

# Virtual reconstruction of a Late Jurassic metriorhynchid skull from Switzerland and its use for scientific illustration and paleoart

Sophie De sousa oliveira<sup>1</sup>, Léa Girard<sup>1,2</sup>, Irena Raselli<sup>3,2</sup>, Jérémy Anquetin<sup>3,2\*</sup>

<sup>1</sup> Université de Rennes 1, Géosciences, CNRS UMR 6118, 35042 Rennes, France

<sup>2</sup> Department of Geosciences, University of Fribourg, 1700 Fribourg, Switzerland

<sup>3</sup> Jurassica Museum, 2900 Porrentruy, Switzerland

\*Corresponding author: jeremy.anquetin@jurassica.ch

## Abstract

The democratization of 3D techniques in recent years provides exciting new opportunities for the study of complex fossils. In the present contribution, we provide a virtual reconstruction of a partial, disarticulated metriorhynchid (Metriorhynchidae, Thalattosuchia, Crocodylomorpha) skull from the Late Jurassic of northwestern Switzerland. This virtual reconstruction was used to produce high quality scientific illustrations of the whole skull for descriptive purposes. The reconstructed skull also served for the estimation of the total body length of the specimen and to propose a life reconstruction of the animal in its paleoenvironment. In an effort for transparency, we review the sources that were consulted for the life reconstruction and explain the choices that we had to make.

**Keywords:** Kimmeridgian, Late Jurassic, Metriorhynchidae, paleoart, Thalattosuchia

Submitted:2022-09-16, published online:2023-07-19. <https://doi.org/10.18563/journal.m3.178>

## INTRODUCTION

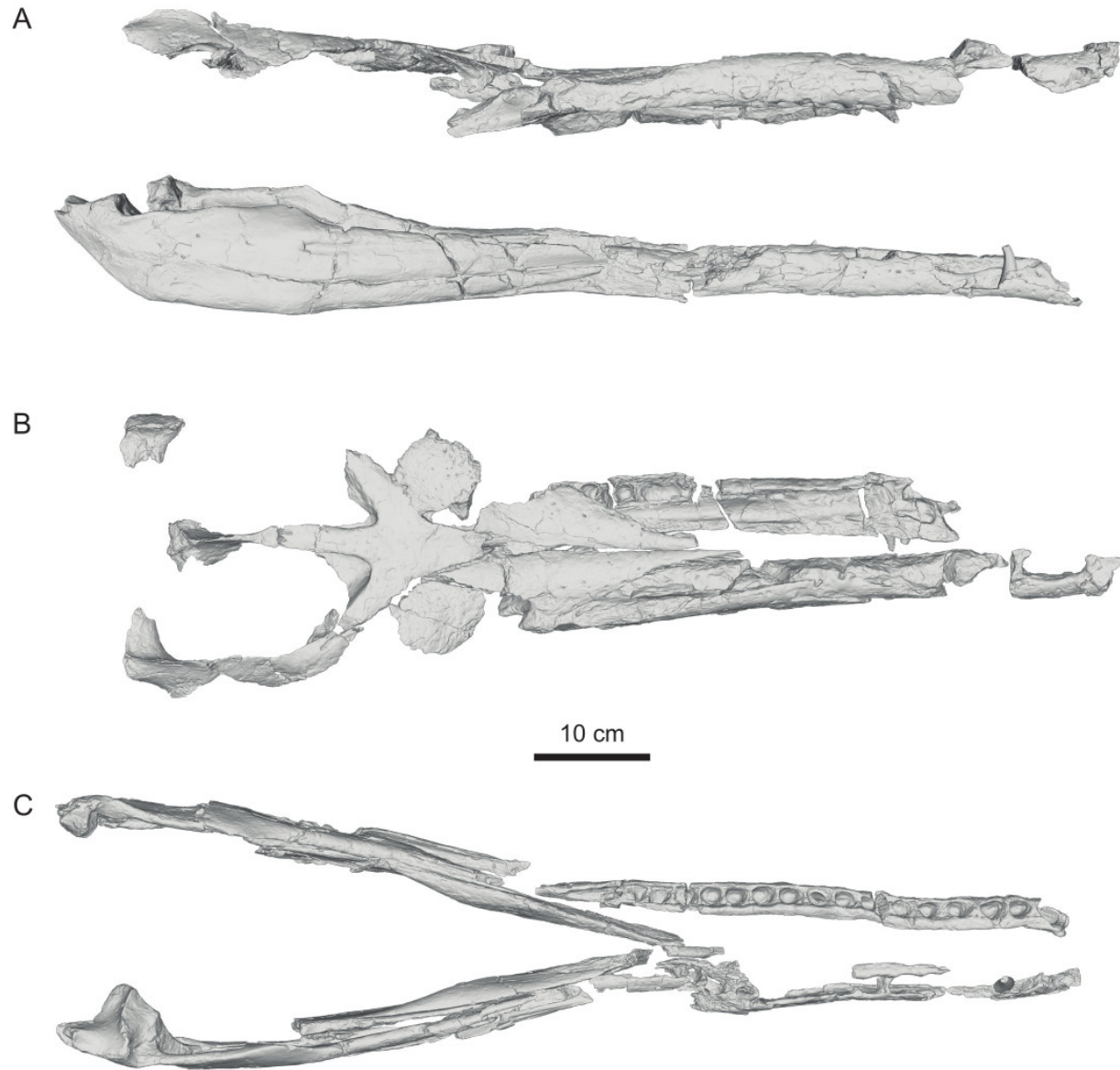
Thalattosuchia Fraas, 1901 is a clade of mainly marine crocodylomorphs that existed from the Early Jurassic to the Early Cretaceous. They are mainly represented by two subclades: the Teleosauridae Geoffroy Saint-Hilaire, 1831 and the Metriorhynchidae Fitzinger, 1843 (Young and Andrade, 2009). While teleosaurids are usually interpreted to remain close to the coast, metriorhynchids are more clearly adapted to a pelagic lifestyle. The latter thus show a variety of specialized characters such as hypertrophied salt glands, forelimbs transformed into flippers, a hypocercal tail, or the loss of osteoderms (Fraas, 1902; Andrews, 1913; Fernández and Gasparini, 2000, 2008; Young et al., 2010; Herrera et al., 2013; Sachs et al., 2019, 2021). The morphological diversity of metriorhynchids long remained underestimated. The description of new material and the efforts put on the revision of old collections in the past two decades have significantly improved our understanding of the group (Andrade et al., 2010; Young et al., 2010, 2011a, 2013, 2020, 2021; Waskow et al., 2018; Abel et al., 2020). The Metriorhynchidae are divided into two major clades: the Metriorhynchinae Lydekker, 1889, gracile fish and invertebrate feeders; and the Geosaurinae Lydekker, 1889, large bodied macrophagous predators. During the Late Jurassic, each clade sees the emergence of derived subclades, the Rhacheosaurini Young et al., 2011a and Geosaurini Cau and Fanti, 2011 respectively (Parrilla-Bel et al., 2013; Young et al., 2020). Metriorhynchines have a slender body with greatly reduced forelimbs and a skull with a long and tubular snout, a high number of small, usually uncarinated teeth, and retracted and separated external nares (Young et al., 2010; Parrilla-Bel et al., 2013). In contrast, geosaurines commonly show a large body size, more robust and shorter snouts (relative to skull length), and large bicarinated teeth. Members of Geosaurini are further

