, observations of living individuals and CT datasets): *Gavialis gangeticus* (Gmelin, 1789), *Crocodylus niloticus* Laurenti, 1768, *Crocodylus porosus* (Schneider, 1801) and *Alligator mississippiensis* (Daudin, 1801).

When we used the test script (see below), several fragmentary OTUs were identified. Due to their instability in the phylogeny, three OTUs related to Dyrosauridae (*Acherontisuchus* Hastings *et al.*, 2011, *Fortignathus* Young *et al.*, 2017 and *Sabinosuchus* Shiller *et al.*, 2016) and two metriorhynchids (‘*Dakosaurus*’ *lissocephalus* Seeley, 1869 and an indeterminate geosaurine from Argentina (Gasparini *et al.*, 2005) were excluded from the longer analyses.

As with previous versions of the HY dataset, reductive coding (Wilkinson, 1995) was used, with character inapplicability scored as ‘-’. In the supplementary character list (Supporting Information, Appendix S1), characters that have inapplicable scorings are denoted with (*). Character construction follows Sereno (2007) and Andrade *et al.* (2011), highlighting the ontological dependence between characters. The net changes resulted in a dataset consisting of 174 OTUs scored for 519 phenotypic characters (509 osteological characters and ten soft tissue characters).

A second dataset was created as part of the CrocTransition Project. The 519 phenotypic character dataset was added to the genotypic matrix compiled by Lee & Yates (2018) [itself an amalgam of nuclear and mitochondrial DNA data from Gatesy *et al.* (2003), Oaks (2011) and GenBank]. This meant three additional extant OTUs were added, namely *Crocodylus mindorensis* Schmidt, 1935, *Crocodylus suchus* (Geoffroy Saint-Hilaire, 1807) and *Paleosuchus palpebrosus* (Cuvier, 1807). Note: the molecular OTU *Crocodylus novaeguineae* (Schmidt, 1928) from Lee & Yates (2018) is treated herein as *Cr. halli*, but in future studies these two species will need to be re-evaluated and separated into two OTUs. These three OTUs were only scored for the molecular and soft-tissue characters. We did not expect a combined phenotype-and-genotype dataset to impact the arrangement of fossil taxa rootward from the crown group (i.e. Thalattosuchia). However, we tested this assumption as the ongoing CrocTransition Project intends to make further use of genotypic data. Note that all in-depth analyses ran herein were under maximum parsimony. Preliminary Bayesian analyses were conducted, but more in-depth analyses will be run in a forthcoming study.

When analysing both datasets, as 39 of the phenotypic characters are morphoclines, we treated them as ordered (see Supporting Information, Appendix S1). A new outgroup taxon was added, *Batrachotomus kurpferzellensis*. *Postosuchus kirkpatricki* Chatterjee, 1985 was previously the outgroup taxon for the HY dataset. Both taxa are non-crocodylomorph loricatans (e.g. Nesbitt, 2011) and were consistently used as the outgroup taxa, but with *Batrachotomus kurpferzellensis* specifically used to root the topology.

The parsimony analyses were conducted using TNT v.1.5 Willi Hennig Society edition (Goloboff *et al.*, 2008; Goloboff & Catalano, 2016). Memory settings were increased with General RAM set to 900 Mb. We ran the analyses using newly created TNT scripts (see Supplementary data files, and available upon request from the corresponding author). The four new scripts presented here are: fourstats.run, fast.run, EqualW.run and ImpliedW.run. The fourstats.run script is an emended version of the stats.run script that comes with TNT. It was emended to calculate the ensemble rescaled consistency and ensemble homoplasy indices. Note, this script must be in the same folder as the data input file and the scripts described below (as they utilize fourstats.run when calculating the descriptive statistics).

The script fast.run implements only a single equal weights analysis. As its name implies, it is a ‘fast’ version of the EqualW script. It is a tester script to check that the data input file is compatible with the longer-running analysis scripts (as our testing found that errors could occur over an hour into the longer analyses). The script produces six output files:

(1) .txt log file (includes the descriptive statistics)
(2) .tre file with the resultant cladograms
(3) .tre file with the strict consensus topology
(4) .txt file with the nodal support values
(5) .svg file of the strict consensus topology
(6) .svg file of the strict consensus with nodal support

This script runs: an initial ‘new technology’ search (xmult:hits 10 replications 10 rss css xss fuse 5 gfuse 10 ratchet 10 drift 10; sec:drift 10 rounds 10 fuse 3; ratchet:numsubs 40 nogiveup; drift:numsubs 40 nogiveup), then runs a ‘traditional methods’ search (bbreak:TBR) on the saved cladograms. Next it calculates the descriptive statistics (length, CI, RI, RC and HI) for one of the fundamental cladograms (tchoose 1; length;run fourstats.run) and the strict consensus topology (tchoose{strict}; length;run fourstats.run). Note: the latter can be less optimal than the fundamental cladograms. After saving the fundamental cladograms (.tre) and strict consensus (.tre) it runs two nodal support analyses, a heuristic Bremer support analysis (hold 2000;subopt 15;bbreak;ttag=;bsupport) and a symmetric resampling analysis (resample = sym replications 100 frequency gc from 0). Finally, it saves two.svg files: (1) strict consensus and (2) the strict consensus with the nodal support values.

The script EqualW.run implements only a single equal weights analysis. This should be used if only one equal weights analysis is desired (i.e. no implied weighting) and once the data input file is compatible (see above for using fast.run as a tester script). The procedure EqualW.run goes through is identical to fast.run, the differences are in the 'new technology' analysis settings (xmult:hits 10 replications 100 rss css xss fuse 5 gfuse 10 ratchet 20 drift 20; sec:drift 10 rounds 10 fuse 3; ratchet:numsubs 40 nogiveup; drift:numsubs 40 nogiveup) and the number of cladograms held per analysis. Note that here hold 20 000 is used, as our testing found holds of greater than 20 000 resulted in unexpected errors when running larger datasets. Note also that sometimes a hold of 20 000 resulted in unexpected errors as well, if other programs where running simultaneously. Workstations with greater memory than a Lenovo ideapad 500 (used for these analyses) might be able to have a higher hold setting.

The final script we introduce is ImpliedW.run. This script implements equal weighting, implied weighting and extended implied weighting analyses (Goloboff, 2014). The settings used are identical to those of EqualW.run. First, an equal weights analysis is run (piwe-), which is then followed by seven different implied weighting analyses, varying in their k value (piwe = 1, piwe = 3, piwe = 7, piwe = 10, piwe = 15, piwe = 20 and piwe = 50), and finally one extended implied weighting analysis, 'xpiwe (*'. By using a range of fitting functions, it shows how strong (k = 1 and k = 3) to how weak (k = 20 and k = 50) homoplastic down-weighting impacts the results. Extended implied weighting is recommended for datasets with large amounts of missing data, due to the artificially high implied weights received by OTUs with high proportions of missing data (Goloboff, 2014). Each of the nine different weight analyses produces the six output files listed above for fast.run, meaning that a correctly running ImpliedW.run script will yield 54 files once completed. Here we used the ImpliedW.run script to analyse both the phenotype-only dataset and the phenotype-and-genotype dataset.

Preliminary undated Bayesian analyses were performed using MrBayes v.3.2.5 (Ronquist *et al.*, 2012). We analysed our phenotype-only dataset using a Markov (Mk) model (Lewis, 2001), assuming only variable characters were scored (v), and with a gamma distribution (G) to model rate heterogeneity across characters (Mkv+G model). For the combined phenotype-and-genotype dataset we used the same molecular partitions and molecular evolution models as Lee & Yates (2018). When analysing both datasets, five independent runs, each with ten chains, ran for five million generations using 50 cores on the Rocket HPC cluster at Newcastle University. Sampling occurred every 5000 generations, with a burn-in of 40%. Parameters were assessed for stationarity and effective sample sizes in tracer (Rambaut *et al.*, 2018). Consensus trees were plotted and formatted in R (R Development Core Team, 2017) using the 'ggtree' R package (Yu *et al.*, 2017). Note, that as MrBayes does not allow ordered characters to have more than six states, cf. '*C.*' *macrospondylus* was re-scored as state (5) for character 56. State (6) for this character is autapomorphic for cf. '*C.*' *macrospondylus*.

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA HAY, 1930 (*SENSU* NESBITT, 2011)

THALATTOSUCHIA FRAAS, 1901 (*SENSU* YOUNG & ANDRADE, 2009)

METRIORHYNCHIDAE FITZINGER, 1843 (*SENSU* YOUNG & ANDRADE, 2009)

METRIORHYNCHINAE FITZINGER, 1843 (*SENSU* YOUNG & ANDRADE, 2009)

RHACHEOSAURINI YOUNG *ET AL.*, 2011

RHACHEOSAURINI INDETERMINATE

(FIGS 1, 2)

Specimen: NMBE 5018135 – anterior cranial rostrum.

Locality: An abandoned quarry near Evilard, Canton Bern, Switzerland (Rieppel, 1979).

Horizon and age: Twannbach Formation. Lower Tithonian, Upper Jurassic.

The specimen, NMBE 5018135, derives from carbonate rock strata exposed in an abandoned quarry near Evilard, Switzerland (Rieppel, 1979). There are no direct data on the fossil-bearing horizon, but all carbonate rocks in the proximity of the fossil site belong to Twannbach Formation (Swiss 'Portlandien', not to be confused with the British Portlandian strata), indicating a Tithonian age for the specimen (Häfeli, 1964; Rieppel, 1979).

