

ARTÍCULO

AN INCOMPLETE METRIORHYNCHID (CROCODYLOMORPHA: THALATTOSUCHIA) CAUDAL VERTEBRA FROM THE LATE JURASSIC OF NORTHERN CHILE, AND COMMENTS ON SOUTH AMERICAN THALATTOSUCHIAN PALEOBIOGEOGRAPHY

Daniel Bajor^{1,2,3}, Jhonatan Alarcón-Muñoz^{1,2,3}, Omar Vicencio-Campos^{4,5}, David Rubilar-Rogers¹

¹ Área de Paleontología, Museo Nacional de Historia Natural, Interior Parque Quinta Normal s/n. Quinta Normal, Santiago, Chile.

² Red Paleontológica U de Chile. Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile.

³ Millenium Nucleus Early Evolutionary Transitions of Mammals, Santiago, Chile.

⁴ Museo Seminario, Seminario San Rafael, Av. Santa Elena 74, Valparaíso, Chile.

⁵ Laboratorio de Ictiología e Interacciones Biofísicas, Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, Valparaíso, Chile.

ABSTRACT

An incomplete isolated thalattosuchian vertebra (SGO.PV.1092) collected near Cerritos Bayos is described, and identified as a mid-caudal vertebra of a metriorhynchid (cf. Metriorhynchidae gen. et sp. indet.). The specimen represents the first three-dimensionally preserved caudal element of this group of pelagic predators from the Jurassic of Chile to be described and figured. It most likely originates from Oxfordian (lower Upper Jurassic) levels of the Cerro Campamento Formation. The paleobiogeographic relevance of incomplete and isolated thalattosuchian axial fossils from South America is commented on, and the implications of the apparent absence of Teleosauroidea in the Jurassic fossil record of the continent is discussed. There is currently no evidence of the metriorhynchid genus *Metriorhynchus*, or any teleosauroid having reached the Southeastern Pacific during this period. Given that historically they used to be considered as important faunistic elements of an Early–Middle Jurassic marine biotic interchange between the western Tethys and the western coast of South America, this lack of evidence calls the proposed pre-Oxfordian stage of the Caribbean Corridor hypothesis as an early dispersal route for Mesozoic marine reptiles into question.

Key words: Chile, Cerritos Bayos, Thalattosuchia, Teleosauroidea, Metriorhynchidae, caudal vertebra, paleobiogeography

RESUMEN

Una vértebra caudal incompleta de metriorrinquido (Crocodylomorpha: Thalattosuchia) del Jurásico Tardío del norte de Chile, y comentarios sobre la paleobiogeografía de los talattosuquios de Sudamérica. Se describe una vértebra incompleta y aislada de un talattosuquio (SGO.PV.1092) colectada cerca de Cerritos Bayos, y se identifica como una vértebra caudal media de un metriorrinquido (cf. Metriorhynchidae gen. et sp. indet.). El espécimen representa el primer elemento caudal con preservación tridimensional de este grupo de depredadores pelágicos del Jurásico de Chile que se ha descrito y representado con figuras. Lo más probable es que provenga de niveles Oxfordianos (Jurásico Superior temprano) de la Formación Cerro Campamento. Se comenta sobre la relevancia paleobiogeográfica de fósiles axiales incompletos y aislados de talattosuquios de Sudamérica, y se discuten las implicancias de la aparente ausencia de Teleosauroidea en el registro fósil del Jurásico del continente. Actualmente no existe evidencia de la llegada del género metriorrinquido *Metriorhynchus*, ni de teleosauroides en el Pacífico sudoriental durante este período. Dado que históricamente se solían considerar como elementos faunísticos importantes de un intercambio biótico marino del Jurásico temprano–medio entre el Tethys occidental y la costa occidental de Sudamérica, esta falta de evidencia arroja dudas sobre la propuesta etapa pre-Oxfordiana de la hipótesis del Corredor Caribeño como una ruta de dispersión temprana de reptiles marinos Mesozoicos.

Palabras clave: Chile, Cerritos Bayos, Thalattosuchia, Teleosauroidea, Metriorhynchidae, vértebra caudal, paleobiogeografía

Institutional abbreviations – **BMMS**, Bürgermeister Müller Museum, Solnhofen, Germany; **CIP**, Centro de Investigaciones Paleontológicas, Villa de Leyva, Colombia; **DMA**, Dinosaurier Museum Altmühltal, Denkendorf, Germany; **MUHNAL**, Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Chile; **NKMB**, Naturkunde Museum Bamberg, Germany; **SGO.PV.**, Área de Paleontología, Museo Nacional de Historia Natural (MNHN), Santiago, Chile; **UOMNH**, University of Oregon Museum of Natural and Cultural History, Eugene, Oregon, USA.

INTRODUCTION

Thalattosuchia is a clade of extinct marine crocodylomorphs (Fraas 1901; Gasparini 1973; Young *et al.* 2024a) that lived during the earliest Jurassic to mid–early Cretaceous interval (Chiarenza *et al.* 2015; Cortés *et al.* 2019; Benani *et al.* 2023; Young *et al.* 2024b). It represents the first known group within Crocodylomorpha to become secondarily aquatic (Martin *et al.* 2016; Wilberg *et al.* 2019). The origins of the clade remain unclear despite two centuries of research, but their divergence may have occurred in the Late Triassic (Wilberg *et al.* 2022; Young *et al.* 2024a). There is also no consensus regarding where Thalattosuchia belongs on the pseudosuchian tree of life. The most commonly recovered phylogenetic scenarios place them: A, as the sister group to Crocodyliformes (Wilberg 2015a, b, 2022); B, close to Metasuchia (Notosuchia + Neosuchia) within Mesoeucrocodylia (Ösi *et al.* 2018; Johnson *et al.* 2020); or C, as the sister group to Tethysuchia (Dyrosauroida + Pholidosauridae) within Neosuchia (Andrade *et al.* 2011; Novas *et al.* 2021; Jouve *et al.* 2026).

Thalattosuchia comprises a handful of known early diverging forms from the Early Jurassic of the western Tethys (Johnson *et al.* 2020; Wilberg *et al.* 2022; Young *et al.* 2024b), and the two considerably more widely distributed lineages of Neothalattosuchia (Young *et al.* 2024a); Teleosauroida and Metriorhynchoidea (Fig. 1). Teleosauroida is a group of semiaquatic animals that are phenotypically very similar to extant crocodylians (especially gavialoids, since most are longirostrine), and generally considered relatively unspecialized to their predominantly marine environment (Hua and Buffrénil 1996; Wilkinson *et al.* 2008; Young *et al.* 2010; Wilberg 2015a; Martin *et al.* 2016; Ösi *et al.* 2018; Séon *et al.* 2020). Metriorhynchoidea is formed by the Metriorhynchidae (Fig. 1); the only group in the evolutionary history of Archosauria (which comprises the lineages of the pterosaurs, dinosaurs and crocodylians) to have acquired a secondarily pelagic lifestyle (Gasparini and Dellapé 1976; Herrera *et al.* 2009, 2021; Young *et al.* 2010; Parrilla-Bel *et al.* 2013; Spindler *et al.* 2021), and early diverging representatives outside of this family (*i.e.*, non-metriorhynchid metriorhynchoids) that show increasing degrees of adaptation to their exclusively marine ecology (Pierce and Benton 2006; Young *et al.* 2010; Wilberg 2015a; Ösi *et al.* 2018; Aiglstorfer *et al.* 2020).