characterized by the presence of denticles on the tooth carinae, a small interalveolar space, and a skull suited for strong bite forces with the articular bone placed high above the tooth row to increase mouth gap and a strongly expressed surangular-dentary groove (Pol and Gasparini, 2009; Young and Andrade, 2009; Andrade et al., 2010; Young et al., 2012; Waskow et al., 2018). Our knowledge of metriorhynchids is hindered by the rareness of relatively complete and 3D-preserved specimens. In this study, we present the 3D reconstruction of a new partial cranium and mandible referable to *Torvoneustes jurensis*, a new geosaurine species from the Late Jurassic of Switzerland (Girard et al., 2023). The disarticulated bones were scanned individually, then reassembled virtually to facilitate the morphological description as well as the scientific illustration of the specimen. This example illustrates how increasingly available 3D techniques can be of major importance for the study of challenging fossil specimens.

## METHODS

### Context of the discovery

The specimen under study (MJSN BSY008-465) consists of a partial metriorhynchid skeleton discovered in 2008 in Courtedoux (Canton of Jura, Switzerland) during systematic excavations related to the construction of the A16 Transjurane highway (Schaefer et al., 2018). The specimen was found on a hardground (level 4000) in the Lower *Virgula* Marls, Chevenez Member, Reuchenette Formation, late Kimmeridgian (Comment et al., 2015). The specimen was initially extracted as a 3-tons block of limestone and superficially acid prepared from the top to preserve the taphonomic arrangement of the bones. Acid preparation was poorly controlled and resulted in damages on several of the more fragile bones. The specimen was finally



**Figure 1.** Virtual reconstruction of the cranium and mandible of *Torvoneustes jurensis* MJSN BSY008-465. (A), cranium and mandible in right lateral view; (B), cranium in dorsal view; (C), mandible in dorsal view. The anterior is to the right.

M3 Id	Description
M3#1037	Left dentary (3 meshes)
M3#1038	Right dentary (3 meshes)
M3#1039	Left ramus (2 meshes)
M3#1040	Right ramus (3 meshes)
M3#1041	Left splenial (2 meshes)
M3#1042	Right splenial (2 meshes)
M3#1043	Frontal and left prefrontal
M3#1044	Left maxilla (4 meshes)
M3#1045	Right maxilla
M3#1046	Left nasal
M3#1047	Right nasal
M3#1048	Parietal
M3#1049	Right postorbital
M3#1050	Right prefrontal
M3#1051	Right premaxilla
M3#1052	Left squamosal
M3#1053	Right squamosal
M3#1054	Reconstruction of the mandible
M3#1055	Reconstruction of the cranium

**Table 1.** List of models derived from the cranium and mandible of *Torvoneustes jurensis* MJSN BSY008-465. Collection : Jurassica Museum.

fully extracted from the rock in 2018 to facilitate both its curation and its study. MJSN BSY008-465 consists of a partial and disarticulated skull for a total of 29 identifiable cranial and mandibular elements, 15 isolated teeth, an incomplete series of vertebrae, a few ribs, as well as elements of the pelvis and limbs. A complete description of this material is given in Girard et al. (2023).

### 3D acquisition

The 29 identifiable cranial and mandibular elements were scanned individually with an Artec Space Spider structured light surface scanner (Artec Group, Inc). This type of scanner allows a resolution of up to 0.1 mm. Each element was placed on a turntable and scanned from multiple angles, keeping a good overlap between each scan. Scan acquisition and post-processing was made with the dedicated software Artec Studio 13 (Artec Group, Inc). Post-processing consisted in background removal, scan alignment, global registration, outlier removal, mesh computation, mesh simplification (with highest accuracy settings), and finally texturing. The 29 surface meshes are provided as .PLY files associated with .PNG texture files (Table 1). They can be opened with a wide range of freeware.

### Virtual reconstruction of the skull

The 3D meshes of 29 identifiable cranial and mandibular elements were imported into Blender 2.8 (available at <https://www.blender.org>) and virtually reassembled by hand. The operator (SDSO) had access to the physical material to check contacts during the process. When contacts or other evidence such as symmetry were absent, the position of the elements was reconstructed based on the published literature (Andrews, 1913; Wilkinson et al., 2008; Andrade et al., 2010; Young et al., 2013; Waskow et al., 2018). It should be noted that some elements

of the skull have undergone a certain degree of deformation. Hence, the skull roof appears more flattened than it should be (Figure 1A). The anterior part of the left maxilla is twisted counterclockwise in the transverse axis so that the few teeth remaining in place are now pointing strongly lingually (Figure 1B). Finally, the two halves of the mandible could not be properly reassembled at the symphysis level (Figure 1C). The reconstructed surface models of the cranium and mandible of MJSN BSY008-465 are provided as .PLY files (Table 1). They should remain correctly aligned one relative to the other when opened together (checked with MeshLab).