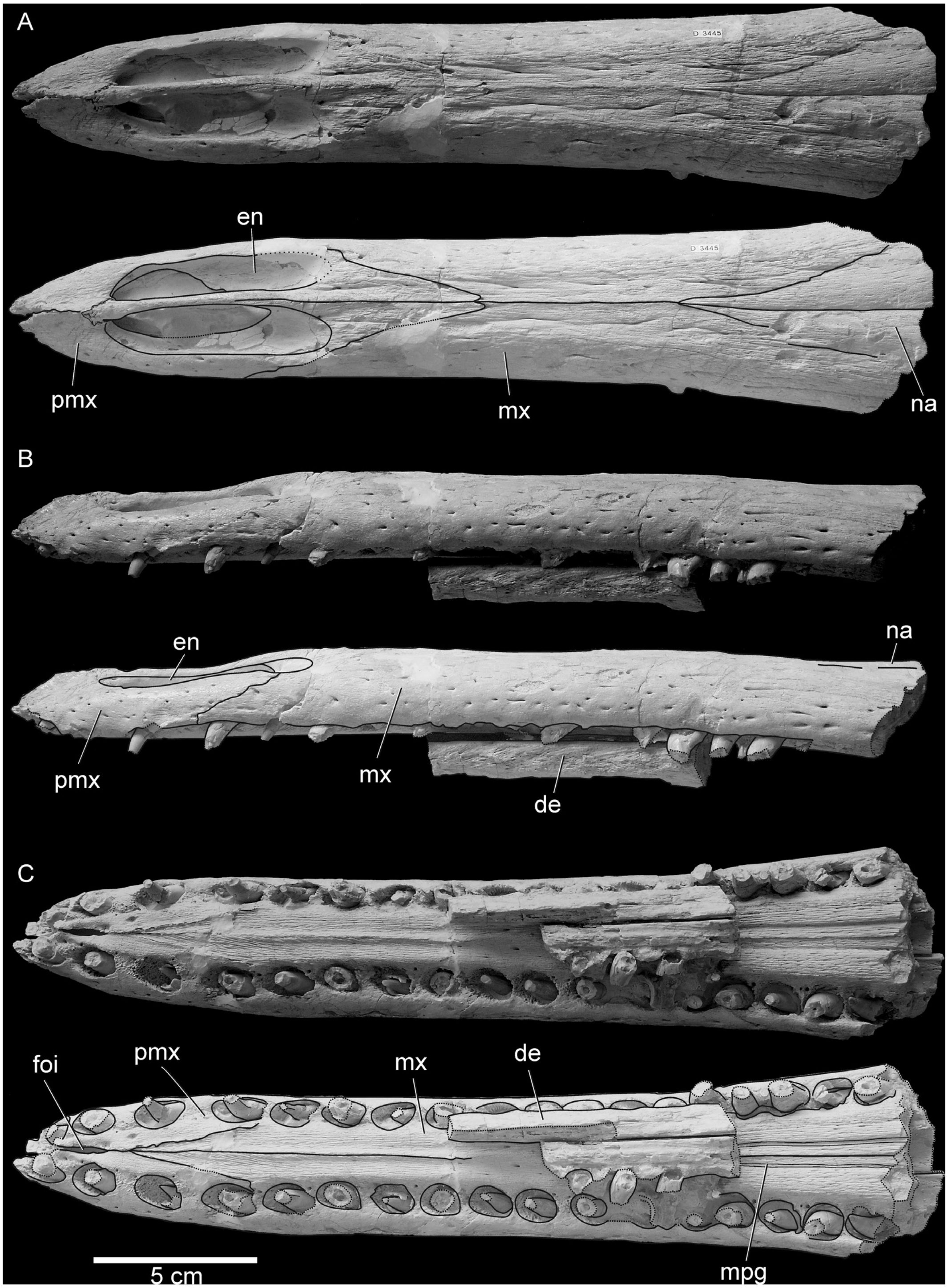

Figure 1. Rhacheosaurini indeterminate NMBE 5018135. A, dorsal view; B, left lateral view; C, palatal view. See text for anatomical abbreviations.

Still, the stratigraphic history of the Swiss 'Portlandien' is complicated, making a proper chronostratigraphic assignment of those strata rather difficult (Rameil, 2005). The succession to the Berriasian Goldberg Formation at the top of the 'Portlandien' is vague and likely diachronous, whereas the base of the 'Portlandien' or Twannbach Formation, respectively, is well defined by the presence of the *virgula* Marls, separating it from the

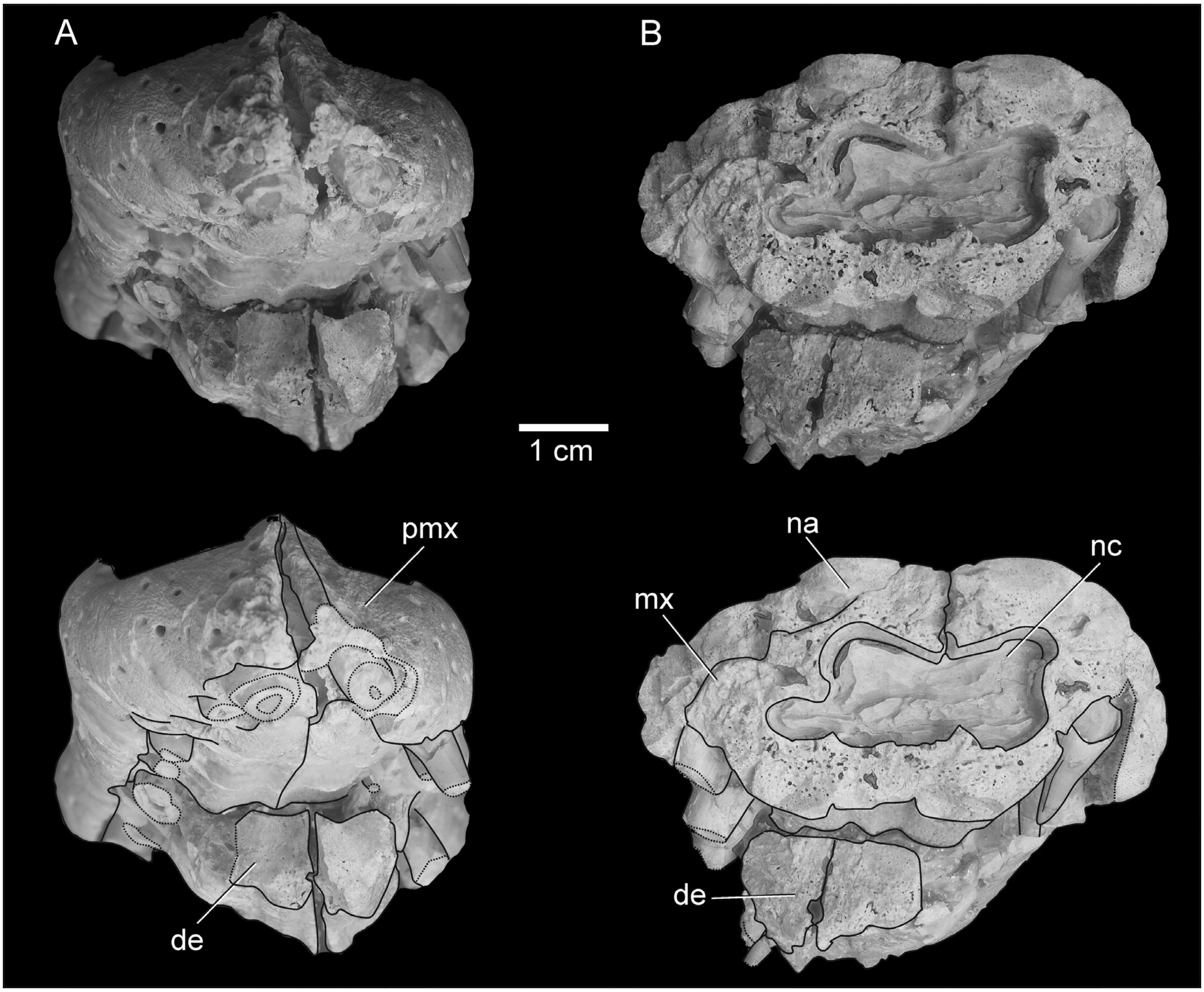

Figure 2. Rhacheosaurini indeterminate NMBE 5018135. A, anterior view; B, posterior view. See text for anatomical abbreviations.

underlying Reuchenette Formation (Rameil, 2005). Those marls are further interpreted to lie approximately at the Kimmeridgian/Tithonian boundary, locating the base of the Twannbach Formation in the lower *Hybonoticeras hybonotum* Sub-Mediterranean Ammonite Biozone (lower Tithonian; Zeiss, 2003; Rameil, 2005; Strasser, 2007). However, due to a lack of index fossils, there is no more information on the biostratigraphy of the Twannbach Formation (Rameil, 2005). Hence, NMBE 5018135 cannot be assigned with certainty to any specific Tithonian Biozone.

The sediments of the Twannbach Formation consist predominantly of thin-bedded limestones, often rich in dolomite, which were deposited in a semi-arid to arid lagoonal to peritidal environment in the north-western Alpine Tethys with temporarily subaerial exposure (Rameil, 2005).

Description

The indeterminate rhacheosaurin NMBE 5018135 was discovered in 1971 by Mr F. Haldemann of Biel, Switzerland. Later, the specimen was given to Prof. Dr H. A. Stalder of the Palaeontological Institute and Museum of the University of Zurich. Based on the similarities with *Geosaurus suevicus* Fraas, 1901 (now *Cricosaurus suevicus*, see: Young & Andrade, 2009) Rieppel (1979) considered the specimen to be *Geosaurus* cf. *suevicus*. Due to the similarity the specimen has with the specimen referred to as '*Cricosaurus*' *macrospondylus* (Koken, 1883) (herein referred to as cf. '*Cricosaurus*' *macrospondylus*; Hua *et al.*, 2000; see below), we instead refer to it as Rhacheosaurini indeterminate. The maximum preserved length is 286 mm, with a width of 40.5 mm and a height of 22 mm at the premaxilla–maxilla suture. The maximum preserved width is 57 mm (at the posterior end of the specimen).

Premaxilla and external nares: In dorsal view, the premaxillae form an anteroposteriorly elongate oval (Fig. 1A). The premaxillary posterior processes are not particularly elongate for a metriorhynchid, although they do terminate approximately level to the 6th (M6) maxillary alveoli. This is due to the posterodorsal retraction and length of the external nares. The suture between the premaxilla and maxilla is almost straight, with the posterodorsal processes converging posteriorly. In dorsal view, the premaxilla only contacts the maxilla along its posterior margins. In lateral view, the external surfaces are slightly convex (Fig. 1A, B), except at the anterior margin of the narial fossa, where the premaxillae become concave. The external surfaces are slightly ornamented, with a short anteroposterior ridge pattern lateral to the external nares (Fig. 1A), which becomes a pitted pattern anterior to the nares (Fig. 2A). The external surfaces of the premaxilla have numerous, large, neurovascular foramina (Figs 1, 2). The presence of numerous, large and conspicuous rostral neurovascular foramina is unusual for a metriorhynchid. It is unclear whether these foramina are osteological correlates for the increased trigeminal innervation and somatosensory receptors seen in extant crocodylians (Soares, 2002). The only other known metriorhynchid that has large, and well separated, neurovascular foramina on the premaxilla and maxilla is cf. '*Cricosaurus*' *macrospondylus* (Hua *et al.*, 2000; RNGHP 990201).

The full extent of the external naris aperture is hard to discern, as the thin premaxillary bones that form the narial fossa are cracked and broken. However, the nares are clearly separated by a fully ossified premaxillary bar. The two narial fossae are anteroposteriorly elongate ovals (Fig. 1A). The anterior margin of the narial fossa is posterior to the P2 alveoli, while the posterior margin of the narial fossa is level to the M4 alveoli. This elongate narial fossae, that stretches between the P2 and M4 is only known to occur in NMBE 5018135, *Cricosaurus elegans* Wagner, 1852 and *C. suevicus* (Fraas, 1902). However, the position of the posterior margin of '*Cricosaurus*' *saltillensis* (Buchy *et al.*, 2006) is hard to discern (Buchy *et al.*, 2013).

In palatal view, three procumbent alveoli are visible (Fig. 1C). The premaxilla–maxilla contact is an anteriorly directed 'V'-shape created by the maxilla palatal anterior process overlapping the premaxilla. The maxillary palatal process terminates level to the anterior margin of the P3 alveoli. Anterior to the maxillary anterior processes is the incisive foramen, which is an elongate anteroposterior oval shape, and positioned medial to the P1 and P2 alveoli. The palatal processes of the premaxilla form the anterior and medial margins of the M1 alveoli (Fig. 1C), but do not contribute to the lateral margins of these alveoli (Fig. 1B). How the premaxilla contributes to the anterior maxillary alveolar margins appears to be highly variable in Metriorhynchidae, and remains a largely overlooked source of variation. Unfortunately, due to preservation, this characteristic cannot be ascertained for any of the German *Cricosaurus* Wagner, 1858 species from the Kimmeridgian-to-Tithonian (e.g. Fraas, 1902; Sachs *et al.*, 2019a; in review) or the unnamed '*Cricosaurus*' subclade consisting of '*Met.*' *palpebrosus*, '*Cricosaurus*' *saltillensis* and cf. '*Cricosaurus*' *macrospondylus* (Hua *et al.*, 2000; Buchy *et al.*, 2013).