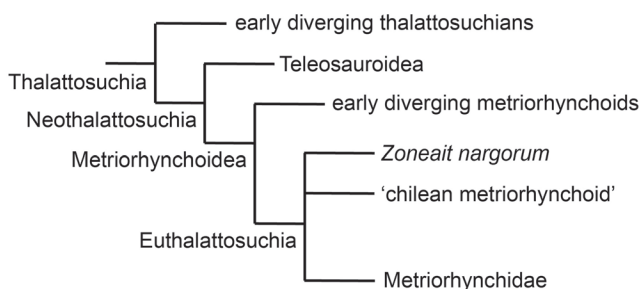


Figure 1. Simplified phylogeny of Thalattosuchia (modified from: Young *et al.* 2024b).

Among their numerous apomorphies, metriorhynchids are characterized by their extended and regionalized caudal vertebral series, which terminates in a hypocercal tailfin (Arthaber, 1906; Andrews 1913; Young *et al.* 2010; Herrera *et al.* 2013, 2026; Parrilla-Bel *et al.* 2013; Parrilla-Bel and Canudo 2015; Ósi *et al.* 2018; Sachs *et al.* 2021; Le Mort *et al.* 2025). The ventral lobe of this structure is formed by the ventrally displaced distal caudal series itself, while its dorsal lobe consists mostly of soft tissue supported by the elongated and anteriorly reoriented neural spines of the vertebrae that participate in the bending zone (Andrews 1913; Ósi *et al.* 2018; Sachs *et al.* 2019, 2021; Spindler *et al.* 2021; Le Mort *et al.* 2025; Herrera *et al.* 2026). Metriorhynchids also possess a foreshortened neck with only five postaxial cervicals (Arthaber, 1906; Andrews 1913; Herrera *et al.* 2013; Parrilla-Bel and Canudo 2015), and ventrally deflected sacral ribs (Hulke 1888; Arthaber 1906; Andrews 1913; Herrera *et al.* 2013, 2017, 2026; Le Mort *et al.* 2022; Hua 2024), differentiating their axial skeleton further from that of teleosauroids. Thus, the cervical, sacral and bending zone caudal regions are diagnostic within *Thalattosuchia* at less exclusive taxonomic levels, and potentially diagnostic traits have also been put forward for other sections of the spinal column (Foffa *et al.* 2018a). Despite this, the axial skeleton of thalattosuchians is generally considered morphologically conserved and quite uniform between the different taxa, making the referral of isolated or incomplete vertebrae and vertebral series to either of its two lineages difficult (Buffetaut 1979; Ferrusquía-Villafranca and Comas-Rodríguez 1988; Wilberg 2015a; Foffa *et al.* 2018a; Hua 2024). Consequently, as opposed to cranial fossils, their postcranial elements are poorly documented in general, and their vertebrae are usually only briefly and superficially described, and often left unprepared (Herrera *et al.* 2013; Young *et al.* 2013; Herrera 2015; Parrilla-Bel and Canudo 2015). Fortunately, this bias is gradually being addressed, with an increasing number of postcranial characters being incorporated into phylogenetic analyses (Young *et al.* 2024a).

Here, we provide a detailed description of an isolated metriorhynchid vertebra (SGO.PV.1092) collected near Cerritos Bayos (Antofagasta Region). The specimen represents the first three-dimensionally preserved caudal element from the Jurassic of northern Chile referred to this group to be described and figured. Given that the possible presence of Teleosauroidea in the Jurassic of the Southeastern Pacific has been tentatively proposed based almost exclusively on postcranial material (Burmeister and Giebel 1861; Huene 1927; Biese 1961; Casamiquela 1970; Chong and Gasparini 1972), being able to distinguish teleosauroid vertebrae from those of metriorhynchoids becomes fundamental in determining whether both thalattosuchian lineages had dispersed from the western Tethys prior to the Cretaceous. The paleobiogeographic implications of the apparent absence of Teleosauroidea in the Jurassic fossil record of South America are commented on.

LOCALITY AND SETTING

SGO.PV.1092 was discovered at what is considered an unknown locality ‘in the vicinity of Cerritos Bayos’, southwest of Calama (Antofagasta Region, northern Chile, Fig. 2B), since no further information is available in the records of the MNHN. According to Duhart *et al.* (2018), the only Mesozoic geological units in the area are the Cerro Campamento and Cerritos Bayos formations. The Cerro Campamento Formation (Fig. 2B) was originally defined by Lira (1989) as the lowermost member of the Cerritos Bayos Formation. It was elevated to formation level by Duhart *et al.* (2018), who described it as a well-stratified succession composed of black calcilutites, fine yellowish brown calcarenites, black bituminous shales, marls containing septarian concretions, oolitic and pisolitic limestones, fossiliferous limestones, conglomeratic calcarenites, and gypsum–anhydrite. Based on its fossil invertebrate fauna, the age of the Cerro Campamento Formation is considered Bathonian?–Kimmeridgian (Duhart *et al.* 2018), spanning the late Middle–early Late Jurassic interval. The overlying Cerritos Bayos Formation, originally defined by García (1967), was later amended by Duhart *et al.* (2018) to exclude the basal calcareous and gypsiferous units, which were reassigned to the Cerro Campamento Formation. The Cerritos Bayos Formation is considered to be Kimmeridgian–Tithonian

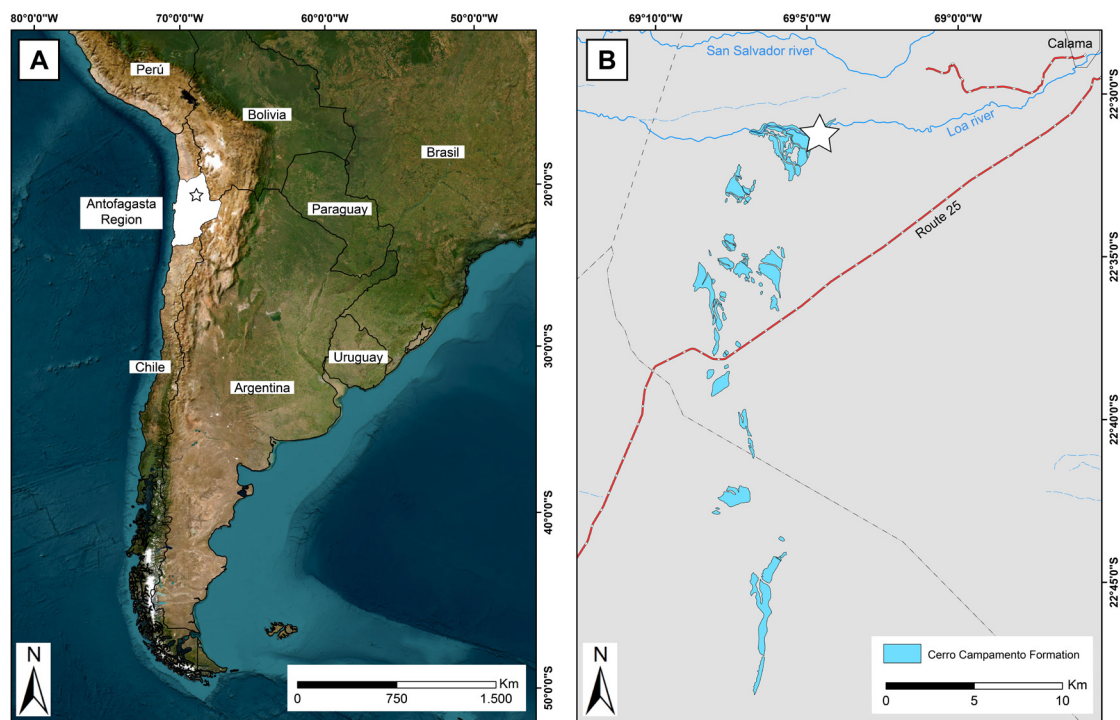


Figure 2. The most likely locality and formation of origin of SGO.PV.1092. The white star marks Cerritos Bayos. **A**, map of southern South America, the region of Antofagasta in northern Chile represented by the area in white (modified from: Esri 2026); **B**, the exposed sections of the Cerro Campamento Formation in Antofagasta Region represented in light blue (modified from: Duhart *et al.* 2018).

in age, encompassing the second half of the Late Jurassic, and remains unfossiliferous, as no fossils are known to have been collected from it (Duhart *et al.* 2018).