### Abbreviations

BMMS, Bürgermeister-Müller-Museum Solnhofen, Germany; DMA, Dinosaurier Museum Altmühltal, Denkendorf, Germany; MJSN, Jurassica Museum (formerly Musée Jurassien des Sciences Naturelles), Porrentruy, Switzerland; NHMUK, Natural History Museum, London, UK; NKMB, Naturkunde-Museum, Bamberg, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

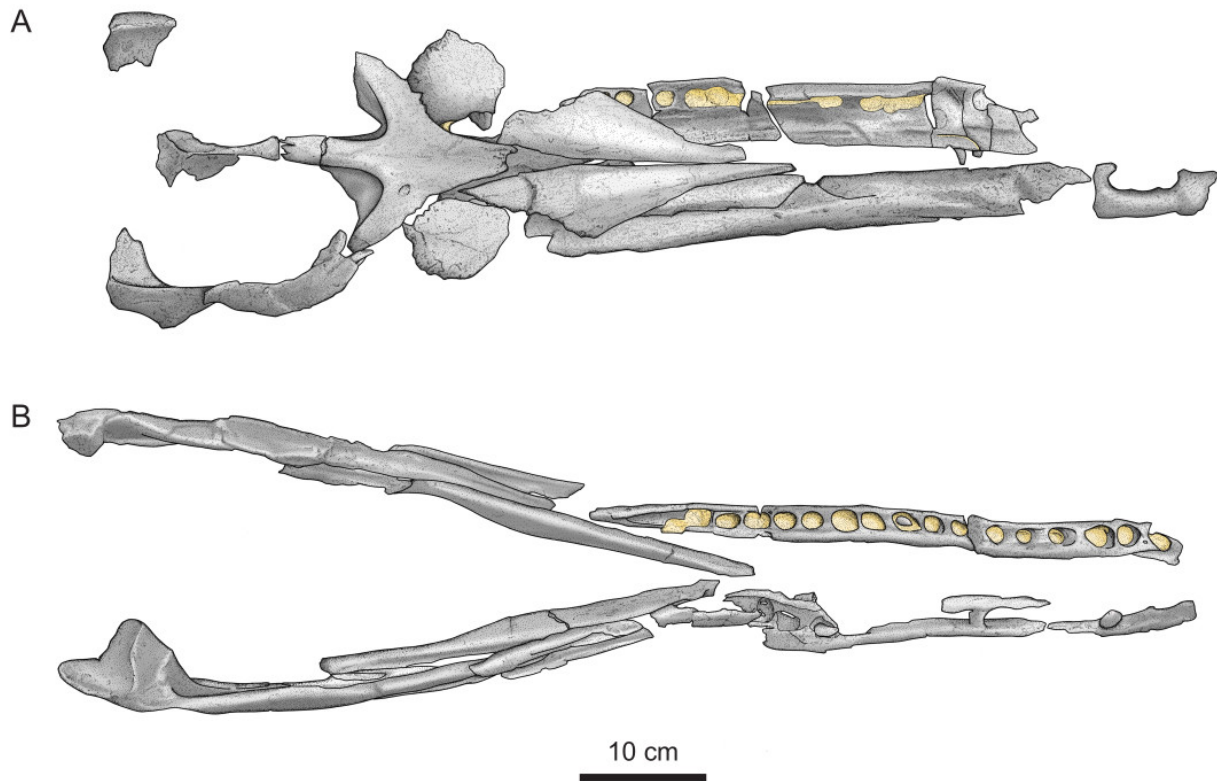
## RESULTS

### Scientific illustrations of the reconstructed skull

The virtual reconstruction of the cranium and mandible of MJSN BSY008-465 greatly facilitated the description and interpretation of the specimen (Girard et al., 2023). It also allowed to produce high quality scientific illustrations of the material for publication. Orthographic views of the cranium and mandible in right lateral and dorsal aspects were extracted from the Blender project. They were used as the basis for the scientific illustrations of the reconstructed skull. These views were imported into Procreate 5.1.6 (on a standard iPad running iPadOS 14) on a 300-dpi A3 canvas in order to obtain a final illustration at 600 dpi in A4 format. The contours and major features (sutures, fractures, foramina, etc.) were first drawn based on these orthographic views. Then the texture and shading (dots and shades of gray) were added based on direct observation of the fossils by the artist (SDSO). Examples of the final illustrations are shown in Figure 2.

### Body length estimation

The body proportions of metriorhynchids depart from those of other crocodylomorphs. Their skull is comparatively longer, whereas their limbs are reduced (Andrews, 1913). Estimating the body size of incomplete metriorhynchids is therefore challenging. Traditional methods to estimate body length in fossil crocodylomorphs rely on regression equations of cranial length-to-total body length (CL-TL) and femur length-to-total body length (FL-TL) in extant species (Sereno et al., 2001; Wu et al., 2001; Farlow et al., 2005). However, it was shown that metriorhynchids do not scale with extant species when body length is regressed against cranial or femoral lengths (Young et al., 2011b). In the same study, Young et al. (2011b) proposed regression equations for metriorhynchids based on measurements in four metriorhynchines and one geosaurine ( $y = 5.506x - 8.162$  for CL-TL;  $y = 12.693x + 25.817$  for FL-TL). These equations



**Figure 2.** Scientific illustrations of the reconstructed cranium and mandible of *Torvoneustes jurensis* MJSN BSY008-465. (A), cranium in dorsal view; (B), mandible in dorsal view. The anterior is to the right. Matrix infill is represented in yellow. Artwork by SDSO.

give diverging body length estimates for MJSN BSY008-465 (Table 2). However, it should be noted that the only available femur of this specimen is missing most of its proximal head (Girard et al., 2023). Hence, the FL-TL estimate is largely underestimated here. A comparison with the femora of the closely related late Kimmeridgian *Torvoneustes carpenteri* (see Wilkinson et al., 2008) suggests that the femur of MJSN BSY008-465 was at least three to five centimeters longer than its present condition, which would give total body length estimates of around 375–400 cm. In order to refine body length estimation for MJSN BSY008-465, we have also experimented a more empirical approach. For this, we extrapolated the total body length from a reconstruction of the axial skeleton for our specimen and measurements of the preserved vertebrae per region of the axial skeleton. Only 22 vertebrae (three cervicals, nine dorsal, and 10 caudals) are known for MJSN BSY008-465, but the total number of vertebrae can be estimated based on available complete metriorhynchid skeletons. There are usually five postaxis cervical, at least 18 dorsal, and two sacral vertebrae (Table 3). A variation in the number of caudal vertebrae is observable in these species ranging from 44 in *Cricosaurus suevicus* (Fraas, 1902), maybe a bit less in *Cricosaurus albersdoerferi* (Sachs et al., 2021), to possibly up to 60 in *Dakosaurus* sp. (Spindler F., pers. comm.). However, since *Torvoneustes* is phylogenetically closer to *Dakosaurus* than any other taxon, it is reasonable to consider that MJSN BSY008-465 had more than 50 caudal vertebrae. Based on this and the measurements of the preserved vertebrae, the total body length of MJSN BSY008-465 can be

Proxy	Proxy length (cm)	Estimated body length (cm)
Cranium	80.8	436.7
Femur (not complete)	24.4	335.5
Empirical reconstruction*	-	385-400

**Table 2.** Body size estimates for specimen MJSN BSY008-465 based on CL-TL and FL-TL regression equations (Young et al., 2011b) and the empirical reconstruction of the axial skeleton (\* see text).

estimated to around 385–400 cm (Figure 3). Since this body length estimate is both relatively congruent with the two obtained from the regression equations of Young et al. (2011b) (when the femur length is corrected) and conservative, this is the one that we retained for the life reconstruction (see below).