Another overlooked potential source of variation is the incisive foramen. In NMBE 5018135, this foramen is entirely bound by the premaxilla (Fig. 1C) and clearly anterior to the maxillary anterior processes. It is positioned medial to the P1 and P2 alveoli. The maxillary contribution to the incisive foramen is a characteristic that requires further checking in specimens.

Maxilla: It is unclear how much of the maxilla is preserved, most likely approximately half (Fig. 1) (based on the Kimmeridgian–Tithonian *Cricosaurus* specimens from Germany and '*Cricosaurus*' *saltillensis* Buchy *et al.*, 2013). The right maxilla preserves 14 alveoli, whereas the left preserves 15 (Fig. 1C). The external surfaces of the maxillae are slightly convex and lightly ornamented. From the premaxilla–maxilla contact, to the anteriormost point of the nasals, the maxilla dorsal surface is lightly ornamented with small pits and occasional grooves. Near the premaxilla–maxilla contact this pattern shifts to the same ridge-groove ornamentation seen on the lateral premaxilla. On the dorsal surface there are anteroposteriorly aligned grooves and ridges, which become less pronounced towards the tooth row. Dorsally, lateral to the nasal anterior processes, the maxilla becomes much more strongly ornamented. Here the external surface is composed of pronounced anteroposteriorly aligned grooves (Fig. 1A).

In lateral view, no discernible reception pits can be seen on the lateral margins of the maxillae or on the palatal surface (Fig. 1B, C). This is a characteristic that NMBE 5018135 shares with *Cricosaurus elegans* and *C. suevicus* to the exclusion of *C. bambergensis* Sachs *et al.*, 2019a, the Solnhofen *Cricosaurus* (Sachs *et al.*, 2019a, in review) and the unnamed '*Cricosaurus*' subclade (Hua *et al.*, 2000; Buchy *et al.*, 2013). As with the premaxilla, the lateral surfaces of the preserved maxilla have numerous large and conspicuous neurovascular foramina (Fig. 1B).

In palatal view, the maxillary shelves are conspicuously ornamented by a ridge-groove pattern, the direction of which shifts along the element. Note that this ornamentation is conspicuous for a thalattosuchian, but in taxa with more defined palatal ornamentation (e.g. *Fruitachampsa*; Clark, 2011), the grooves in NMBE 5018135 could be considered fine and shallow. However, anteriorly they curve medially from the alveolar margin to the midline intermaxillary suture. The orientation shifts to being almost anteroposterior towards the end of the preserved maxilla. Between the M1 and M6 alveoli, the intermaxillary suture forms a pronounced, raised ridge. The preserved dentary obscures exactly when this ridge flattens out (Fig. 1C).

All of the alveoli have *in situ* tooth crowns of varying degrees of preservation. The alveoli are somewhat irregularly shaped, being varying shapes of almost circular to differently aligned subovals. The M1 and M2 alveoli are noticeably anteriorly procumbent, the M3 alveoli are less so and posteriorly the alveoli become more vertically oriented. The interalveolar spacing is somewhat variable, and only at the posterior–maxilla do the interalveolar spaces reduce to a thin lamina. Posterior to the M11 alveoli, the interalveolar spacing begin to narrow. As with other metriorhynchids there are paired 'palatal grooves', or anteroposterior sulci, on either side of the maxilla midline (see: Andrews, 1913; Foffa & Young, 2014). These palatal grooves can only be observed posterior to the preserved dentary (adjacent to the M11–M15 alveoli). The preserved dentary most likely obscures exactly where the grooves disappear, but it probably would have been between the M5 and M11 alveoli.

Nasals: Little of the nasals is preserved, only the anterior processes. The anterior processes form the characteristic converging triangular shape seen in thalattosuchians (e.g. see: Fraas, 1902; Andrews, 1913) (Fig. 1A). The anterior processes terminate level to the M11 alveoli. Light ornamentation is present on the external surface, composed of anteroposteriorly aligned grooves, especially on the anterior and lateral margins. Closer to the internasal suture, the ornamentation is less dense and, in addition to the grooves, includes anteroposteriorly aligned rows of small pits.

Dentary: A small fragment of symphyseal dentary is preserved. The left preserved dentary is *in situ* between the M5 and M11 alveoli, while the smaller right dentary fragment is preserved *in situ* between the M7 and M11 alveoli. It is clear that, at least in this region of the dentary, the maxilla was noticeably wider than the dentary. However, given the preservation of the specimen, we cannot be certain that the dentary was this narrow. Three tooth fragments are preserved in the right dentary (Fig. 1B, C).

Dentition: No complete tooth crowns are preserved. However, from parts that are preserved, the dentition is single cusped, distally curved, subconical with a pointed apex. Two thin carinae extend mesiodistally from the base to the crown to the apex. No serrations are visible on the carinae. The exposed surfaces appear largely smooth, with no conspicuous enamel ornamentation.

GEOSAURINAE LYDEKKER, 1888 (*SENSU* YOUNG & ANDRADE, 2009)

GEOSAURINI LYDEKKER, 1888 (*SENSU* CAU & FANTI, 2011)

Taxonomic note: Previously, the nominal authority given for the *Geosaurus* Cuvier, 1824-stem family group has been Lydekker (1889). It is in fact Lydekker (1888).

'E-CLADE' INDETERMINATE ('ENGLISH ROSTRUM')

(FIGS 3D–F, 9G)

Specimen: CAMSM J18212 – anterior cranial rostrum.

Locality: Chettisham (north of Ely), Cambridgeshire, UK.

Horizon and age: Kimmeridge Clay Formation. Kimmeridgian, Upper Jurassic.

CAMSM J18212 derives from rocks of the Kimmeridge Clay Formation in Chettisham, Cambridgeshire, UK. A specific horizon was not reported (Watson, 1911: 9). Nevertheless, the Kimmeridge Clay Formation in the proximity of Ely, and hence Chettisham, is reported to contain only the Lower Kimmeridge Clay (Gallois & Bazley, 1980). This section extends from the *Rasenia cymodoce* to the *Aulacostephanus autissiodorensis* Subboreal Tethyan Ammonite Biozones, covering most of the subboreal Kimmeridgian (Zeiss, 2003; Gallois, 2004). A stratigraphic assignment of CAMSM J18212 below stage-level is hence not possible. The Kimmeridge Clay Formation in the provenience consists of clays, calcareous clay and micritic limestones, and the most common macrofossils are ammonites (Gallois & Bazley, 1980). A fine-grained, calcareous sediment is associated with the specimen.

Description

The 'English rostrum' (CAMSM J18212) has rarely been mentioned in the literature. The first mentioned was by Watson (1911: 9), where he referred it to *Met. hastifer* (Eudes-Deslongchamps, 1868a). However, as the rostrum of the *Me. hastifer* holotype (MNHN.F RJN 119) is broken just anterior to the premaxilla–maxilla

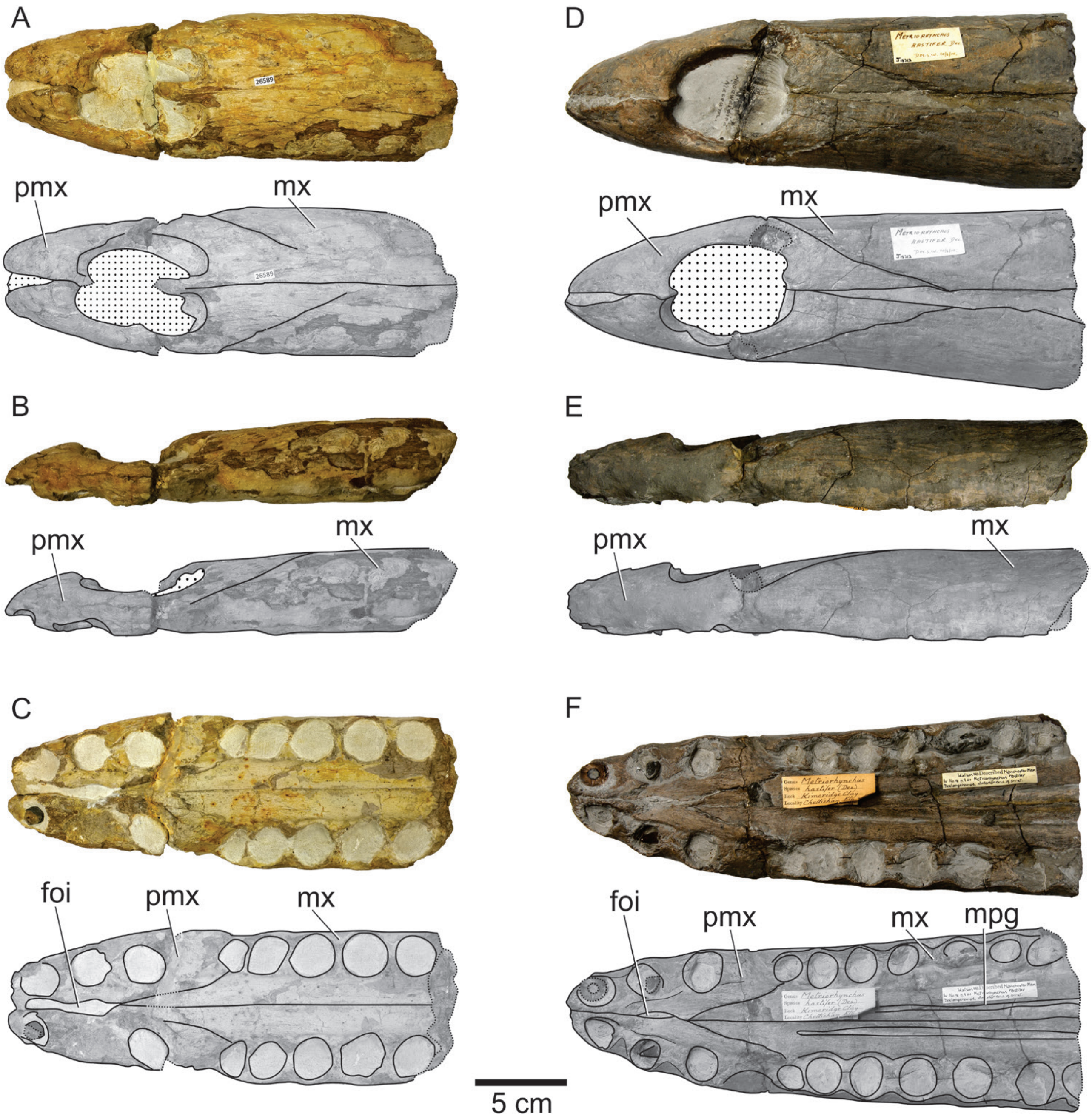

Figure 3. Comparative plate of the two 'E-clade' cranial rostra. The 'Swiss rostrum' NMO 26589 in: A, dorsal view; B, left lateral view; C, palatal view. The 'English rostrum' CAMSM J18212 in: D, dorsal view; E, left lateral view; F, palatal view. See text for anatomical abbreviations.

suture, and lacks transversely oval maxillary alveoli, this referral cannot be supported. Watson (1911) considered there to be a similarity between the dental morphology of CAMSM J18212 and a specimen Phillips (1871) referred to as *Steneosaurus longirostris*. Based on the figure and description given by Phillips (1871: 388 and diagram CXC), it is more likely that his *Steneosaurus longirostris* is a specimen of *Torvoneustes* Andrade *et al.*, 2010, as the figured tooth crown shows a shift in enamel ornamentation from long apicobasally aligned ridges to noticeably shorter ridges apically, and the crown apex is blunt. Grange & Benton (1996: 510) briefly mentioned CAMSM J18212 in their overview of Kimmeridge Clay Formation metriorhynchids. Abel *et al.* (2020) were the first to include CAMSM J18212 in a phylogenetic analysis, where they found it to be a member of the 'E-clade', an enigmatic group of poorly known geosaurins from the Kimmeridgian-to-Tithonian of Europe.