In marked contrast, a diverse marine vertebrate fauna is known from the Oxfordian (~161.5–154.8 Ma, lower Upper Jurassic) levels of the Cerro Campamento Formation, comprising different osteichthyan (Otero 2022), ichthyopterygian (Otero *et al.* 2023) and sauropterygian (Otero *et al.* 2020a, b) lineages, as well as rhamphorhynchine pterosaurs (Alarcón-Muñoz *et al.* 2021) and metriorhynchid thalattosuchians (Soto-Acuña *et al.* 2015). Given this rich fossil record of marine vertebrates, the confirmed presence of metriorhynchid crocodylomorphs, the coloration of the specimen studied herein, as well as that of the neural canal infill, these authors consider that SGO.PV.1092 most likely originates from the Oxfordian levels of the Cerro Campamento Formation.

MATERIALS AND METHODS

SGO.PV.1092 is a well-preserved, though incomplete mid-caudal vertebra from the distal pre-flexural region of the caudal series that lacks most of its posterior articular face and its neural arch (Fig. 3). Although its precise provenance (locality and horizon) is not documented, according to the records of the MNHN, it was collected near the locality Cerritos Bayos. The specimen most likely originates from the Oxfordian levels of the Cerro Campamento Formation. SGO.PV.1092 is curated in the Paleontology Area of the Museo Nacional de Historia Natural de Chile (MNHN) in Santiago de Chile.

SGO.PV.1092 was examined first-hand and photographed at the MNHN, and did not require prior preparation. Measurements were taken with a digital caliper, and the taxonomic identification and comparative analysis were carried out relying on the published literature.

RESULTS

Systematic paleontology

Crocodylomorpha Hay 1930 (*sensu* Nesbitt 2011)

Thalattosuchia Fraas 1901 (*sensu* Young *et al.* 2024a)

Neothalattosuchia Young *et al.* 2024a

Metriorhynchoidea Fitzinger 1843 (*sensu* Young *et al.* 2024a)

Euthalattosuchia Young *et al.* 2024a

Metriorhynchidae Fitzinger 1843 (*sensu* Young *et al.* 2024a)

cf. Metriorhynchidae gen. et sp. indet.

Material – SGO.PV.1092, an incomplete mid-caudal vertebra from the distal pre-flexural region, that lacks most of its posterior articular face and the neural arch.

Locality, horizon and age – Cerritos Bayos, Antofagasta Region, northern Chile. Cerro Campamento Formation, Oxfordian.

Description

SGO.PV.1092 is a partial vertebra that lacks most of its posterior articular face and only preserves the basalmost region of the neural arch (Fig. 3). The specimen is dark grayish-brown, while the adhering sandstone matrix (*i.e.*, the infill of the neural canal) is cream in color (Fig. 3A). The anteroposterior length of the centrum is 39.2 mm, and its mediolateral width is 16.95 mm (measured approximately at mid-height and mid-length, respectively). It is cylindrical in shape, and expands cranially and caudally to form the thickened rims of the articular faces. This expansion gives it an hourglass-shape in ventral view, with concave lateral margins (Fig. 3C). The centrum is devoid of nutritive foramina and lacks a hypapophysis. While the anterior articular face is practically complete (only showing slight erosion dorsolaterally and ventrolaterally on the right side, Fig. 3D), the posterior one consists only of the central portion of its dorsal region, lacking its borders. Still, enough of it is preserved to determine the amphicoelous morphology of the centrum. The anterior articular face, which lacks a notochordal pit, is subcircular (being slightly taller than wide, 28.4 mm x 26.9 mm, Table 1) and its surface is evenly and gently concave rather than flat, or possessing a wide flat to convex border around a central concavity. The base of the neural arch forms part of the dorsolateral region of its rim on each side, creating the false impression of a dorsally truncated vertically oval shape in anterior view (Fig. 3D). The dorsal rim is slightly concave below the neural canal. Short and weakly developed longitudinal ridges are present on the ventrolateral surfaces of the centrum, adjacent to the rim.

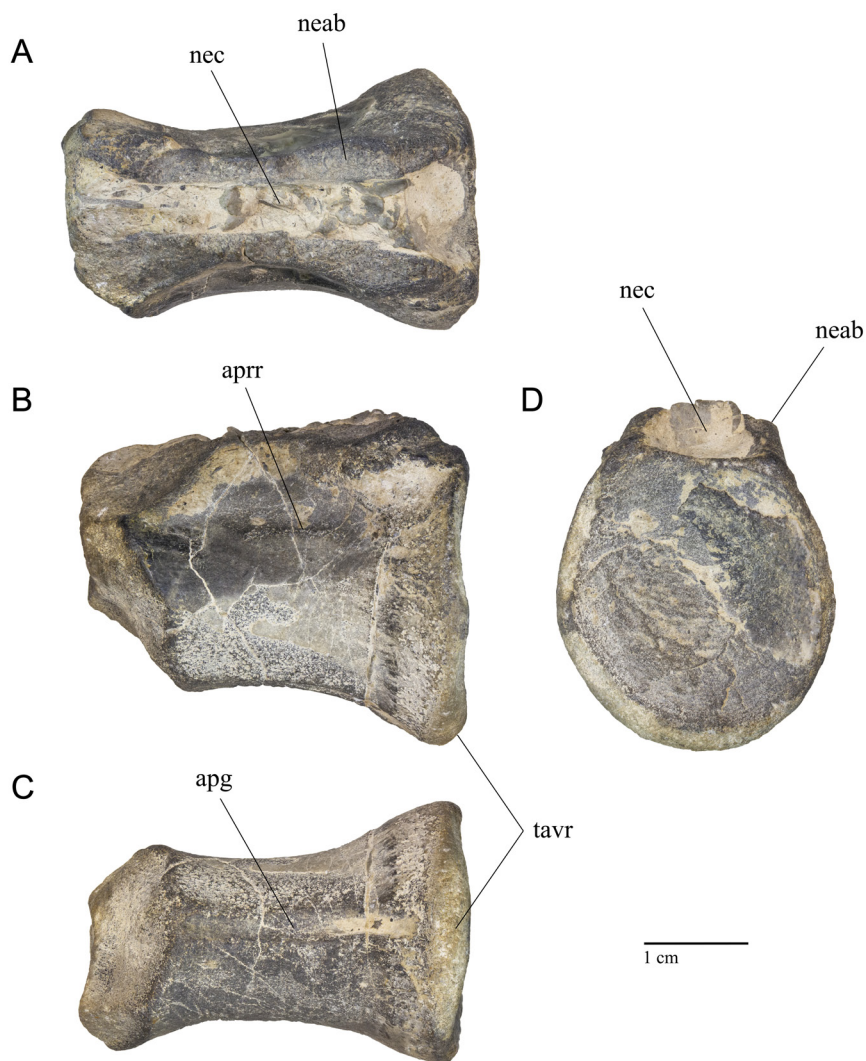


Figure 3. The partial mid-caudal vertebra (SGO.PV.1092) in different views. These are: **A**, dorsal; **B**, right lateral; **C**, ventral and **D**, anterior. **Abbreviations:** **apg**, anteroposterior groove; **aprr**, anteroposterior rugous ridge; **neab**, neural arch base; **nec**, neural canal; **tavr**, thickened anteroventral rim.