### Life reconstruction of the specimen

The morphology and proportions of the head were directly derived from the virtual reconstruction presented herein (see above). *Torvoneustes carpenteri* and *Torvoneustes coryphaeus*, two closely related species, were also taken into consideration based on the available literature (Grange and Benton, 1996; Wilkinson et al., 2008; Young et al., 2013). From the virtual reconstruction of the skull, it appears that the upper and lower teeth are alternated without occlusion and that they do not protrude from the jaws laterally. This corresponds to the condition observable in *Torvoneustes mexicanus* (Barrientos-Lara et al., 2016). The right femur and fibula of MJSN BSY008-465 are



Taxon	postaxis vertebrae	dorsal vertebrae	sacral vertebrae	caudal vertebrae	Sources
Geosaurinae					
<i>Dakosaurus</i> sp.	4/5	19/20	2	>50 (possibly up to 60)	DMA-JP-2009/001 (Spindler F., pers. comm.)
Metriorhynchinae					
<i>Cricosaurus bambergensis</i>	5	18	2	54	NKMB-P-Watt14/274 (Sachs et al., 2019)
<i>Cricosaurus suevicus</i>	5	18	2	44	SMNS 9808 (Fraas, 1902)
<i>Rhacheosaurus gracilis</i>	?	19	2	50	NHMUK R.3948 (Andrews, 1913)

**Table 3.** Number of vertebrae per region of the axial skeleton in selected complete metriorhynchid specimens.

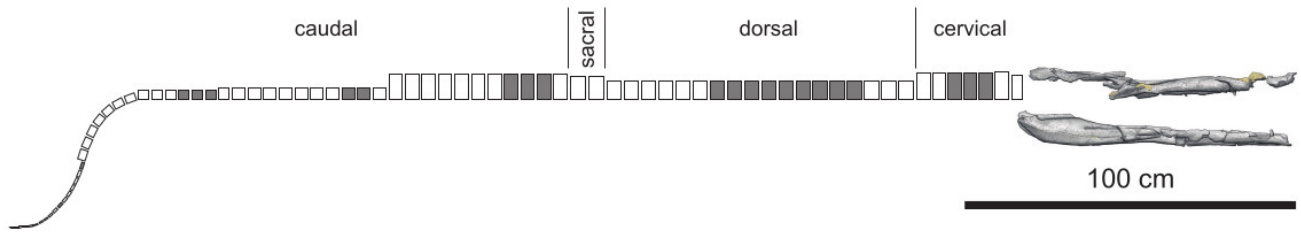
preserved (Girard et al., 2023), which gives a good idea of the size of the hindlimbs in this specimen. The missing proximal head of the femur was taken into account for limb size estimates. The length of the humerus in our specimen was estimated thanks to the humerus/femur ratio in *Torvoneustes carpenteri* (Wilkinson et al., 2008). The more distal parts of the fore- and hindlimbs were drawn based notably on *Dakosaurus* sp. DMA-JP-2009/001, an exquisitely preserved specimen from the Late Jurassic limestones of Painten (Germany) currently under formal description (Spindler F., pers. comm.), and *Cricosaurus bambergensis* NKMB-P-Watt14/274 (Sachs et al., 2019). The rare complete articulated skeletons reveal that metriorhynchids had a long and slender body (e.g., *Rhacheosaurus gracilis* NHMUK R.3948, *Cricosaurus suevicus* SMNS 9808, *Cricosaurus bambergensis* NKMB-P-Watt14/274, *Cricosaurus albersdoerferi* BMMS-BK 1–2, *Dakosaurus* sp. DMA-JP-2009/001). The tail is usually about as long as the rest of the body and the size of the caudal vertebrae indicates that it remains relatively thick for the first three quarters of its length, as noted by Fraas (1902) on *Cricosaurus suevicus* SMNS 9808. The position and angle of the tail bend have been variably represented by paleoartists. The bend is often positioned too anteriorly, whereas the angle is sometimes too great (more than 45° from the horizontal plane). Similarly, the upper lobe of the tail fluke is often represented as much developed as the lower lobe. This is in contradiction with currently available specimens (e.g., *Rhacheosaurus gracilis* NHMUK R.3948), which tend to have a tail bend located in the last quarter of the tail forming an angle of less than 45° and a moderately developed upper lobe representing less than half of the lower lobe (Andrews, 1913; Sachs et al., 2019, 2021; Spindler et al., 2021). It was proposed early on that metriorhynchids had a smooth skin instead of the typical scaly integument of reptiles (e.g., Fraas, 1901, 1902). However, fossilized evidence was missing and the closely related teleosaurids were known to have scales (Westphal, 1962). As a result, metriorhynchids were sometimes represented with a smooth skin and sometimes with scales. However, Spindler et al. (2021) recently described soft-tissue preservation in several Late Jurassic metriorhynchids from Painten and Wattendorf, Germany. They showed that metriorhynchids had a uniform

type of smooth and flexible skin reinforced by straight, mostly transverse fibers. The metriorhynchid skin is therefore convergent with that of ichthyosaurs and plesiosaurs. In contrast, teleosaurids had a scaly integument similar to that of modern crocodiles (Spindler et al., 2021).