Premaxilla and external nares: In dorsal view, the premaxilla is an anteroposteriorly elongate rhombus (Fig. 3D). The premaxillary posterior processes are particularly elongate, terminating approximately level to the 5th (M5) maxillary alveoli (similar to the condition seen in *Tyrannoneustes lythrodectikos* Young *et al.*, 2013; Foffa & Young, 2014). This suture between the premaxilla and maxilla is almost straight, with the posterodorsal processes convergingly posteriorly. The premaxilla only contacts the maxilla along its posterior margins. In lateral view, the external surfaces are slightly convex (Fig. 3D, E). The external surfaces have little ornamentation, with a low-relief anteroposteriorly oriented ridge pattern present posterior to the external nares.

The external naris aperture cannot be observed due to matrix infilling the narial fossa. The narial fossa is a slight anteroposterior oval and there is no evidence of an ossified internarial bar. The anterior margin of the narial fossa is posterior to the P2 alveoli, while the posterior margin of the narial fossa is almost level to the posterior margin of the M1 alveoli.

In palatal view, three round and widely spaced alveoli can be seen (Fig. 3F). The premaxilla–maxilla contact is an anteriorly directed 'V'-shape created by the maxilla palatal anterior process overlapping the premaxilla. The maxillary palatal process terminates level to the anterior margin of the P3 alveoli. Anterior to the maxillary anterior processes is the incisive foramen, which is an elongate anteroposterior oval shape, and positioned medial to the P2 alveoli. The palatal processes of the premaxilla form the anterior margin of the M1 alveolar margin (as with *Tyrannoneustes lythrodectikos*; Foffa & Young, 2014).

Maxilla: Approximately the anterior third of the maxilla is preserved (only seven alveolar pairs are present) (Fig. 3F). The external surfaces of the maxillae are slightly convex and lightly ornamented. On the dorsal surface there are anteroposteriorly aligned grooves and ridges, which become less pronounced towards the tooth row (Fig. 3D). Adhering matrix on the rostrum makes it hard to determine if there is a shift in ornamentation pattern as in *Tyrannoneustes lythrodectikos* (Foffa & Young, 2014). In lateral view, there could be slight reception pits on the lateral margins of the maxillae, but given the preservation of the specimen we cannot be certain (Fig. 3E).

In palatal view, the unusual mediolaterally expanded maxillary alveoli are visible. This morphology is only shared with members of the 'E-clade' (see: Abel *et al.*, 2020), such as the specimen Lepage *et al.* (2008) referred to as *Met.* cf. *hastifer*. The 'Swiss rostrum' (NMO 26589) has a somewhat intermediate condition in alveolar shape. The interalveolar spacing is narrow, although not uniformly so (unlike in *Plesiosuchus* Owen, 1884 and *Dakosaurus* Quenstedt, 1856 where the interalveolar spaces are uniformly thin laminae; see: Young *et al.*, 2012). As with *Plesiosuchus* and *Dakosaurus*, it looks as though the reduced interalveolar spacing is due to an increase in alveolar/tooth diameter. Paired palatal grooves are present on either side of the maxilla midline. Unusually, these grooves continue anteriorly along the maxilla, terminating level to the M2 alveoli (Fig. 3F). In *Tyrannoneustes lythrodectikos* these grooves terminate level to the M4 alveoli (Foffa & Young, 2014).

'E-CLADE' INDETERMINATE ('SWISS ROSTRUM')

(FIGS 3A–C, 9F)

Specimen: NMO 26589 – anterior cranial rostrum.

Locality: An abandoned quarry near Oberbuchsiten, Canton Solothurn, Switzerland.

Horizon and age: Villigen Formation. Upper Oxfordian or lower Kimmeridgian, Upper Jurassic.

NMO 26589 derives from carbonate rocks exposed near Oberbuchsiten, Canton Solothurn, Switzerland. Data on the fossil-bearing stratum of NMO 26589 is equivocal. The specimen is said to derive from the Wettingen Member of the Villigen Formation, but Wettingen Member is not a subunit of the Villigen Formation, as the sediments of the Wettingen Member date from the *Crussoliceras divisum* to the *Aulacostephanus eudoxus* Sub-Mediterranean Ammonite Biozone (lower to middle Kimmeridgian). Whereas the Villigen Formation extends from the *Epipeltoceras bimammatum* to the *Subnebrodites planula* Mediterranean Ammonite Biozone (upper Oxfordian to lower-most Kimmerdigian) and is hence older than the Wettingen Member (Gygi & Persoz, 1986; Gygi, 2000; Zeiss, 2003). Furthermore, the Wettingen Member is reported to be not present in the provenience but is in parts indistinguishable from the Villigen Formation in its lithology (Gygi & Persoz, 1986; Gygi, 2000). We hence argue that the fossil-bearing stratum of NMO 26589 likely belonged to the Villigen Formation. The facies of both units are similar, consisting predominantly of bedded micritic limestones (Gygi, 2000). The most common macrofossils of the Villigen Formation in the provenience are ammonites and siliceous sponges (Gygi, 2000).

Description

The 'Swiss rostrum' (NMO 26589) has, to our knowledge, only been mentioned once in the literature. Abel *et al.* (2020) added NMO 26589 in their phylogenetic analyses; they found it to be a member of the 'E-clade'. The specimen is approximately 24 cm long and has a maximum preserved width of 8 cm.

Overall the Swiss and English rostra are similar. The 'Swiss rostrum' differs from CAMSM J18212 in four ways: (1) that the premaxillary posterior process terminates level to the M4 alveoli (unlike the M5 in CAMSM J18212), (2) the narial fossa anterior margin is level to approximately the middle of the P2 alveoli (unlike the anterior margin being posterior to the P2 in CAMSM J18212), (3) the narial fossa posterior margin is almost level to the anterior margin of the M1 alveoli (unlike CAMSM J18212 where the narial fossa posterior margin is almost level to the posterior margin of the M1 alveoli) and (4) there are no discernible palatal grooves preserved in the anterior maxilla of the 'Swiss rostrum', whereas these grooves continue anteriorly until level to the M2 alveoli in the 'English rostrum' (compare Fig. 3C to F). Less of the maxilla is preserved in NMO 26589 than in CAMSM J18212 (only the first five alveolar pairs, whereas CAMSM J18212 preserves the first seven alveolar pairs). Otherwise, the description for CAMSM J18212 largely applies to NMO 26589.

RESULTS

As our study is focused on the narial retraction of metriorhynchids, we will only discuss the internal relationships of Metriorhynchidae (the strict consensus topologies with nodal support values, for all 18 parsimony analyses are in Supporting Information, Appendix S2). Moreover, metriorhynchid internal relationships were not affected by the addition of the genotypic data in the Bayesian analyses and for most of the parsimony analyses (see Supporting Information, Appendix S2), as the phenotypic dataset strict consensus topologies are identical to those of the phenotype and genotype dataset. The only exception is the extended implied weighting analyses. There, the addition of the genotypic data alters the resultant topology, a result that makes sense given how the protocol works (for details see: Goloboff, 2014).

The internal relationships of Metriorhynchidae are identical in the unweighted parsimony analyses, the extended implied weighting analyses and in most of the implied weighted analyses (k = 10, k = 15, k = 20 and k = 50) from both datasets. In the strong homoplasy down-weighting analyses (k = 1 and k = 3) from both datasets, there are three differences (Fig. 4): (1) *Geosaurus lapparenti* (Debelmas & Strannoloubsky, 1956) becomes the basalmost member of Geosaurina, (2) *Met. geoffroyii* and *Mec. superciliosus* (Blainville, 1853) are sister-taxa and (3) the two Chilean metriorhynchid species form a clade '*Mec.*' *casamiquelai* and '*Mec.*' *westermanni* that is recovered as the sister-taxon to Metriorhynchidae (i.e. they are no longer recovered as basal geosaurines). The k = 7 weighting regime from both datasets yields an intermediate topology, where *Geosaurus lapparenti* is still recovered as the basalmost member of Geosaurina and '*Mec.*' *casamiquelai* and '*Mec.*' *westermanni* are not metriorhynchids, but *Mec. geoffroyii* is within Rhacheosaurini (i.e. no longer united with *Mec. superciliosus*).

The topology found in the unweighted analysis differs from those reported in Abel *et al.* (2020) in only one respect: the position of *Met. geoffroyii*. Rather than being recovered as the sister-taxon to *Mec. superciliosus*, *Mec. geoffroyii* is recovered as the sister-taxon to the '*Cricosaurus*' + *Rhacheosaurus* von Meyer, 1831 + *Cricosaurus* subclade. As noted above, when strongly down-weighting homoplastic characters, *Mec. geoffroyii* and *Mec. superciliosus* are united once more.

The metriorhynchid phylogram from the Bayesian analyses are similar to those from the parsimony unweighted analysis and in most of the weighted analyses (Figs 5, 6). The major difference is the position of *Mec. geoffroyii*, as it is found to be the sister-taxon to Rhacheosaurini (i.e. basal to *Maledictosuchus* Parrilla-Bel *et al.*, 2013). Due to the preliminary nature of the Bayesian analyses, we refrain from commenting on these differences, especially as they are poorly supported (Figs 5, 6).

In our phylogenetic analyses, the Swiss rhacheosaurin is consistently recovered as the sister-taxon to cf. '*Cricosaurus*' *macrospondylus*, but note that the cf. '*C.*' *macrospondylus* OTU is solely based on a partial skeleton from the Valanginian of France (Hua *et al.*, 2000). Assessing the validity of that referral to '*Cricosaurus*' *macrospondylus* by Hua *et al.* (2000) is beyond the scope of this paper and will be addressed in a forthcoming study. The 'Swiss rostrum' and 'English rostrum' are consistently recovered within 'E-clade', regardless of optimality criteria or weighting regime. This supports the referral of the two 'rostra' OTUs to 'E-clade' made by Abel *et al.* (2020).

As the external specifiers for Rhacheosaurini are *Met. geoffroyii* and *Gracilineustes leedsi* (Andrews, 1913), our unweighted parsimony and most of our weighted parsimony analyses suggest *Maledictosuchus* is not a member of Rhacheosaurini. However, given that our strong homoplastic down-weighting analyses, and the Bayesian analyses, found *Mec. geoffroyii* to be outside of Rhacheosaurini, the transition from basal metriorhynchines to basal rhacheosaurins is less understood than we previously thought.