In lateral view (Fig. 3B), the ventral margin of the centrum is concave anteroposteriorly (whereas it is convex mediolaterally). The neurocentral sutures cannot be discerned, making them qualify as closed (Brochu 1996). An anteroposteriorly oriented rugose ridge can be observed on the dorsolateral surface of the centrum (present on both sides but better preserved on the right, where it measures 9.1 mm in length), shifted anteriorly with respect to the centrum mid-length. In ventral view (Fig. 3C), a shallow anteroposterior groove extends along the midline across the entire preserved length of the centrum, reaching the border of the thickened rim of the anterior articular face but not extending onto it, flanked by a pair of rounded ridges. Only the anterior three-quarters of the ventral surface are preserved, precluding the description of the posterior region of the centrum. In dorsal view (Fig. 3A), the broken neural arch reveals the infill of the neural canal. The canal is tubular, with parallel margins along most of its anteroposterior length (being approximately 4.8 mm in width), and widening anteriorly and posteriorly near the articular faces. The bases of the neural arch extend along the entire length of the centrum. The fractured and/or eroded regions reveal the trabecular (or ‘osteoporotic-like’) internal microstructure of the centrum.

Taxonomic affinities and position within the vertebral column

Based on the combination of the following characteristics shown by the vertebral centrum we confidently identify the specimen as belonging to a thalattosuchian crocodylomorph: the anteroposterior elongation, the concave ventral margin in lateral- and concave lateral margins in ventral views (*i.e.*, hourglass or spool shape), the amphicoelous morphology, the lack of a hypapophysis and nutritive foramina, the subcircular anterior articular face that lacks a notochordal pit, and the markedly trabecular (or ‘osteoporotic-like’) internal osseous structure (Andrews 1913; Buffetaut 1979; Hua and Buffrénil 1996; Cau and Fanti 2015; Parrilla-Bel and Canudo 2015; Kean *et al.* 2020; Young *et al.* 2024b).

The pair of longitudinal ridges separated by a groove that run along the ventral surface of the centrum places the specimen in the caudal series (Andrews 1913). As mentioned in the description, the height and width of the complete articular face are subequal, and the centrum itself also has a subcircular cross-section (see Table 1). This is consistent with the observations of Andrews (1913) in metriorhynchid caudal centra, whereas those of teleosauroids are taller than wide (Andrews 1913; Johnson *et al.* 2018).

We interpret the anteroposteriorly oriented rugous ridge on the dorsolateral surfaces of the centrum as the vestigial transverse process (or caudal rib). These structures are strongly dorsoventrally compressed and rapidly decrease in size posteriorly along the caudal series (Andrews 1913; Parrilla-Bel and Canudo 2015). The position of the transverse processes represents another taxonomically informative morphological trait; while teleosauroid caudal ribs emerge from the neural arch, in metriorhynchids they are borne on the centrum (Andrews 1913). Based on the combination of possessing a subcircular (rather than vertically oval) articular face and cross-section at mid-length, and a vestigial caudal rib that is borne on the centrum (rather than on the neural arch), we identify the specimen as belonging to a metriorhynchid.

In the anterior portion of the tail of metriorhynchids, the pair of ridges on the ventral surface of the centrum bear the articulation facets for the hemapophyses (or chevrons) in their posterior region (Hulke 1888; Andrews 1913; Herrera *et al.* 2013; Sachs *et al.* 2021). The absence of these articular facets, combined with the extensive participation of the bases of the neural arch in its rim dorsolaterally, indicate that the well-preserved articular face is the anterior one. Regarding the position of the centrum, the vestigial morphology of the transverse process indicates that it is likely the first caudal that lacks them. In Metriorhynchidae, these processes are no longer present at positions 12-20, depending on the species and individual in question (Arthaber 1906; Andrews 1913; Herrera *et al.* 2013; Le Mort *et al.* 2022), showing inter- as well as intraspecific variation. Therefore, considering that the caudal vertebral count of some metriorhynchids is up to over 50 (Young *et al.* 2010; Herrera *et al.* 2026), the identification of SGO. PV.1092 can be narrowed down to representing a mid-caudal vertebra from the tail stock (*i.e.*, the proximal region of the tail), approximately the 16th position.

As mentioned in the introduction, thalattosuchian vertebrae generally receive little attention due to their perceived low diagnostic value, therefore detailed measurements are, unfortunately, hardly ever reported. Admittedly, one of the reasons for this is that sufficiently complete caudal series in which the exact position of each element is known are only preserved in fully articulated skeletons, such as a referred specimen of *Dakosaurus maximus* (DMA-JP-2009/001, Herrera *et al.* 2026), or the holotypes of *Cricosaurus albersdoerferi* (BMMS-BK 1-2, Sachs *et al.* 2021) and *C. bambergensis* (NKMB-PWatt14/274, Sachs *et al.* 2019). These are left semi-prepared in order to retain anatomical integrity, partially embedded within a slab of the sedimentary rock that contains them. This leaves the vertebrae visible in only one view (usually lateral), and in some cases partially obscured by other skeletal elements. The problem with less complete material is that, while taking their detailed measurements is possible once prepared, their exact position within the vertebral series remains uncertain, precluding precise comparisons – such as in the present case. What complicates matters even further is that the measurements chosen to be reported (*e.g.*, sometimes only one articular face is considered) and/or the way they are taken (*e.g.*, centrum length can be measured at mid-height, or between the dorsal or ventral margins of the articular faces, which tend to result in different

Table 1. The measurements of cf. Metriorhynchidae indet. (SGO.PV.1092) summarized. Length refers to the total length of the centrum, measured at mid-height. Height and width were measured at mid-length. Anterior height- and width refer to the dimensions of the anterior articular face. All measurements are in millimeters.

	Length	Height	Width	Ant. height	Ant. width
cf. Metriorhynchidae indet.					
SGO.PV.1092	39.2	17.5	16.95	28.4	26.9

values) can differ markedly between studies. Therefore, as for the dimensions of SGO.PV.1092 (Table 1), the lack of overlapping information in the literature precludes determining its affinities through size comparisons.