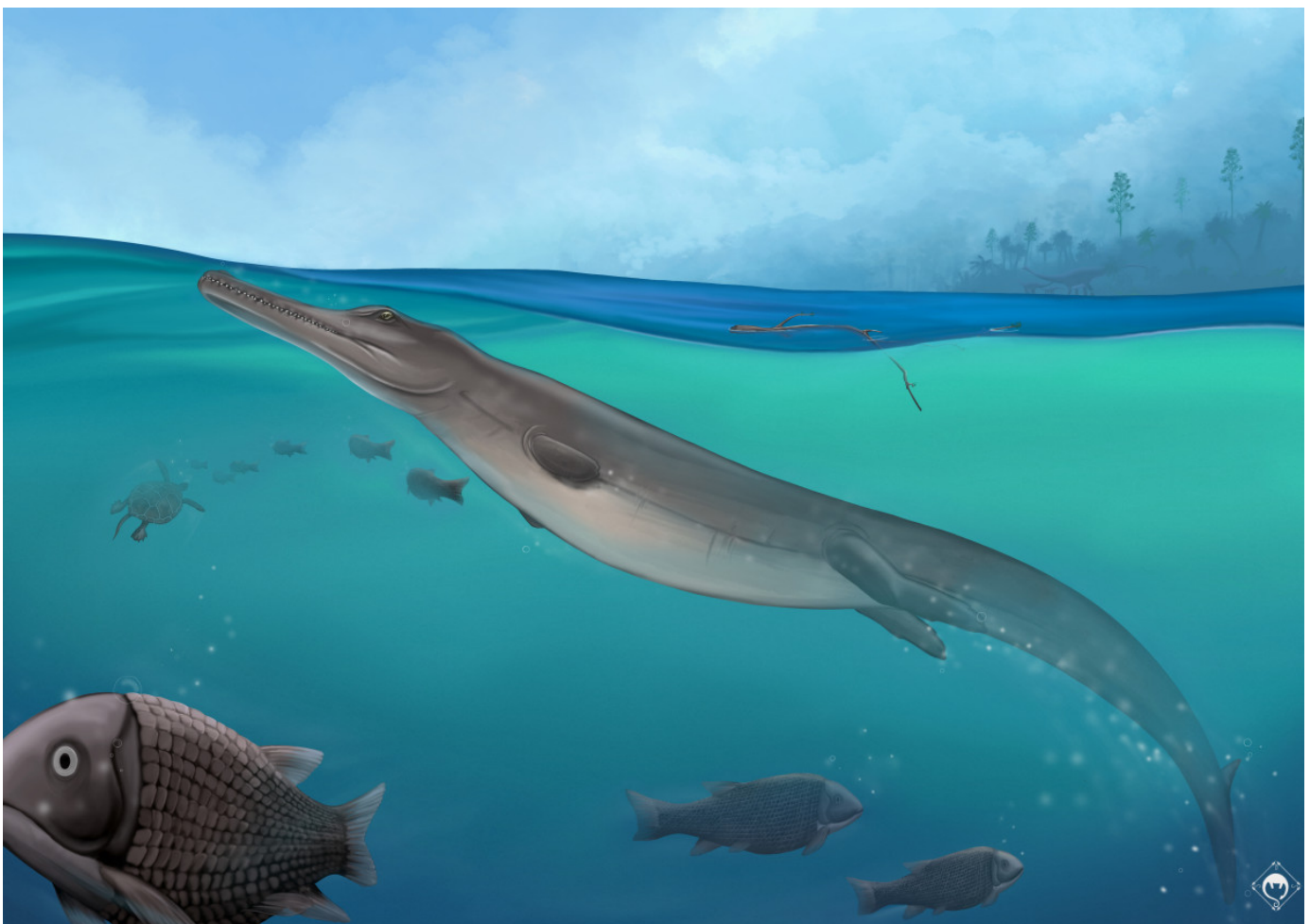
Several other important aspects of the external appearance were also considered to produce the final life reconstruction of MJSN BSY008-465 (Figure 4). Metriorhynchids are often represented with a high degree of dorsoventral flexion of their axial skeleton. Yet, this is not consistent with the morphology of their vertebrae. Propulsion in metriorhynchids was probably ensured by lateral undulation of their body and tail (Massare, 1988). We therefore opted for a less dynamic posture in our reconstruction. The presence of extraoral tissues (lips) must be considered for animals that became so profoundly adapted to a pelagic lifestyle like metriorhynchids (Witton, 2018). The number of foramina on the premaxilla, maxilla and dentary can be used as a proxy to determine the type of extraoral tissue in fossil amniotes (Morhardt, 2009). More specifically, animals with lips or cheeks tend to have few foramina on their jaw bones, whereas the absence of extraoral flexible tissues is usually marked by a high density of foramina (typically more than 50 per bones). On MJSN BSY008-465, we counted close to 50 foramina on the maxilla and dentary despite the imperfect preservation of these bones. This would suggest that this specimen lacked extraoral tissues. We also checked this condition on several teleosaurids (e.g., "*Steneosaurus*" sp., MJSN TCH006-1439) from the same stratigraphical layer (Schaefer et al., 2018). They consistently have more than 50 foramina on the maxilla and dentary and, therefore, also lacked extraoral tissues according to Morhardt (2009).

### Reconstruction of the environment

Most of the elements of the partial skeleton MJSN BSY008-465 were found in close association on a 2.5 m<sup>2</sup> area (Girard et al., 2023). Except for the forelimbs, elements of all regions of the skeleton are known. This strongly suggests that the specimen came to rest on the sea bottom very close to its place of death, and, by extension, that this pelagic animal occasionally visited the moderately shallow paleoenvironment represented



**Figure 3.** Tentative reconstruction of the axial skeleton of MJSN BSY008-465 based on the estimated vertebral count and on the measurements of known vertebrae (in gray). Note that the position of the preserved vertebrae in the reconstruction is speculative.



**Figure 4.** Life reconstruction of *Torvoneustes jurensis* MJSN BSY008-465 in its paleoenvironment. Artwork by SDSO.

by the Lower *Virgula* Marls (see above; Comment et al., 2015). Therefore, it was decided to represent our specimen in this paleoenvironment rather than in open sea, in contrast to many other metriorhynchid life reconstructions. The fact that metriorhynchids commonly visited shallow, coastal environments is further substantiated by their presence in several localities of the Solnhofen Archipelago (e.g., Arratia et al., 2015). Teeth of hybodont sharks and of the lepisosteiforme fish *Scheenstia* were found associated the metriorhynchid skeleton MJSN BSY008-465. These are common representatives of the Lower *Virgula* Marls vertebrate fauna (Leuzinger et al., 2017a, 2017b). Several *Scheenstia* were represented in the reconstruction (Figure 4). Coastal marine turtles (Thalassochelydia) are also iconic representatives of the Lower *Virgula* Marls vertebrate fauna (Püntener et al., 2017). One in particular, *Thalassemys bruntrutana* (MJSN SCR011-87), was found in the same stratigraphical horizon as the metriorhynchid skeleton MJSN BSY008-465 and is represented by a relatively complete carapace and plastron (Püntener et al., 2015). A recently referred specimen from Wattendorf (Germany) provided additional insights into the shell outline and flipper morphology of this turtle (Joyce et al., 2021) permitting the inclusion of this turtle in the reconstruction (Figure 4). In addition to their richness in marine vertebrates, the Lower *Virgula* Marls are also remarkable for the number of floated wood remains that they contain, including pieces of trunk and ramified branches (Püntener and Billon-Bruyat, 2017). Most, if not all, of these remains can be referred to the extinct conifer *Protocupressinoxylon purbeckensis* (Philippe et al., 2010). The fact that many wood remains correspond to elongate, slender ramified branches devoid of epibionts suggests that they were not transported for a long time. A floating branch is represented in the proposed reconstruction (Figure 4). This element was drawn based on one of the best preserved sample in the collection (MJSN SCR008-45). The closeness of emerged land is evoked with the presence of an island in the background with silhouettes of the 20-m tall *Protocupressinoxylon purbeckensis* (Figure 4). Only a few meters below the Lower *Virgula* Marls are several layers of dinosaur track bearing laminites that produced more than 14,000 documented tracks (Marty et al., 2007, 2018; Razzolini et al., 2017; Castanera et al., 2018). Parallel sauropod trackways formed by individuals of different size, including young ones, are relatively common and seem to suggest a gregarious behavior (Paratte et al., 2019). At a larger scale, multiple dinosaur tracksites are known in the Late Jurassic of the Jura Mountains, which indicate that large dinosaurs either lived or at least travelled through the emerged lands of the Jura carbonate platform at that time. A small group of diplodocid sauropod dinosaurs was represented on the background of the reconstruction to evoke this phenomenon (Figure 4).