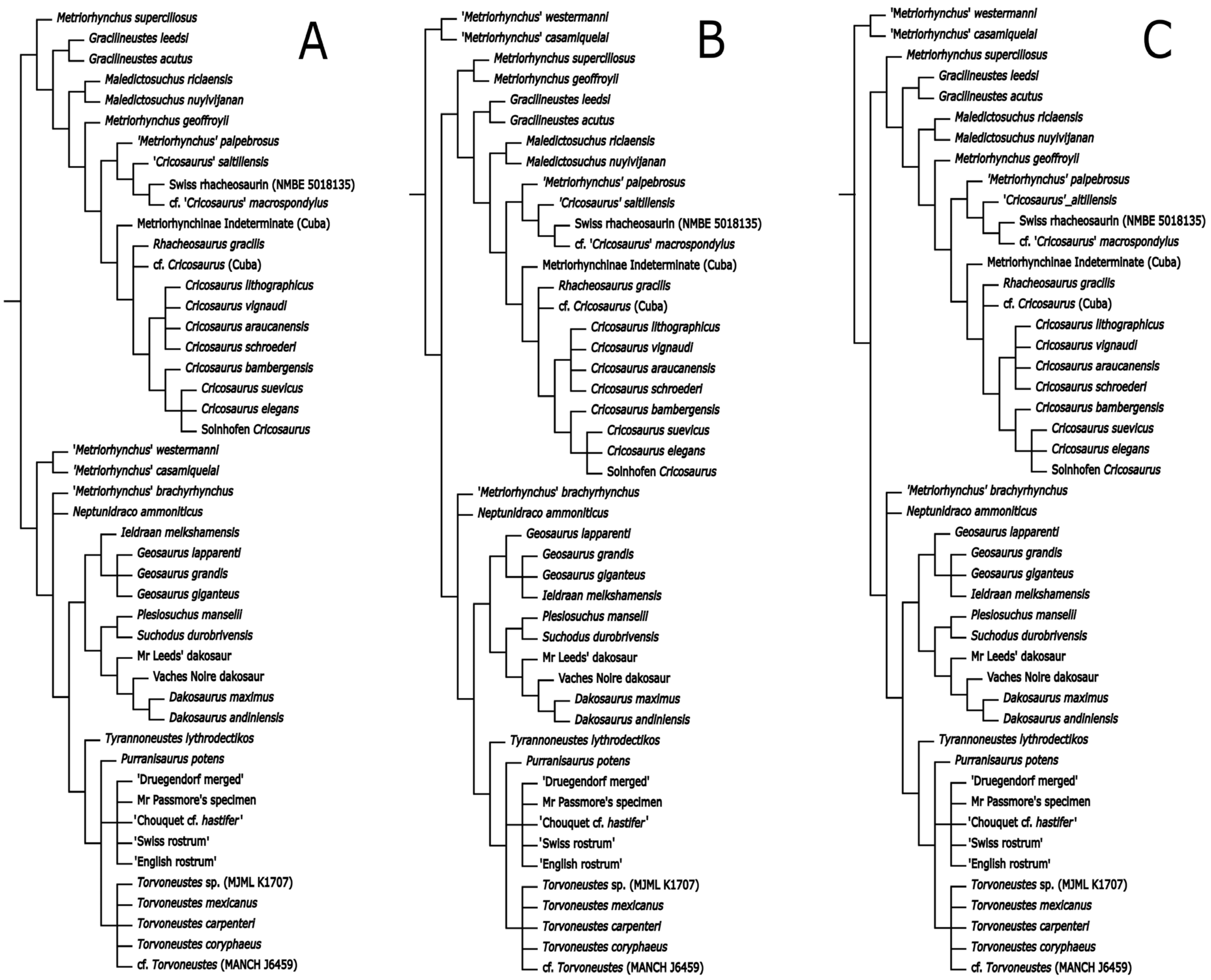

Figure 4. Strict consensus topologies of Metriorhynchidae found in the parsimony analyses. A, unweighted, extended implied weighting and weak down-weighting topology (k = 10, k = 15, k = 20 and k = 50) (both datasets); B, strong down-weighting topology (k = 1 and k = 3) (both datasets); C, intermediate down-weighting topology (k = 7) (both datasets).

DISCUSSION

NARIAL FOSSA-EXTERNAL NARES POSITION

Symplesiomorphically, most metriorhynchids had a dorsally oriented narial fossa, bound entirely by the premaxilla, that is not posterodorsally retracted (Fig. 7). The anterior margin is approximately level to the posterior margin of the P1 alveoli, while the posterior margin terminates approximately level to the posterior margin of the P3 alveoli, in the region of the inflexion point of the premaxillary lateral margins. It is important to note that, in basal species, there is a broad gap between the posterior margin of the narial fossa and the premaxilla–maxilla contact. This general morphology is present in most of the middle Callovian metriorhynchids from the Oxford Clay Formation, *Met. superciliosus*, '*Met.*' *brachyrhynchus* (Eudes-Deslongchamps, 1868b) and *Tyrannoneustes lythrodectikos* (see: Andrews, 1913; Foffa & Young, 2014; Figs 8, 9). These specimens also have an incomplete premaxillary internarial bar (or septum). Often incomplete or broken, a partial internarial bar is preserved in almost all metriorhynchids. Currently, only members of Rhacheosaurini are known to have a fully ossified internarial bar that divides the external nares in two (see: Parrilla-Bel *et al.*, 2013; but note that our phylogenetic analyses suggest *Maledictosuchus riclaensis* Parrilla-Bel *et al.*, 2013 is not a rhacheosaurin and also does not preserve a fully ossified internarial bar, as the bar is partially reconstructed in the holotype). Still, the proximal end of the bar is frequently preserved in non-rhacheosaurins,

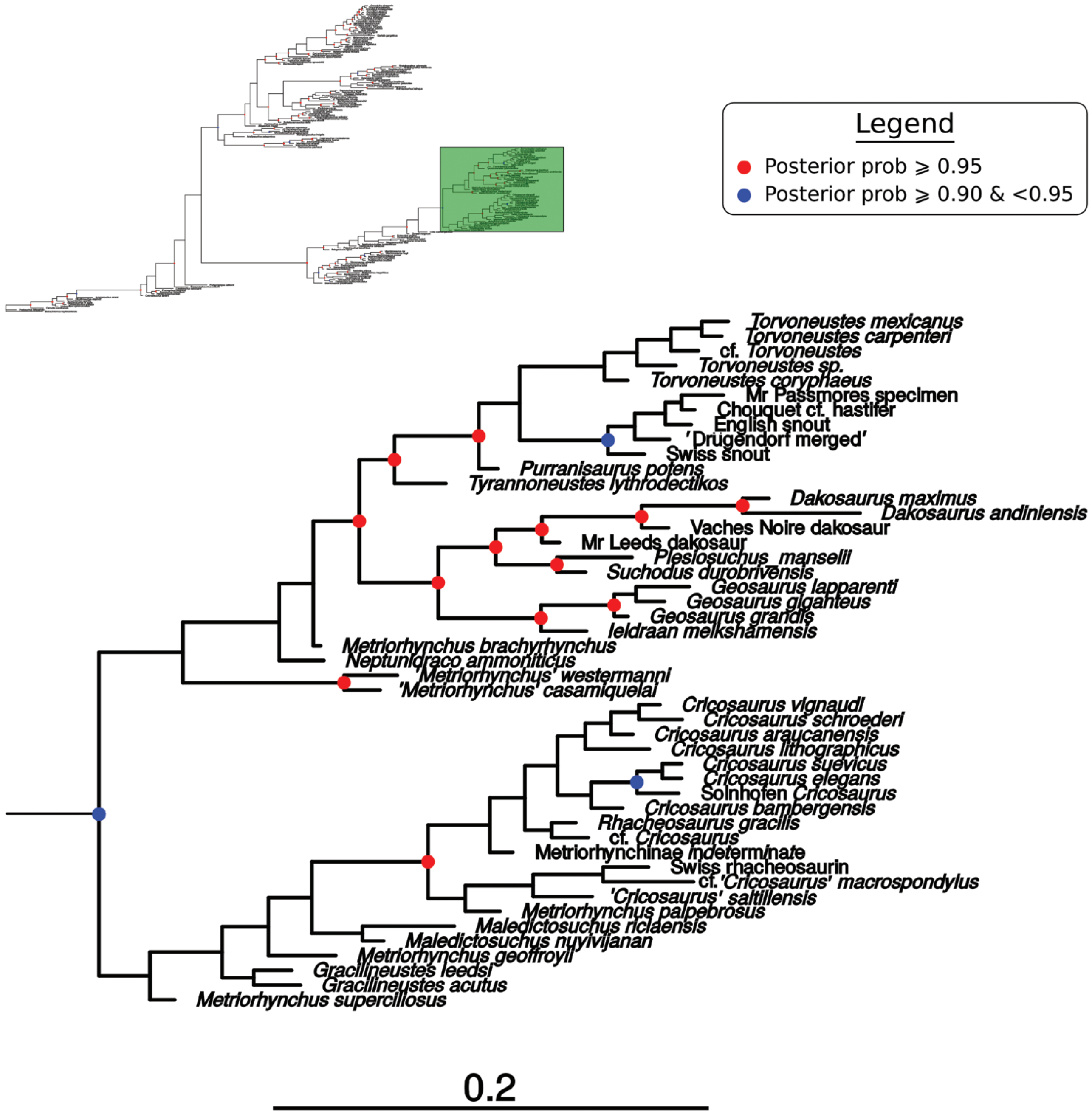

Figure 5. Phylogram of Metriorhynchidae found in the phenotypic only dataset Bayesian analysis. Nodes with strong support (PP ≥ 0.95) are in red, nodes with low support (PP between ≥0.90 and <0.95) are in blue and nodes with poor support (PP < 0.90) are unlabelled.

as is a 'V'-shaped depression with articular surfaces on the narial anterior border (see Fig. 8). It appears that in non-rhacheosaurins, the internarial bar is only partially ossified or fragile, such that it is not preserved in its entirety.

As such, we can assume that the basal condition of narial fossa for Metriorhynchidae, Metriorhynchinae and Geosaurinae is: dorsally oriented, bound solely by the premaxilla, is not posterodorsally retracted (being situated largely between the P1 and P3 alveoli) and has a partially ossified internarial bar (Fig. 7). Moreover, the shape of the external naris varies. In these basal forms the narial fossa is typically 'heart-shaped' with the posterior margin noticeably wider than the anterior margin (Figs 8, 9). However, within Rhacheosaurini the external nares become elongate