Regarding early diverging (*i.e.*, non-metriorhynchid) metriorhynchoids, their postcranial skeleton in general, and the caudal region of their vertebral column in particular is poorly known, hindering detailed comparisons. Based on the brief descriptions available in the scientific literature, SGO.PV.1092 differs from *Magyarosuchus fitosi* (from the late Toarcian, latest Early Jurassic, of the Kiszegrecse Marl Formation in Hungary) in that the articular faces of the mid-caudal vertebrae in the latter are oval in shape (Ösi *et al.* 2018), as in teleosauroids (Andrews 1913; Johnson *et al.* 2018). Two of the few known early diverging metriorhynchoids have been discovered in the Eastern Pacific; *Zoneait nargorum* from the late Aalenian–early Bajocian (~170.9 Ma, early Middle Jurassic) of the Weberg Member of the Snowshoe Formation in Oregon, western USA (Wilberg 2015a), and the only South American taxon, referred to as ‘the Chilean metriorhynchoid’ (originally described as ‘*Ichthyosaurus acutirostris*’) from the early–middle Bajocian (~170.9–169.6 Ma, mid-Middle Jurassic) of the Lautaro Formation in the Atacama Region (Tavera 1981). Although the holotype of the former (UOMNH F39539) preserves a mid-caudal vertebra, it is incomplete and partially surrounded by matrix (Fig. 11 in Wilberg 2015a). The latter consists of a small (~18.3 cm in length), incomplete and poorly preserved skull (Tavera 1981), considered lost since 1991 (pers. comm. with Dr. Alfonso Rubilar Rodríguez). According to our current knowledge, non-metriorhynchid metriorhynchoids reached their peak diversity in the Toarcian (~184.2–174.7 Ma, late Early Jurassic), and their most recent representative is *Teleidosaurus calvadosii* from the Bathonian (~168.2–165.3 Ma, mid-Middle Jurassic) of France (Hua 2020). Given the above, we consider the identification of SGO.PV.1092 as a metriorhynchid (rather than a non-metriorhynchid metriorhynchoid) mid-caudal vertebra reaffirmed, due to its deduced Oxfordian (~161.5–154.8 Ma, early Late Jurassic) age. However, due to the uncertainty that stems from not knowing the precise provenance and age of the fossil, and our limited knowledge of the mid-caudal axial anatomy in early diverging metriorhynchoids, our identification at the family level cannot be considered unequivocal.

DISCUSSION

The thalattosuchian fossil record of northern Chile – though far from being as rich as that of Argentina – is key in improving our understanding of the internal genealogic relationships of Metriorhynchidae, since it encompasses the early Bajocian–Oxfordian interval, which includes the earliest stages of their evolution (Gasparini and Chong 1977; Gasparini 1980; Tavera 1981; Gasparini *et al.* 2000, 2008; Fernández *et al.* 2011; Soto-Acuña *et al.* 2012, 2015, 2018). Curiously, this fossil record is almost exclusively cranial, which increases the scientific value of the fossil presented here. The only axial elements that can be confidently identified as thalattosuchian are the first few cervical vertebrae preserved in articulation with a partial skull referred to “*Metriorhynchus*” *casamiquelai* (SGO.PV.249) from the Callovian of Sierra Moreno (Soto-Acuña *et al.* 2012), and material referred to Metriorhynchidae indet. consisting of partially preserved cervical and dorsal vertebrae associated with cranial remains (MUHNCAL.27177), and an articulated series

of heavily eroded 11 caudal centra from the distal region of the tail, preserved in blocks of sedimentary rock (MUHNCAL.27152) from the Oxfordian of the Cerro Campamento Formation (Soto-Acuña *et al.* 2015), both in the Antofagasta Region. This makes SGO.PV.1092 the only three-dimensionally preserved thalattosuchian caudal vertebra from the Jurassic of Chile to be described and figured to date. Since the possible presence of Teleosauroida in the Jurassic of the Southeastern Pacific has been tentatively proposed based almost exclusively on postcranial material (Burmeister and Giebel 1861; Huene 1927; Biese 1961; Casamiquela 1970; Chong and Gasparini 1972), the detailed description and identification of this vertebra also bears paleobiogeographic significance.

On the apparent absence of Teleosauroida in the Southeastern Pacific during the Jurassic, and its paleobiogeographic implications

To explain the disjunct distribution of Thalattosuchia in the western Tethys and the Eastern Pacific during the pre-Oxfordian Jurassic, Gasparini and Chong (1977) proposed the existence of a dispersal route in the Caribbean region. Over the years that followed, several studies provided further evidence for this paleobiogeographic hypothesis based on shared taxa in the marine reptile faunas of the two regions (Gasparini 1979, 1981, 1985; Vignaud and Gasparini 1996; Gasparini and Fernández 1997; Gasparini *et al.* 1997, 2000, 2007; Gasparini and Iturralde-Vinent 2001), where Teleosauroida and the metriorhynchid

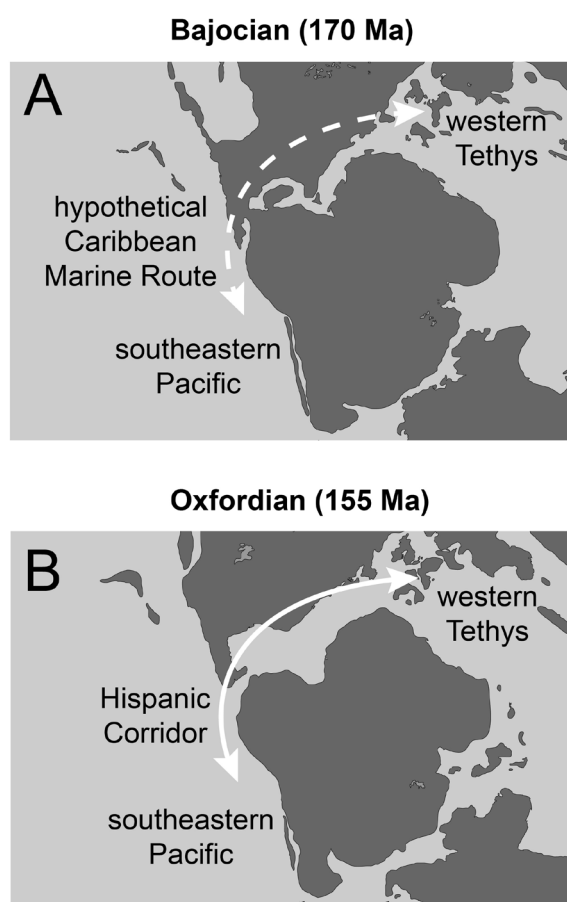


Figure 4. Maps of the dispersal routes proposed to explain the disjunct distribution of Mesozoic marine reptiles during the Jurassic (modified from: Scotese 2021). **A**, the hypothetical Caribbean Marine Route (Bajocian); **B**, the fully open marine strait known as the Hispanic Corridor (Oxfordian).