## CONCLUSION

Apart from rare exceptionally preserved specimens from plattenkalk localities (e.g., Sachs et al., 2019, 2021; Spindler et al., 2021), metriorhynchids are often represented by incomplete, flattened material. In this context, the associated skeleton MJSN BSY008-465 is an important specimen despite the disarticulated

state of its skull (Girard et al., 2023). We used increasingly available 3D techniques to produce 3D models of all identifiable elements of the skull and to reconstruct the cranium and mandible of the specimen virtually. The virtual reconstruction of the cranium and mandible of MJSN BSY008-465 was determinant to many aspects of the study of this specimen. The fragility of the material and absence of many contacts prevent the mounting of the cranium and mandible for description, photography, and illustration. The virtual model can be manipulated easily and greatly facilitated the description of the material (Girard et al., 2023). It was also used to produce high quality scientific drawings (Figure 2), to estimate the total body length of the specimen, and to propose a life reconstruction of the animal in its environment (Figure 4). This is yet another example of the added value of 3D data for paleontology. In the near future, the virtual and life reconstructions of the metriorhynchid MJSN BSY008-465 will also be used for public outreach purposes at the Jurassica Museum (MJSN). Life reconstructions of extinct organisms are, by definition, all flawed. This is primarily due to fossil incompleteness, but also to the misconceptions or preconceived ideas of scientists and paleoartists. Unfortunately, the chance is rarely given to the latter to explain their published life reconstructions. In the present contribution, we have tried to be as transparent as possible about the sources that were used and the choices that we had to make for the proposed life reconstruction of *Torvoneustes jurensis* MJSN BSY008-465 (Figure 4). Considering the composite nature of a life reconstruction in paleoart, where science-based interpretation and artistic vision seemingly merge, we would like to encourage future works to transparently distinguish between these two components. Similar to the distinction between results and interpretation in a scientific study, the separation between science-based interpretation and artistic vision enables a considerable degree of reproducibility and reduces the risk of wrong conclusions. Thus, we think that including a section with a clear statement on study-based information and reasoning behind the artistic choices in a published life reconstruction will not only add scientific value to the reconstruction, but also clarify its adaptability for closely related studies.

## ACKNOWLEDGEMENTS

We are grateful to Renaud Roch and Patrick Röschli (Jurassica Museum) for their help with fossil preparation and illustration techniques respectively. Frederik Spindler (Dinosaurier Museum Altmühltal) kindly provided information about the vertebral count in *Dakosaurus* sp. DMA-JP-2009/001. SDSO and LG were supported by a grant from the Swiss-European Mobility Programme (University of Fribourg). This work was funded by a grant from the Swiss National Science Foundation (SNF 205321\_175978) to JA and IR. The Paleontology A16 project was funded by the Federal Roads Office (FEDRO, 95%) and the Republic and Canton of Jura (RCJU, 5%). Finally, the authors would like to thank Frederik Spindler and Sven Sachs for their comments on an earlier version of this work.