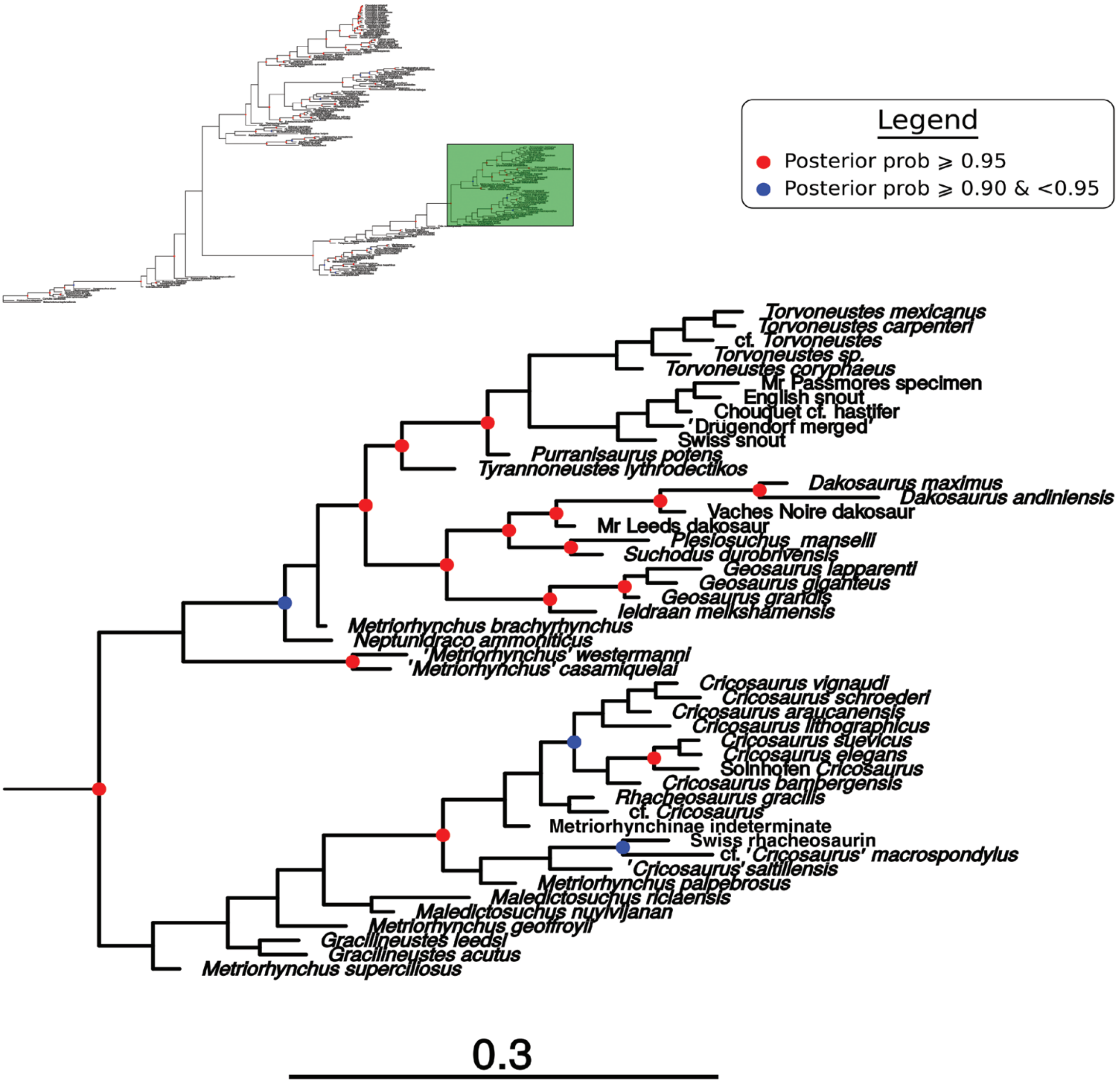

Figure 6. Phylogram of Metriorhynchidae found in the phenotypic and genotypic dataset Bayesian analysis. Nodes with strong support (PP ≥ 0.95) are in red, nodes with low support (PP between ≥0.90 and <0.95) are in blue and nodes with poor support (PP < 0.90) are unlabelled.

ellipsoids (Fig. 8F–J) and within Geosaurini a wide oval external naris morphotype evolves (Fig 9C–H).

The backwards migration of the posterior margin of the narial fossa occurs independently multiple times in Metriorhynchidae, but it does not always co-occur with the backwards migration of the anterior margin of the narial fossa (Fig. 7); thus, it is not a true posterodorsal retraction. Here the posterior margin of the narial fossa is either level to the premaxilla–maxilla contact or almost level to it. This results in a proportionally longer narial fossa in dorsal view. Within Metriorhynchinae this occurs once, in taxa more derived than *Met. superciliosus* (Figs 7, 8A), thus appearing by at least the middle Callovian (seen in *Gracilineustes leedsi* and *Maledictosuchus riclaensis*). In Geosaurinae, the posterior margin backwards migration is seen in the late Kimmeridgian Geosaurini taxa *Torvoneustes carpenteri* (Wilkinson *et al.*, 2008), *Plesiosuchus manselii* and *Dakosaurus maximus* (Plieninger, 1846), as well as all members

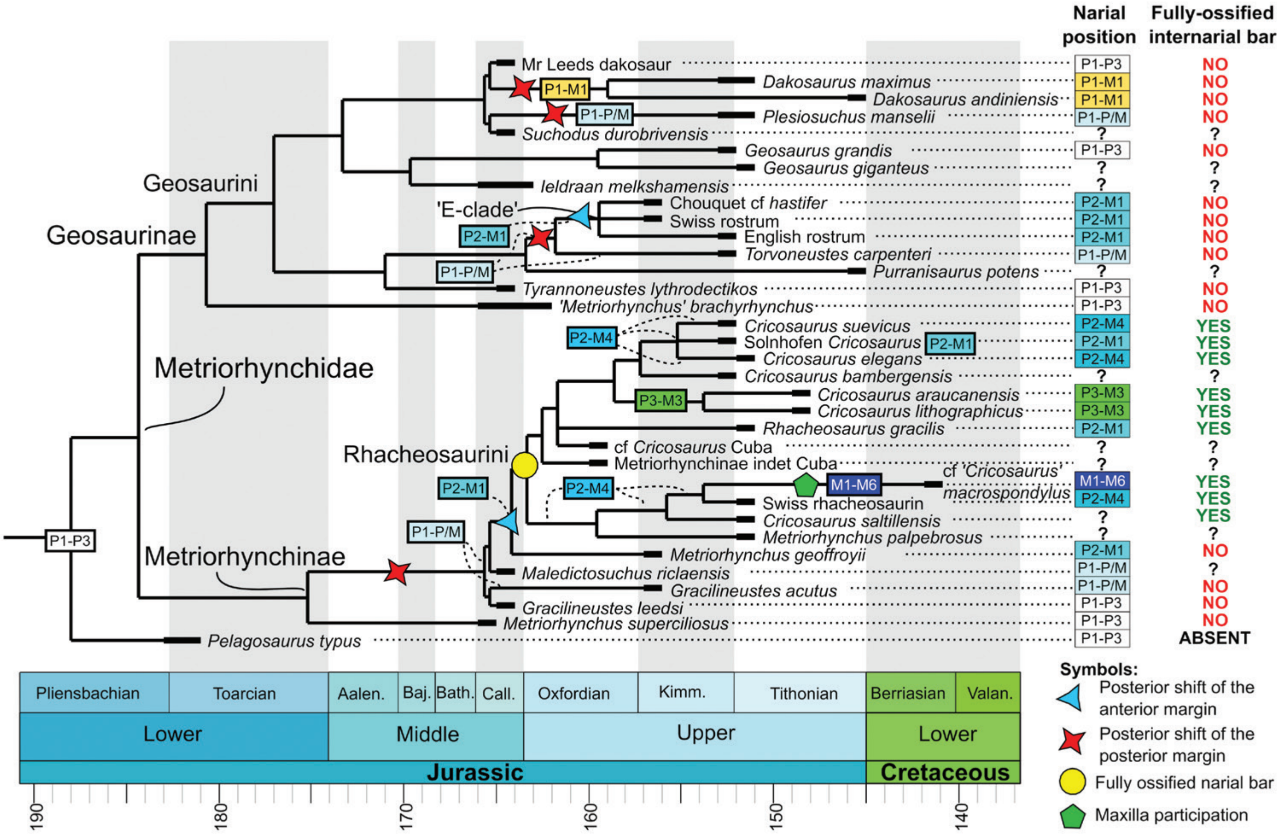

Figure 7. Time-calibrated tree of Metriorhynchoidea with mapped narial fossa morphologies. It maps when the maxilla participates in the border of the narial fossa, the development of the internarial bar, narial position relative to the upper tooth-row, and where the anterior and posterior margins of the narial fossa begin to posteriorly retract. This tree uses the topology of Figure 4A (due to it being the most frequently recovered topology), and has been pruned to remove as many taxa lacking the anterior cranial rostrum as possible. The only taxon that is recovered in a different position and impacts narial character optimisation is *Met. geoffroyii*; in the more basal positions it can be recovered in, there would be one further incidence of anterior margin of the narial fossa retracting in Metriorhynchinae.

of the 'E-clade' (Figs 7, 9D–I). It appears to have evolved independently three times (Fig. 7), as the early Tithonian *Geosaurus grandis* (Wagner, 1858) (Fig. 9H) and an undescribed geosaurine from the Kimmeridge Clay Formation (Fig. 9C) retain the basal condition, as do the Callovian Geosaurini taxa. This margin reaches approximately level to the middle of the M1 alveoli in the *D. maximus* neotype, resulting in the largest known narial fossa for a geosaurine (Fig. 9I). Therefore, the backwards migration of the posterior margin of the narial fossa occurred at least four times in Metriorhynchidae (although that assumes it occurred once in the subclade *Torvoneustes* + 'E-clade', a poorly understood region of the topology; see Abel *et al.*, 2020).

Within Metriorhynchinae, true retraction of the narial fossa is seen in the clade *Met. geoffroyii* + Rhacheosaurini (Fig. 7). In these taxa, the anterior margin is posterior to the P1 alveoli, being approximately level to the anterior margin of the P2 alveoli, or more posterior (Fig. 8). The posterior margin of the narial fossa is also displaced posteriorly, being at least posterior to the premaxillary tooth-row. This is seen in *Met. geoffroyii* (Fig. 8B) and *Cricosaurus* sp. nov. from the upper Kimmeridgian of southern Germany, with the narial fossa positioned between the PM2 and M1 alveoli (Sachs *et al.*, in review). Further displacement is observed in the Kimmeridgian-to-Tithonian *Cricosaurus* species from southern Germany, with the posterior margin becoming level to approximately the M4 alveoli in *Cricosaurus suevicus* and *C. elegans* (Fig. 8G–H). This suggests that within the German *Cricosaurus* subclade there was rapid elongation of the narial fossa. Also from southern Germany, the early Tithonian species *Rhacheosaurus gracilis* has the narial fossa positioned approximately between the P2 and M2 alveoli (Fig. 8E). The narial fossa of '*Cricosaurus*' *saltillensis* from the early