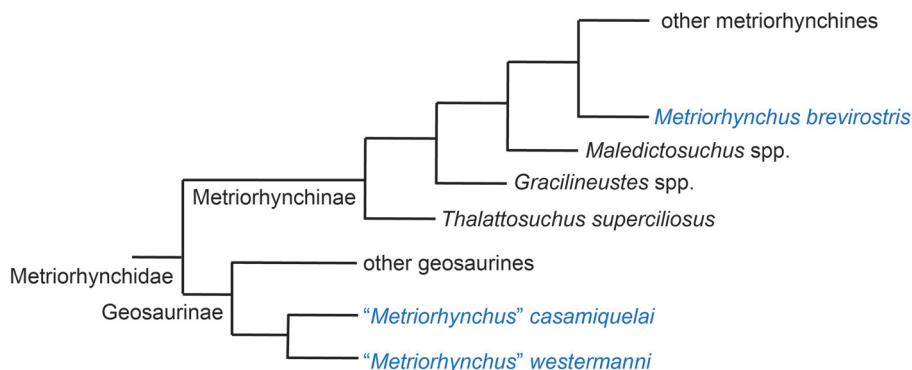


Figure 5. Simplified phylogeny of Metriorhynchidae (modified from: Young *et al.* 2024b). The only valid species of the metriorhynchine genus *Metriorhynchus* (*M. brevirostris*), and the two currently recognized Chilean species (“*M.*” *casamiquelai* and “*M.*” *westermanni*) are shown in blue.

genus *Metriorhynchus* played a key role. Since, according to Iturralde-Vinent (2003, 2006), there is no geological evidence for a marine corridor connecting the western Tethys and Eastern Pacific before the Oxfordian, an updated two-stage version of the Caribbean Corridor hypothesis was put forward (Fig. 4). During the first stage of the opening of the Caribbean Corridor, the Caribbean Marine Route would have connected the two regions (Iturralde-Vinent 2006). The author envisioned it as a hypothetical system of ephemeral channels that would have formed periodically during the Early and Middle Jurassic at times of sea level highstands, enabling pulses of dispersal for marine organisms. During the second stage, the Hispanic Corridor, a true marine strait that opened in the Oxfordian, established stable interchange between the marine faunas of the western Tethys and Eastern Pacific (Iturralde-Vinent 2006).

However, *Metriorhynchus* is currently considered monospecific, with *M. brevirostris* being the only species recognized as valid (Young *et al.* 2021). The generic name of the two nominal species described from northern Chile, “*Metriorhynchus*” *casamiquelai* (Callovian, Gasparini and Chong 1977) and “*M.*” *westermanni* (Callovian–Oxfordian, Gasparini 1980; Gasparini *et al.* 2008; Fernández *et al.* 2011) has been used in the scientific literature in quotation marks since Young *et al.* (2012) first demonstrated that it was erroneous. Additionally, *Metriorhynchus* and the Chilean taxa are not closely related in terms of phylogenetic distance (Young *et al.* 2021, 2024a, b). Metriorhynchidae is currently divided into two subfamilies (Fig. 5). Metriorhynchinae (Young and Andrade 2009) comprises forms with a long, gracile rostrum and a high tooth count, and are considered piscivorous (Young *et al.* 2010; Parrilla-Bel *et al.* 2013). In contrast, Geosaurinae (Young and Andrade 2009) are characterized by their comparatively short, deep and wide rostra, and lower tooth count. Their dentition consists of larger tooth crowns with serrated carinae, and their representatives are considered macrophagous carnivores (Andrade *et al.* 2010; Young *et al.* 2010; Foffa and Young 2014; Herrera *et al.* 2026). While the monotypic *Metriorhynchus* is a metriorhynchine genus, the two currently recognized Chilean species are consistently recovered as stem-geosaurines in phylogenetic analyses (Fig. 5), forming a small clade that represents the sister group to the rest of Geosaurinae (Foffa *et al.* 2018b; Cau 2019; Girard *et al.* 2023; Young *et al.* 2021, 2024a, b; Herrera *et al.* 2026). Therefore, there is no evidence for the presence of the genus *Metriorhynchus* in South America, precluding the use of its distribution as indirect evidence for a dispersal route between the western Tethys and the Eastern Pacific.

Despite their comparatively unspecialized anatomy, Teleosauroida had already reached a wide distribution by the late Toarcian, being present in the fossil record of several European countries, Morocco, Madagascar and China (Young 1948; Buffetaut *et al.* 1981; Johnson *et al.* 2020; Wilberg *et al.* 2022; Benani *et al.* 2023), and they remained widely distributed during the rest of the Jurassic as well. Dubious to

anecdotic reports of their presence in the Southeastern Pacific have also appeared in the scientific literature (Burmeister and Giebel 1861; Huene 1927; Biese 1961; Casamiquela 1970; Chong and Gasparini 1972), however, they are invariably based on fragmentary remains, most often tentatively assigned to, or associated with Teleosauroidea due to their Early Jurassic age rather than taxonomically informative characters. The published pre-Bajocian ‘thalattosuchian’ fossils from South America are currently considered to lack diagnostic features that would justify their inclusion in this clade (Wilberg *et al.* 2022; Young *et al.* 2024a, b), and to complicate matters further, the reassessment of these fossils is not possible, since they have been considered lost for decades (Gasparini *et al.* 2000). Currently, the only confirmed record of Teleosauroidea from South America is represented by a gigantic specimen (CIP-0001) with an estimated total body length of 9.6 m from the late Barremian (~123.6–121.4 Ma, mid-Early Cretaceous) of Colombia, which is also the most recent record of the group worldwide (Cortés *et al.* 2019). With the identification of SGO.PV.1092 as a metriorhynchid vertebra, this remains unchanged.

Aside from thalattosuchians, the disjunct distribution of certain ichthyopterygian and sauropterygian taxa was also considered as evidence for the Caribbean Corridor hypothesis (Gasparini 1985; Gasparini and Fernández 1997; Gasparini *et al.* 1997, 2007). However, ichthyosaurs likely originated before the Great Dying (~251.9 Ma), and the oldest plesiosaur remains are Rhaetian in age (~205.7–201.4 Ma, latest Triassic), with both groups considered pelagic from the earliest stages of their evolutionary history (Wintrich *et al.* 2017; Kear *et al.* 2023). Furthermore, fossil evidence suggests that they were capable of circumnavigating Pangea in both polar regions during the Early and Middle Jurassic (Zammit 2011; Kear 2012; Zverkov *et al.* 2020). Conversely, the Caribbean Marine Route, a hypothetical system of ephemeral channels that would have formed periodically during sea level highstands in the rift valley system of west-central Pangea (the zone of separation between North- and South America), represents an environment that is not consistent with the ecology of pelagic forms, making its role as a dispersal route questionable in their case. Additionally, this rift valley system was partially occupied by rivers and lakes (Iturralde-Vinent 2003, 2006), which would have made the waters of the hypothetical Caribbean Marine Route brackish due to their freshwater input. As opposed to ichthyosaurs, plesiosaurs, and most likely metriorhynchid crocodylomorphs, this would have been a perfect dispersal route for marine semiaquatic forms. Given the demonstrated dispersal ability of Teleosauroidea, the persisting lack of records of their fossils in the Jurassic of the Eastern Pacific is a mystery, especially considering the repeated opportunities of colonization that an intermittently open Caribbean Marine Route should have provided them.

A thorough revision of the entirety of the evidence supporting such a marine route presented since the 1970s is beyond the scope of this contribution. Nevertheless, the currently available thalattosuchian fossil record suggests that neither Teleosauroidea, nor the metriorhynchid genus *Metriorhynchus* should be included among the taxa whose distribution is used to support the pre-Oxfordian stage of the Caribbean Corridor hypothesis. In particular, the apparent absence of teleosauroids in western South America until the Cretaceous represents a weak point in the hypothesis, calling the existence of a sufficiently developed Caribbean Marine Route as to allow the dispersal of Mesozoic marine reptiles into question.