## BIBLIOGRAPHY

- Abel, P., S. Sachs, and M. T. Young. 2020. Metriorhynchid crocodylomorphs from the lower Kimmeridgian of Southern Germany: evidence for a new large-bodied geosaurin lineage in Europe. *Alcheringa: An Australasian Journal of Palaeontology*, 44:312–326. <https://doi.org/10.1080/03115518.2019.1701079>
- Andrade, M. B., M. T. Young, J. B. Desojo, and S. L. Brusatte. 2010. The evolution of extreme hypercarnivory in Metriorhynchidae (Mesoeucrocodylia: Thalattosuchia) based on evidence from microscopic denticle morphology. *Journal of Vertebrate Paleontology*, 30:1451–1465. <https://doi.org/10.1080/02724634.2010.501442>
- Andrews, C. W. 1913. *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay, Part II*. British Museum (Natural History), London, 206 p.
- Arratia, G., H.-P. Schultze, H. Tischlinger, and G. Viohl. 2015. Solnhofen. Ein Fenster in Die Jurazeit. Verlag Dr. Friedrich Pfeil, München, 620 p.
- Barrientos-Lara, J. I., Y. Herrera, M. S. Fernández, and J. Alvarado-Ortega. 2016. Occurrence of *Torvoneustes* (Crocodylomorpha, Metriorhynchidae) in marine Jurassic deposits of Oaxaca, Mexico. *Revista Brasileira de Paleontologia*, 19:415–424. <https://doi.org/10.4072/rbp.2016.3.07>
- Castanera, D., M. Belvedere, D. Marty, G. Paratte, M. Lapaire-Cattin, C. Lovis, and C. A. Meyer. 2018. A walk in the maze: variation in Late Jurassic tridactyl dinosaur tracks from the Swiss Jura Mountains (NW Switzerland). *PeerJ*, 6:e4579. <https://doi.org/10.7717/peerj.4579>
- Cau, A., and F. Fanti. 2011. The oldest known metriorhynchid crocodylian from the Middle Jurassic of North-eastern Italy: *Neptunidraco ammoniticus* gen. et sp. nov. *Gondwana Research*, 19:550–565. <https://doi.org/10.1016/j.gr.2010.07.007>
- Comment, G., A. Lefort, J. Koppka, and P. Hantzpergue. 2015. Le Kimméridgien d’Ajoie (Jura, Suisse) : lithostratigraphie et biostratigraphie de la Formation de Reuchenette. *Revue de Paléobiologie*, 34:161–194. <https://doi.org/10.5281/zenodo.34341>
- Farlow, J. O., G. R. Hurlburt, R. M. Elsey, A. R. C. Britton, and W. Langston. 2005. Femoral dimensions and body size of *Alligator mississippiensis*: estimating the size of extinct mesoeucrocodylians. *Journal of Vertebrate Paleontology*, 25:354–369. [https://doi.org/10.1671/0272-4634\(2005\)025\[0354:FDABSO\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0354:FDABSO]2.0.CO;2)
- Fernández, M., and Z. Gasparini. 2000. Salt glands in a Tithonian metriorhynchid crocodyliform and their physiological significance. *Lethaia*, 33:269–276. <https://doi.org/10.1080/00241600750053835>
- Fernández, M., and Z. Gasparini. 2008. Salt glands in the Jurassic metriorhynchid *Geosaurus*: implications for the evolution of osmoregulation in Mesozoic marine crocodyliforms. *Naturwissenschaften*, 95:79–84. <https://doi.org/10.1007/s00114-007-0296-1>
- Fitzinger, L. J. F. J. 1843. *Systema Reptilium. Fasciculus Primus, Amblyglossae*. Braumüller et Seidel, Vienna, 134 p. <https://doi.org/10.5962/bhl.title.4694>
- Fraas, E. 1901. Die Meerkrokodile (Thalattosuchia n. g.) eine neue Sauriergruppe der Juraformation. *Ahreshefte Des Vereins Für Vaterländische Naturkunde in Württemberg*, 57:409–418.
- Fraas, E. 1902. Die Meer-Crocodilier (Thalattosuchia) des oberen Jura unter specieller Berücksichtigung von *Dacosaurus* und *Geosaurus*. *Palaeontographica*, 49:1–72.
- Geoffroy Saint-Hilaire, É. 1831. *Recherches Sur de Grands Sauriens Trouvés à l’état Fossile Aux Confins Maritimes de La Basse-Normandie, Attribués d’abord Au Crocodile, Puis Déterminés Sous Les Noms de Teleosaurus et Steneosaurus*. Firmin Didot, Paris, 138 p.
- Girard, L., S. De sousa oliveira, I. Raselli, J. E. Martin, and J. Anquetin. 2023. Description and phylogenetic relationships of a new specimen of Metriorhynchidae (Crocodylomorpha, Thalattosuchia) from the Kimmeridgian of Switzerland. *PeerJ*. <https://doi.org/10.7717/peerj.15512>
- Grange, D. R., and M. J. Benton. 1996. Kimmeridgian metriorhynchid crocodiles from England. *Palaeontology*, 39: 497–514.
- Herrera, Y., M. S. Fernández, and Z. Gasparini. 2013. Postcranial skeleton of *Cricosaurus araucanensis* (Crocodyliformes: Thalattosuchia): morphology and palaeobiological insights. *Alcheringa: An Australasian Journal of Palaeontology*, 37: 285–298. <https://doi.org/10.1080/03115518.2013.743709>
- Joyce, W. G., M. Mäuser, and S. W. Evers. 2021. Two turtles with soft tissue preservation from the platy limestones of Germany provide evidence for marine flipper adaptations in Late Jurassic thalassochelydians. *PLOS ONE*, 16:e0252355. <https://doi.org/10.1371/journal.pone.0252355>
- Leuzinger, L., C. Püntener, and J.-P. Billon-Bruyat. 2017a. *Vertébrés Mésozoïques – Poissons*. Office de la culture, Paléontologie A16, Porrentruy, 250 p.
- Leuzinger, L., G. Cuny, E. Popov, and J.-P. Billon-Bruyat. 2017b. A new chondrichthyan fauna from the Late Jurassic of the Swiss Jura (Kimmeridgian) dominated by hybodonts, chimaeroids and guitarfishes. *Papers in Palaeontology*, 3:471–511. <https://doi.org/10.1002/spp2.1085>
- Lydekker, R. 1889. On the remains and affinities of five genera of Mesozoic reptiles. *Quarterly Journal of the Geological Society*, 45:41–59. <https://doi.org/10.1144/GSL.JGS.1889.045.01-04.04>
- Marty, D., J. Ayer, D. Becker, J.-P. Berger, J.-P. Billon-Bruyat, L. Braillard, W. A. Hug, and C. A. Meyer. 2007. Late Jurassic dinosaur tracksites of the Transjurane highway (Canton Jura, NW Switzerland): overview and measures for their protection and valorisation. *Swiss Bulletin Für Angewandte Geologie*, 12:75–89.
- Marty, D., M. Belvedere, N. L. Razzolini, M. G. Lockley, G. Paratte, M. Cattin, C. Lovis, and C. A. Meyer. 2018. The tracks of giant theropods (*Jurabrontes curtedulensis* ichnogen.