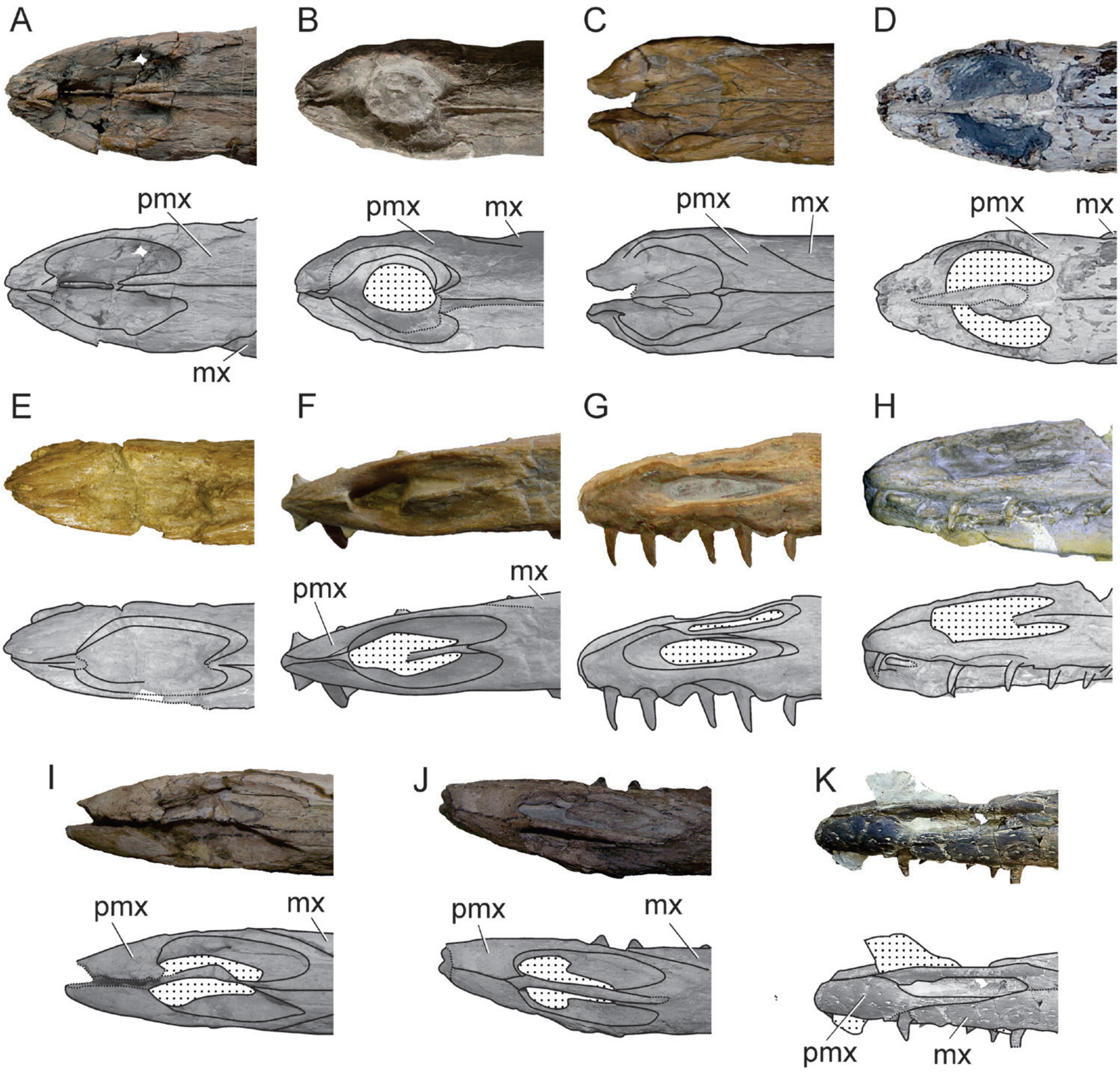

Figure 8. Comparative plate of metriorhynchine anterior cranial rostra. A, *Met. superciliosus*, referred specimen PETMG R10; B, *Met. geoffroyii*, holotype MHNG V-2232; C, *Gracilineustes leedsi*, referred specimen NHMUK PV R 3105 (holotype of '*Met.*' *laeve*); D, *Maledictosuchus riclaensis*, holotype MPZ 2001/130a; E, *Rhacheosaurus gracilis*, referred specimen NHMUK PV R 3961; F, '*Rhacheosaurus*' *gracilis*, referred specimen SMF R. 4071; G, *Cricosaurus suevicus*, lectotype SMNS 9808; H, *Cricosaurus elegans*, holotype SNSB-BSPG AS I 504; I, *Cricosaurus araucanensis*, holotype MLP 72-IV-7-1; J, *Cricosaurus* sp., referred specimen MOZ-PV 6111; K, cf. '*Cricosaurus*' *macrospondylus*, referred specimen RNGHP 990201. See text for anatomical abbreviations. Not to scale.

Tithonian of Mexico would at least have been positioned from the P2 to M2 (see: Buchy *et al.*, 2013). The narial fossae of the three Tithonian forms from Argentina, *C. lithographicus* Herrera *et al.*, 2013c, *C. araucanensis* (Gasparini & Dellapé, 1976) (Fig. 8I) and *Cricosaurus* sp. (MOZ-PV 6111) (Fig. 8J) are positioned level to the P3 and at least the M3 (Fig. 7). As such, these species have the most retracted external nares of any known Jurassic metriorhynchid.

However, in the Early Cretaceous, the most extreme posterodorsal retraction so far observed is seen in the cf. '*Cricosaurus*' *macrospondylus* referred specimen. In this specimen, the anterior margin of the narial fossa is almost level with the anterior maxilla, while

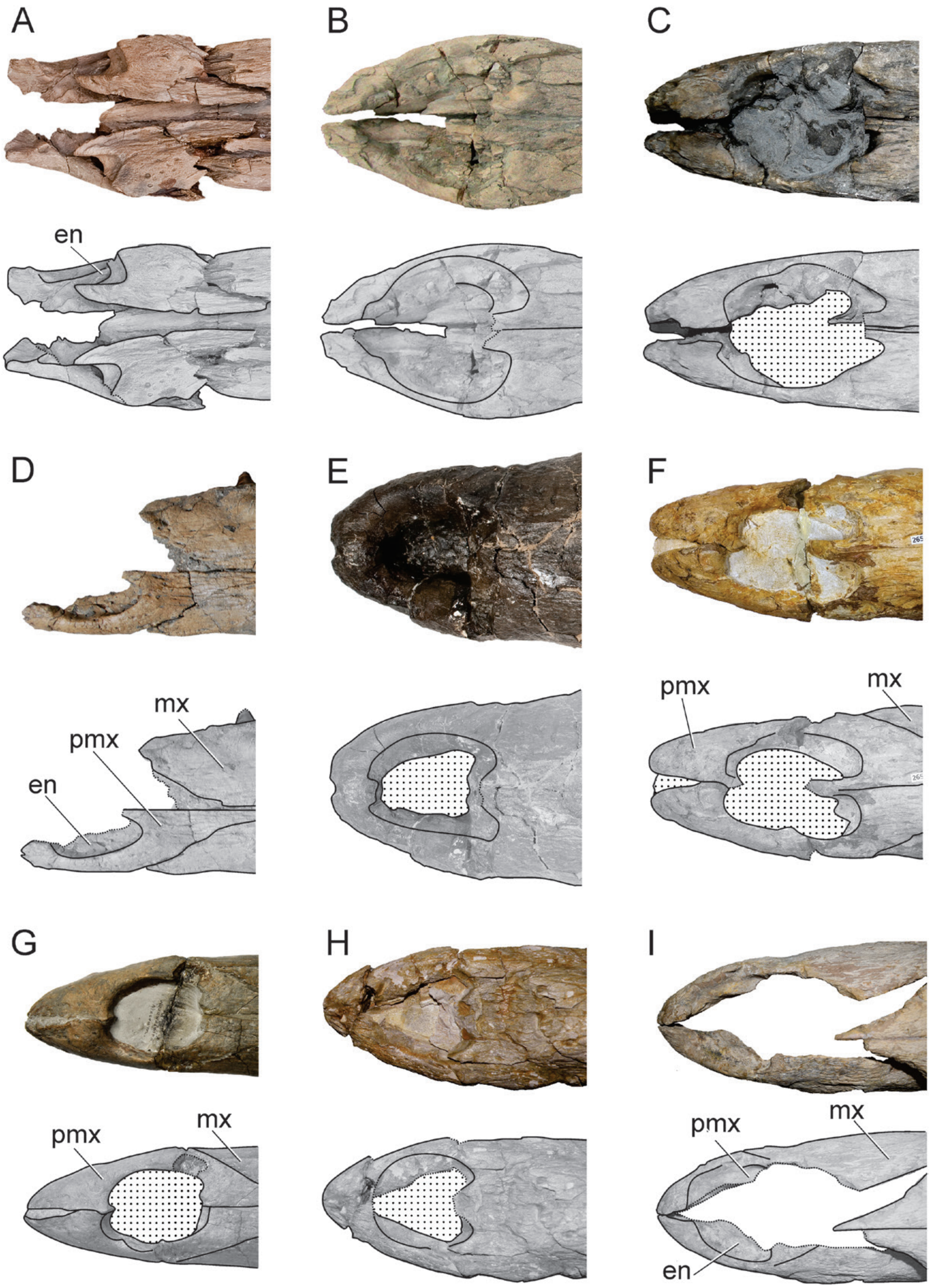

Figure 9. Comparative plate of geosaurine anterior cranial rostra. A, '*Met.*' *brachyrhynchus*, referred specimen NHMUK PV R 3804 (holotype of '*Met.*' *cultridens*); B, *Tyrannoneustes lythrodectikos*, referred specimen PETMG R176; C, undescribed geosaurine DORCM G.0114; D, *Torvoneustes carpenteri*, holotype BRSMG Ce17365; E, *Plesiosuchus manselii*, holotype NHMUK PV OR 40103; F, 'Swiss rostrum', NMO 26589; G, 'English rostrum', CAMSM J18212; H, *Geosaurus grandis*, holotype SNSB-BSPG AS VI 1; I, *Dakosaurus maximus*, neotype SMNS 8203. See text for anatomical abbreviations. Not to scale.

the posterior margin is posterior to the M6 alveoli (Hua *et al.*, 2000; Figs 7, 8K). This is the only known metriorhynchid where the narial fossa is not entirely enclosed by the premaxilla, as the posterolateral margin is partially formed by the maxilla.

As such, within Rhacheosaurini there are three occurrences of noticeable posterodorsal retraction (Fig. 7). The most extreme occurring in the unnamed '*Cricosaurus*' *saltillensis*–cf. '*C*.' *macrospondylus* subclade, another in the Tithonian *Cricosaurus* species of Argentina and the elongation seen in the Kimmeridgian-to-Tithonian *Cricosaurus* species of southern Germany.

Interestingly, there is also evidence of narial retraction in Geosaurini (Fig. 7). There is gradual retraction in an unnamed clade of geosaurins from the Kimmeridgian-to-Tithonian of Europe (the 'E-clade'; see: Abel *et al.*, 2020). One specimen, the 'Swiss rostrum', has the narial fossa positioned level to the middle of the P2 alveoli and level to the anterior margin of the M1 (Fig. 3A–C); whereas the 'English rostrum' has the narial fossa positioned posterior to the P2 and level to the anterior margin of the M1 (Fig. 3D–F). The 'Chouquet cf. *hastifer*' has the narial fossa in a similar position to these cranial rostra specimens (Lepage *et al.*, 2008), and the Passmore specimen has the anterior margin of the narial fossa almost level to the posterior margin of the P2 alveolus.

SUSTAINED SWIMMER ECOMORPHOTYPE?

While symplesiomorphically metriorhynchids had evolved extensive pelagic adaptations, such as enlarged salt exocrine glands, loss of osteoderms, modification of the forelimbs into hydrofoil-like flippers and regionalization of the caudal vertebral column, including a hypocercal tail (e.g. Fraas, 1902; Andrews, 1913; Fernández & Gasparini, 2000, 2008), posterodorsal retraction of the external nares only evolved in more derived species. Posterodorsal retraction of the external nares is observed in other pelagically adapted clades, those that include sustained swimmers [see Massare (1994) and the references therein]. The absence of this classic pelagic adaptation for most metriorhynchids fits with the known distribution of Metriorhynchidae, being most commonly found in lagoonal, coastal and shallow marine deposits (e.g. Lepage *et al.*, 2008; Sachs *et al.*, 2019a; Abel *et al.*, 2020). Contemporaneous ophthalmosaurid ichthyosaurs and plesiosaurians may have acted as a barrier to dispersal into deeper water ecosystems, and prevented metriorhynchids from occupying higher tier trophic levels. However, during the Late Jurassic there is evidence from the subboreal seaway of the UK that shallow marine ecosystems were being restructured (see: Foffa *et al.*, 2018a). This coincides with the numerical and trophic diversification of geosaurins (e.g. Young *et al.*, 2011, 2012, 2013; Young, 2014; Foffa *et al.*, 2018a, b), ichthyosaurs (e.g. Maisch & Matzke, 2000; Sander, 2000; McGowan & Motani, 2003; Moon, 2019) and plesiosaurs (e.g. Benson & Druckenmiller, 2014; Fischer *et al.*, 2017, 2018; Sachs & Kear, 2017; Sachs *et al.*, 2017, 2018; Madzia *et al.*, 2019). It is during this time-span that the first instances of posterodorsal retraction in both Rhacheosaurini and Geosaurini are known (although the backwards migration of the posterior margin had already occurred in basal metriorhynchines by the middle Callovian).