CONCLUSIONS

SGO.PV.1092 is an incomplete mid-caudal element from the distal pre-flexural region of the vertebral column of a marine crocodylomorph, which we identify as cf. *Metriorhynchidae* indet. Though the specimen was collected at an unknown locality in the vicinity of Cerritos Bayos (Antofagasta Region, northern Chile), it likely originates from Oxfordian (lower Upper Jurassic) levels of the Cerro Campamento Formation. Isolated or incomplete thalattosuchian vertebrae and vertebral series are generally considered poorly diagnostic at best (Buffetaut 1979; Ferrusquía-Villafranca and Comas-Rodríguez 1988; Wilberg 2015a; Foffa *et al.* 2018a; Hua 2024), and receive considerably less attention than cranial fossils (Herrera *et al.* 2013; Young *et al.* 2013; Herrera 2015; Parrilla-Bel and Canudo 2015). The detailed description of

SGO.PV.1092 is a step towards diminishing this bias, which is relevant for the still poorly understood Jurassic fossil record of the Southeastern Pacific, where the possible presence of Teleosauroida has been proposed based almost exclusively on postcranial material from Chile and Argentina (Burmeister and Giebel 1861; Huene 1927; Biese 1961; Casamiquela 1970; Chong and Gasparini 1972). These fossils are, on the one hand, poorly documented and currently not considered sufficiently informative to be included even within the more inclusive Thalattosuchia (Wilberg *et al.* 2022; Young *et al.* 2024a, b), and on the other hand, considered lost (Gasparini *et al.* 2000), precluding their revision. Therefore, there is currently no evidence to support the dispersal of the semiaquatic Teleosauroida from the western Tethyan realm into the Southeastern Pacific prior to the Cretaceous, diminishing the likelihood of the intermittent formation of a system of ephemeral semi-marine channels (*i.e.*, the Caribbean Marine Route, Iturralde-Vinent 2003, 2006) connecting the two regions during the Early and Middle Jurassic, that would have allowed the dispersal of Mesozoic marine reptiles.

ACKNOWLEDGEMENTS

D.B. and J.A.-M. were financed during 2020-2024 by the ANID grant for PhD studies in Chile. D.B. and J.A.-M. would also like to thank ANID - MILENIO - NCN2023_025 for their financial support.

REFERENCES

- AIGLSTORFER, M., P. HAVLIK and Y. HERRERA. 2020. The first metriorhynchoid crocodyliform from the Aalenian (Middle Jurassic) of Germany, with implications for the evolution of Metriorhynchoidea. *Zoological Journal of the Linnean Society*, 188(2): 522-551. <https://doi.org/10.1093/zoolinnean/zlzz072>
- ALARCÓN-MUÑOZ, J., R.A. OTERO, S. SOTO-ACUÑA, A.O. VARGAS, J. ROJAS and O. ROJAS. 2021. First record of a Late Jurassic rhamphorhynchine pterosaur from Gondwana. *Acta Palaeontologica Polonica*, 66(3): 571-583. <https://doi.org/10.4202/app.00805.2020>
- ANDRADE, M.B., R. EDMONDS, M.J. BENTON and R. SCHOUTEN. 2011. A new Berriasian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. *Zoological Journal of the Linnean Society*, 163(S1): S66-S108. <https://doi.org/10.1111/j.1096-3642.2011.00709.x>
- 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(5): 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. London, British Museum (Natural History).
- ARTHABER, G. 1906. Beiträge zur Kenntnis der Organisation und der Anpassungserscheinungen des Genus *Metriorhynchus*. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, pp. 287-320.
- BENANI, H., A. NEHILI, L.A. OUZZAOUIT, S. JOUVE, L. BOUDAD, M. MASROUR, N. JALIL and T.Y. ARRAD. 2023. Discovery of the teleosauroid crocodylomorph from the early Jurassic of Chaara cave, Middle Atlas of Morocco. *Journal of African Earth Sciences*, 198: 104804. <https://doi.org/10.1016/j.jafrearsci.2022.104804>
- BIESE, W. 1961. El Jurásico de Cerritos Bayos. Facultad de Ciencias Físicas y Matemáticas, Instituto de Geología, Universidad de Chile, Publicación 19: 1-61.
- BROCHU, C.A. 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology*, 16(1): 49-62. <https://doi.org/10.1080/02724634.1996.10011283>
- BUFFETAUT, E. 1979. Jurassic marine crocodilians (Mesosuchia: Teleosauridae) from central Oregon: first record in North America. *Journal of Paleontology*, 53(1): 210-215.
- BUFFETAUT, E., G. TERMIER and H. TERMIER. 1981. A teleosaurid (Crocodylia, Mesosuchia) from the Toarcian of Madagascar and its palaeobiogeographical significance. *Paläontologische Zeitschrift*, 55(3/4): 313-319. <https://doi.org/10.1007/BF02988145>

- BURMEISTER, H. and C. GIEBEL. 1861. Die Versteinerungen von Juntas im Thal des Río de Copiapó. *Abhandlungen der Naturforschenden Gesellschaft zu Halle*, 6: 1-34.
- CASAMIQUELA, R. 1970. Los vertebrados Jurásicos de la Argentina y de Chile. *Actas del IV. Congreso Latinoamericano de Zoología*, Caracas, 1968, 2: 873-890.
- CAU, A. 2019. A revision of the diagnosis and affinities of the metriorhynchoids (Crocodylomorpha, Thalattosuchia) from the Rosso Ammonitico Veronese Formation (Jurassic of Italy) using specimen-level analyses. *PeerJ*, 7:e7364. <https://doi.org/10.7717/peerj.7364>
- CAU, A. and F. FANTI. 2015. High evolutionary rates and the origin of the Rosso Ammonitico Veronese Formation (Middle–Upper Jurassic of Italy) reptiles. *Historical Biology*, 28(7): 952-962. <https://doi.org/10.1080/08912963.2015.1073726>
- CHIARENZA, A.A., D. FOFFA, M.T. YOUNG, G. INSACCO, A. CAU, G. CARNEVALE and R. CATANZARITI. 2015. The youngest record of metriorhynchid crocodylomorphs, with implications for the extinction of Thalattosuchia. *Cretaceous Research*, 56: 608-616. <https://doi.org/10.1016/j.cretres.2015.07.001>
- CHONG, G. and Z. GASPARINI. 1972. Presencia de Crocodilia marinos en el Jurásico de Chile. *Revista de la Asociación Geológica Argentina*, 27(4): 406-409.
- CORTÉS, D., H.C.E. LARSSON, E.E. MAXWELL, M.L. PARRA RUGE, P. PATARROYO and J.A. WILSON. 2019. An Early Cretaceous teleosauroid (Crocodylomorpha: Thalattosuchia) from Colombia. *Ameghiniana*, 56(5): 365-379. <https://doi.org/10.5710/AMGH.26.09.2019.3269>
- DUHART, P., J. MUÑOZ, D. QUIROZ, A. MESTRE and G. VARAS. 2018. Carta Sierra Gorda, Región de Antofagasta. SERNAGEOMIN, Carta Geológica de Chile, Serie Geológica Básica 198. Escala 1:100,000, 1 CD con anexos. Santiago, Chile.
- ESRI 2026. “World Imagery” [base map, South America]. ArcGis Online.
- FERNÁNDEZ, M.S., A. PAULINA-CARABAJAL, Z. GASPARINI and G. CHONG. 2011. A metriorhynchid crocodyliform braincase from northern Chile. *Journal of Vertebrate Paleontology*, 31(2): 369-377. <https://doi.org/10.1080/02724634.2011.550361>
- FERRUSQUÍA-VILLAFRANCA, I. and O. COMAS-RODRÍGUEZ. 1988. Reptiles marinos Mesozoicos en el sureste de México y su significación geológico-paleontológica. *Revista de la Inst. Geología de la Univ. Nat. Autón. México*, 7(2): 168-181.
- FITZINGER, L. 1843. *Systema Reptilium*. Vienna: Braumüller et Seidel, 106 p.
- FOFFA, D. and M.T. YOUNG. 2014. The cranial osteology of *Tyrannoneustes lythrodictikos* (Crocodylomorpha: Metriorhynchidae) from the Middle Jurassic of Europe. *PeerJ*, 2: e608. <https://doi.org/10.7717/peerj.608>
- FOFFA, D., M.T. YOUNG and S.L. BRUSATTE. 2018A. Filling the Corallian gap: new information of Late Jurassic marine reptile faunas from England. *Acta Palaeontologica Polonica*, 63(2): 287-313. <https://doi.org/10.4202/app.00455.2018>
- FOFFA, D., M.T. YOUNG, S.L. BRUSATTE, M.R. GRAHAM and L. STEEL. 2018B. A new metriorhynchid crocodylomorph from the Oxford Clay Formation (Middle Jurassic) of England, with implications for the origin and diversification of Geosaurini. *Journal of Systematic Palaeontology*, 16(13): 1123-1143. <https://doi.org/10.1080/14772019.2017.1367730>
- FRAAS, E. 1901. Die Meerkrokodile (Thalattosuchia n.g.) eine Sauriergruppe der Juraformation. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg*, 57: 409-418.
- GARCÍA, F. 1967. Geología del Norte Grande de Chile. Simposium sobre el Geosinclinal Andino, 1962, Santiago. Sociedad Geológica de Chile, 3: 1-138.
- GASPARINI, Z. 1973. Revisión de ?*Purranisaurus potens* Rusconi, 1948 (Crocodilia, Thalattosuchia) y los Thalattosuchia como un nuevo infraorden de los Crocodilia. *Actas V. Congreso Geológico Argentino*, 3: 423-431.
- GASPARINI, Z. 1979. Comentarios críticos sobre los vertebrados Mesozoicos de Chile. *Libro de Resúmenes II. Congreso Geológico Chileno*, H15-30.
- GASPARINI, Z. 1980. Un nuevo cocodrilo marino (Crocodylia, Metriorhynchidae) del Caloviano del norte de Chile. *Ameghiniana*, 17(2): 97-103.
- GASPARINI, Z. 1981. Los Crocodylia fósiles de la Argentina. *Ameghiniana*, 18(3-4): 177-205.