- & ichnosp. nov.) from the Late Jurassic of NW Switzerland: palaeoecological & palaeogeographical implications. *Historical Biology*, 30:928–956. <https://doi.org/10.1080/08912963.2017.1324438>
- Massare, J. A. 1988. Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. *Paleobiology*, 14:187–205. <https://doi.org/10.1017/S009483730001191X>
- Morhardt, A. C. 2009. Dinosaur smiles: do the texture and morphology of the premaxilla, maxilla, and dentary bones of sauropsids provide osteological correlates for inferring extra-oral structures reliably in dinosaurs? Master Thesis, Western Illinois University, Macomb, Illinois, USA, 55 p.
- Paratte, G., V. Friedli, and G. Comment. 2019. PaléOdyssée : 20 Ans de Recherches Au Fil de La Transjurane. Office de la culture et Société jurassienne d'émulation, Porrentruy, Switzerland, p.
- Parrilla-Bel, J., M. T. Young, M. Moreno-Azanza, and J. I. Canudo. 2013. The first metriorhynchid crocodylomorph from the Middle Jurassic of Spain, with implications for evolution of the subclade Rhacheosaurini. *PLoS ONE*, 8:e54275. <https://doi.org/10.1371/journal.pone.0054275>
- Philippe, M., J.-P. Billon-Bruyat, J. C. Garcia-Ramos, L. Bocat, B. Gomez, and L. Piñuela. 2010. New occurrences of the wood *Protocupressinoxylon purbeckensis* Francis: Implications for terrestrial biomes in southwestern Europe at the Jurassic/Cretaceous boundary. *Palaeontology*, 53:201–214. <https://doi.org/10.1111/j.1475-4983.2009.00926.x>
- Pol, D., and Z. Gasparini. 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Palaeontology*, 7:163–197. <https://doi.org/10.1017/S1477201908002605>
- Püntener, C., and J.-P. Billon-Bruyat. 2017. Plantes Mésozoïques – Bois. Office de la culture, Paléontologie A16, Porrentruy, 90 p.
- Püntener, C., J. Anquetin, and J.-P. Billon-Bruyat. 2015. *Thalassemys bruntrutana* n. sp., a new coastal marine turtle from the Late Jurassic of Porrentruy (Switzerland), and the paleobiogeography of the Thalassemyidae. *PeerJ*, 3:e1282. <https://doi.org/10.7717/peerj.1282>
- Püntener, C., J. Anquetin, and J.-P. Billon-Bruyat. 2017. Vertébrés mésozoïques – Tortues. Office de la culture, Paléontologie A16, Porrentruy, 358 p.
- Razzolini, N. L., M. Belvedere, D. Marty, G. Paratte, C. Lovis, M. Cattin, and C. A. Meyer. 2017. *Megalosauripus transjuranicus* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland and implications for tridactyl dinosaur ichnology and ichnotaxonomy. *PLOS ONE*, 12:e0180289. <https://doi.org/10.1371/journal.pone.0180289>
- Sachs, S., M. Young, P. Abel, and H. Mallison. 2019. A new species of the metriorhynchid crocodylomorph *Cricosaurus* from the Upper Jurassic of southern Germany. *Acta Palaeontologica Polonica*, 64:343–356. <https://doi.org/10.4202/app.00541.2018>
- Sachs, S., M. Young, P. Abel, and H. Mallison. 2021. A new species of *Cricosaurus* (Thalattosuchia, Metriorhynchidae) based upon a remarkably well-preserved skeleton from the Upper Jurassic of Germany. *Palaeontologia Electronica*, 24:a24. <https://doi.org/10.26879/928>
- Schaefer, K., C. Püntener, and J.-P. Billon-Bruyat. 2018. Vertébrés Mésozoïques – Crocodiliens. Office de la culture, Paléontologie A16, Porrentruy, 184 p.
- Sereno, P. C., H. C. E. Larsson, C. A. Sidor, and B. Gado. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, 294:1516–1519. <https://doi.org/10.1126/science.1066521>
- Spindler, F., R. Lauer, H. Tischlinger, and M. Mäuser. 2021. The integument of pelagic crocodylomorphs (Thalattosuchia: Metriorhynchidae). *Palaeontologia Electronica*, 24:a25. <https://doi.org/10.26879/1099>
- Waskow, K., D. Grzegorzczak, and P. M. Sander. 2018. The first record of *Tyrannoneustes* (Thalattosuchia: Metriorhynchidae): a complete skull from the Callovian (late Middle Jurassic) of Germany. *PalZ*, 92:457–480. <https://doi.org/10.1007/s12542-017-0395-z>
- Westphal, F. 1962. Die Krokodilier des deutschen und englischen oberen Lias. *Palaeontographica*, Abt. A, 118:23–118.
- Wilkinson, L. E., M. T. Young, and M. J. Benton. 2008. A new metriorhynchid crocodylian (Mesoeucrocodylia: Thalattosuchia) from the Kimmeridgian (Upper Jurassic) of Wiltshire, UK. *Palaeontology*, 51:1307–1333. <https://doi.org/10.1111/j.1475-4983.2008.00818.x>
- Witton, M. P. 2018. *The Palaeoartist's Handbook: Recreating Prehistoric Animals in Art*. Crowood Press, Marlborough, 224 P.
- Wu, X.-C., A. P. Russell, and S. L. Cumbaa. 2001. *Terminonaris* (Archosauria: Crocodyliformes): new material from Saskatchewan, Canada, and comments on its phylogenetic relationships. *Journal of Vertebrate Paleontology*, 21:492–514. [https://doi.org/10.1671/0272-4634\(2001\)021\[0492:TACNMF\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2001)021[0492:TACNMF]2.0.CO;2)
- Young, M. T., and M. B. Andrade. 2009. What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. *Zoological Journal of the Linnean Society*, 157:551–585. <https://doi.org/10.1111/j.1096-3642.2009.00536.x>
- Young, M. T., M. A. Bell, and S. L. Brusatte. 2011a. Craniofacial form and function in Metriorhynchidae (Crocodylomorpha: Thalattosuchia): modelling phenotypic evolution with maximum-likelihood methods. *Biology Letters*, 7:913–916. <https://doi.org/10.1098/rsbl.2011.0357>
- Young, M. T., S. L. Brusatte, M. Ruta, and M. B. Andrade. 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. <https://doi.org/10.1111/j.1096-3642.2009.00571.x>

Young, M. T., M. A. Bell, M. B. Andrade, and S. L. Brusatte. 2011b. Body size estimation and evolution in metriorhynchid crocodylomorphs: implications for species diversification and niche partitioning. *Zoological Journal of the Linnean Society*, 163:1199–1216. <https://doi.org/10.1111/j.1096-3642.2011.00734.x>

Young, M. T., M. B. Andrade, S. Etches, and B. L. Beatty. 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. <https://doi.org/10.1111/zoj.12082>

Young, M. T., S. Sachs, P. Abel, D. Foffa, Y. Herrera, and J. J. N. Kitson. 2020. Convergent evolution and possible constraint in the posterodorsal retraction of the external nares in pelagic crocodylomorphs. *Zoological Journal of the Linnean Society*, 189:494–520. <https://doi.org/10.1093/zoolinlean/zlaa021>

Young, M. T., A. Brignon, S. Sachs, J. J. Hornung, D. Foffa, J. J. N. Kitson, M. M. Johnson, and L. Steel. 2021. Cutting the Gordian knot: a historical and taxonomic revision of the Jurassic crocodylomorph *Metriorhynchus*. *Zoological Journal of the Linnean Society*, 192:510–553. <https://doi.org/10.1093/zoolinlean/zlaa092>

Young, M. T., S. L. Brusatte, M. B. Andrade, J. B. Desojo, B. L. Beatty, L. Steel, M. S. Fernández, M. Sakamoto, J. I. Ruiz-Omeñaca, and R. R. Schoch. 2012. The cranial osteology and feeding ecology of the metriorhynchid crocodylomorph genera *Dakosaurus* and *Plesiosuchus* from the Late Jurassic of Europe. *PLoS ONE*, 7:e44985. <https://doi.org/10.1371/journal.pone.0044985>