Unfortunately, we do not have enough data to test whether shifts in postcranial anatomy occured prior to the shift in narial position or vice versa, but we do have some data for the southern German *Cricosaurus* subclade. *Cricosaurus bambergensis*, the basalmost species of this subclade, retains the symplesiomorphic metriorhynchid tail fluke: (1) the posteriormost preflexural vertebra has a rod-like hemapophysis, (2) the flexural vertebrae have anteriorly oriented neural spines, but not strongly oriented anteriorly, (3) the flexural hemapophyses contact one another along their anterior–posterior margins and (4) the distalmost post-flexural hemapophyses return to a 'rod-like' morphology (see Sachs *et al.* 2019a, in review). However, the 'Solnhofen *Cricosaurus*' and *C. suevicus* share the following synapomorphies: (1) the posteriormost preflexural vertebra has a dorsoventrally deep hemapophysis with a midline flange, (2) the flexural vertebrae have strongly anteriorly oriented neural spines, (3) the flexural hemapophyses contact one another along their posteroventral–anterodorsal margins and (4) the distalmost post-flexural hemapophyses retain their dorsoventrally deep profile (i.e. they do not return to a 'rod-like' morphology; see: Sachs *et al.*, 2019a, in review). Interestingly, while both of these species share tail fluke synapomorphies, the 'Solnhofen *Cricosaurus*' had fewer vertebrae in the tail displacement unit (Sachs *et al.*, in review) and has the posterior margin of the narial fossa being approximately level to the M1 alveoli, whereas *C. suevicus* had three more vertebrae in the tail displacement unit (Sachs *et al.*, in review) and the posterior margin of the narial fossa shifted to being level to the M4 alveoli.

Therefore, a deeper and better supported tail fluke evolved prior to narial elongation (P2–M4), at least in this subclade. But this does not explain the narial position shift from P1–P3 to P2–M1 that had already occurred. Unfortunately, most metriorhynchid species are known from skull material or incomplete postcrania. Discovery of more complete fossil specimens is needed to dissect the evolution of a potential 'sustained swimmer' ecomorphotype in Metriorhynchidae.

Unique disadvantage?

We propose the hypothesis that metriorhynchids were uniquely 'disadvantaged' when retracting their external nares. Teleosauroids and basal metriorhynchoids have the external nares bound by the premaxilla, positioned anteriorly in the premaxilla and lack an internarial bar (e.g. Andrews, 1913; Pierce & Benton, 2006; Foffa *et al.*, 2019; Johnson *et al.*, 2020; Sachs *et al.*, 2019b). This is different from the semi-aquatic forms basal to the other major Mesozoic marine reptile groups. In the case of Middle Triassic sauropterygians, Early Jurassic pleurosaurids and Late Cretaceous non-hydropelvian mosasauroids, the external nares are bound by multiple bones (premaxilla, maxilla and nasals in basal sauropterygians and early pleurosaurids; premaxilla, maxilla and often the prefrontal in many mosasauroids), positioned posteriorly relative to the premaxilla and had an internarial bar (e.g. Páramo, 2000; Rieppel, 2000; Dupret, 2004; Voeten *et al.*, 2018). This highlights that metriorhynchids convergently evolved narial characters that other Mesozoic clades had 'pre-adapted' prior to their pelagic postcranial adaptations. Further retraction of the external nares occurred in Pistosauria, Late Jurassic pleurosaurids and hydropelvian mosasaurids (e.g. Páramo-Fonseca, 2000; Rieppel *et al.*, 2002; Dupret, 2004; Bardet *et al.*, 2005). In some derived plesiosaur clades, the external nares were bound by the maxilla, frontal and prefrontal (see: O'Keefe, 2008). In Late Jurassic pleurosaurids, the external nares extended posteriorly such that the prefrontals partially bound the openings (Watson, 1914; Dupret, 2004). This character suite is even found in the Cisuralian mesosaurids, where the premaxilla, septomaxilla and nasals bound the separated nares (Piñeiro *et al.*, 2012), as well as in the Triassic thalattosaurians and saurosphargids, whose retracted external nares are bound by the premaxilla, maxilla and nasals (Nicholls, 1999; Müller, 2005; Li *et al.*, 2011, 2014).

A similar shift occurs in Triassic phytosaurian archosauriforms. While phytosaurians are generally recovered from fluvial and lacustrine strata, some species are known from marine deposits [see Butler *et al.* (2019) and the references therein]. The Middle Triassic species *Diandongosuchus fuyuanensis* Li *et al.*, 2012 had the external nares bound by the premaxilla and maxilla, positioned posteriorly relative to the premaxilla and had an internarial bar formed by premaxillary and maxillary processes (Stocker *et al.*, 2017). Within Phytosauridae the posterodorsal retraction of the external nares is extreme, with the nares typically dorsal to the antorbital fenestrae. The separated nares of phytosaurids are bound by the nasals and septomaxilla or nasals, septomaxilla and paranasals (see: Hungerbühler *et al.*, 2013; Butler *et al.*, 2019).

Moreover, in the basalmost known Lower Triassic ichthyosauriforms, the external nares are separated by the nasals, bound by multiple bones and are close to the orbits (e.g. Jiang *et al.*, 2016). Narial evolution in ichthyosaurs is interesting, as during the Jurassic there is a shift from the large, oval and elongate nares of basal neoichthyosaurians to the smaller narial apertures seen in ophthalmosaurids (see: Fischer *et al.*, 2014; Campos *et al.*, 2020; and the references therein). Ophthalmosaurid narial evolution is complex, with a shift in the relative position and what bones bound the openings (ranging from the premaxilla, maxilla, lacrimals, nasals and prefrontals; for an overview see: Campos *et al.*, 2020). Furthermore, in derived platypterygiine ophthalmosaurids, each naris is divided into two openings by a nasomaxillary process, creating a complex nasal region constituting of an anterior and a posterior opening, with the premaxilla, maxilla, nasal and lacrimal all contributing to these openings (Fischer *et al.*, 2014; Campos *et al.*, 2020). The repeated subdivisions of the external nares in Ophthalmosauridae has led to the interesting hypothesis that one of these openings could be for salt exocrine gland drainage (Campos *et al.*, 2020).

One pertinent difference between metriorhynchids and other Mesozoic marine reptiles is the presence of a well-developed secondary bony palate. In metriorhynchids and non-pelagic thalattosuchians the secondary palate is formed by shelf-like processes of the premaxilla, maxilla and palatines that contact with their corresponding bone along the midline of the skull. Posteriorly, the narial airway becomes the nasopharyngeal duct, which is formed by the palatines ventrally and laterally, and the vomer dorsally and medially, until it reaches the internal nares (secondary choanae) where the pterygoid contributes dorsally. The formation of a complex secondary palate is convergent with the mammalian bony secondary palate. This raises the question: could a secondary palate make a posterior shift in the nasopharyngeal soft tissues 'harder' to achieve?

In basal cetaceans ('archaeocetes') there is no internarial bar, the external naris is positioned close to the end of the cranial rostrum and is largely bound by the premaxilla, but with the nasals forming the posteromedial border [see figures in Marx *et al.* (2016)]. The earliest example of noticeable posterodorsal retraction is in Basilosauridae (note this clade could be a paraphyletic grouping), with basal mysticetes and odontocetes retaining this relatively anteriorly positioned external naris (see: Uhen, 2007; Marx *et al.*, 2016; and the references therein). Interestingly, in sirenians the mesorostral fossa (external nares) was retracted and elongated prior to becoming obligately aquatic (see: Domning, 2001; Díaz-Berenguer *et al.*, 2018). These mammalian examples suggest that a secondary palate does not necessarily make posterodorsal narial retraction inherently more difficult to evolve. Especially as noticeable narial retraction evolved early during the semi-aquatic phase in sirenians, and within 15 million years of the cetacean land-to-sea transition (by the time the tail fluke was present).

In sum, narial retraction is yet another example of a morphofunctional complex that evolved during the land-to-sea transition. The pronounced asynchrony in metriorhynchid postcranial marine adaptations and narial retraction looks to be unique amongst secondarily marine tetrapods. It is unclear why it took approximately 5–10 Myr from the time extensive postcranial adaptations evolved (Bathonian–Callovian) to when narial retraction began (Kimmeridgian–Tithonian) and why it took another 20 Myr for the external nares to be noticeably retracted (Valanginian).

CONCLUSIONS

Although metriorhynchids evolved extensive osteological adaptations to living in a marine environment, posterodorsal retraction of the external nares is rare and only begins to occur in the Late Jurassic. Retraction of the posterior margin of the narial fossa always occurred prior to the backwards shift of the anterior margin. This change occurs at least four times in Metriorhynchidae: in metriorhynchines more derived than *Met. superciliosus*, in two Late Jurassic geosaurin genera that do no retract the anterior margin (*Dakosaurus* and *Plesiosuchus*) and in the geosaurine subclade *Torvoneustes* + 'E-clade'. However, the posterior shift in the anterior margin of the narial fossa only occurred twice: once in the clade *Met. geoffroyii* + Rhacheosaurini and also in the poorly known 'E-clade' in Geosaurini.

Only within Rhacheosaurini did noticeable narial elongation and/or retraction occur. This supports previous studies that found Rhacheosaurini species to be the best adapted to an epipelagic lifestyle (e.g. Parrilla-Bel *et al.*, 2013). Curiously, posterodorsal elongation/retraction occurred three times in Rhacheosaurini. Within at least one of these rhacheosaurin subclades a deeper and better supported tail fluke evolved prior to posterodorsal narial elongation. It hints that a 'sustained swimmer' ecomorphotype may have been evolving in Rhacheosaurini.

The level of homoplasy in narial position within Metriorhynchidae was unexpected, but given the multiple instances of dermatocranial ornamentation reduction/loss in Metriorhynchidae (e.g. Young *et al.*, 2013b; Young, 2014), the multiple instances of tooth count reduction and acquisition of contiguously serrated dentition in Geosaurini lineages (e.g. Foffa *et al.*, 2018c), as well as the parallel evolution of humeral diaphysis reduction (Young *et al.*, 2010), metriorhynchids repeatedly converged on the same morphologies. Presumably similar selection pressures were acting on the disparate lineages of metriorhynchids. Metriorhynchidae is an excellent exemplar of rampant parallel evolution, a confounding problem generally in crocodylomorph systematics, and a reminder that similar ecomorphotypes do evolve repeatedly and contemporaneously.

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SUPPORTING INFORMATION

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

Appendix S1. Character list and scoring sources for the phylogenetic analyses.
Appendix S2. Descriptive statistics and phylogenetic results.