- GASPARINI, Z. 1985. Los reptiles marinos Jurásicos de América del Sur. *Ameghiniana*, 22(1-2): 23-34.
- GASPARINI, Z. and G. CHONG. 1977. *Metriorhynchus casamiquelai* n. sp. (Crocodylia, Thalattosuchia), a marine crocodile from the Jurassic (Callovian) of Chile, South America. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 153(3): 341-360. DOI: 10.1127/njgpa/153/1977/341
- GASPARINI, Z. and D. DELLAPÉ. 1976. Un nuevo cocodrilo marino (Thalattosuchia, Metriorhynchidae) de la Formación Vaca Muerta (Jurásico, Tithoniano) de la Provincia de Neuquén (República Argentina). *Actas I. Congreso Geológico Chileno*, Santiago, 1: C1-C21.
- GASPARINI, Z. and M.S. FERNÁNDEZ. 1997. Tithonian marine reptiles of the Eastern Pacific. In: Callaway, J.M. & Nicholls, E.L. (Eds.), *Ancient marine reptiles*. Academic Press, San Diego, 435-450.
- GASPARINI, Z., M.S. FERNÁNDEZ, M. DE LA FUENTE and L. SALGADO. 2007. Reptiles marinos Jurásicos y Cretácicos de la Patagonia argentina: su aporte al conocimiento de la herpetofauna Mesozoica. *Ameghiniana*, Publicación Especial 11: 125-136.
- GASPARINI, Z. and M. ITURRALDE-VINENT. 2001. Metriorhynchid crocodiles (Crocodyliformes) from the Oxfordian of Western Cuba. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 9: 534-542. DOI: 10.1127/njgpm/2001/2001/534
- GASPARINI, Z., A. PAULINA-CARABAJAL and G. CHONG. 2008. Un nuevo espécimen de cocodrilo marino del Jurásico Medio del norte de Chile: revalidación de *Metriorhynchus westermanni* (Crocodyliformes: Metriorhynchidae). *Revista Geológica de Chile*, 35(2): 335-346. <http://dx.doi.org/10.4067/S0716-02082008000200008>
- GASPARINI, Z. L. SPALLETTI and M.S. FERNÁNDEZ. 1997. Significado paleobiogeográfico de los reptiles marinos Bajocianos (Jurásico Medio) de la Cuenca Neuquina, Argentina. *Actas del VIII Congreso Geológico Chileno*, Universidad Católica del Norte, Departamento de Ciencias Geológicas, Antofagasta, pp. 484-488.
- GASPARINI, Z., P. VIGNAUD and G. CHONG. 2000. The Jurassic Thalattosuchia (Crocodyliformes) of Chile: a paleobiogeographic approach. *Bulletin de la Société Géologique de France*, 171(6): 657-664. <https://doi.org/10.2113/171.6.657>
- GIRARD, L.C., S. DE SOUSA OLIVEIRA, I. RASELLI, J.E. MARTIN and J. ANQUETIN. 2023. Description and phylogenetic relationships of a new species of *Torvoneustes* (Crocodylomorpha, Thalattosuchia) from the Kimmeridgian of Switzerland. *PeerJ*, 11:e15512. <https://doi.org/10.7717/peerj.15512>
- HAY, O.P. 1930. Second bibliography and catalogue of the fossil vertebrata of North America, vol. 2. Washington, D.C., Carnegie Institute Washington. 1094 p.
- HERRERA, Y. 2015. Metriorhynchidae (Crocodylomorpha: Thalattosuchia) from Upper Jurassic-Lower Cretaceous of Neuquén Basin (Argentina), with comments on the natural casts of the brain. En: Fernández, M. & Herrera, Y. (Eds.), *Reptiles extintos – volumen en homenaje a Zulma Gasparini*. *Publicación Electrónica de la Asociación Paleontológica Argentina*, 15(1): 159-171.
- HERRERA, Y., M.S. FERNÁNDEZ and Z. GASPARINI. 2013. Postcranial skeleton of *Cricosaurus araucanensis* (Crocodyliformes: Thalattosuchia): morphology and palaeobiological insights. *Alcheringa*, 37(3): 285-298. <https://doi.org/10.1080/03115518.2013.743709>
- HERRERA, Y., M.S. FERNÁNDEZ, S.G. LAMAS, L. CAMPOS, M. TALEVI and Z. GASPARINI. 2017. Morphology of the sacral region and reproductive strategies of Metriorhynchidae: a counter-inductive approach. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, 106(4): 247-255. <https://doi.org/10.1017/S1755691016000165>
- HERRERA, Y., M.S. FERNÁNDEZ and J.A. VARELA. 2009. Morfología del miembro anterior de *Geosaurus araucanensis* Gasparini y Dellapé, 1976 (Crocodyliformes: Thalattosuchia). *Ameghiniana*, 46(4): 657-667.
- HERRERA, Y., M.S. FERNÁNDEZ and V.V. VENNARI. 2021. *Cricosaurus* (Thalattosuchia, Metriorhynchidae) survival across the J/K boundary in the High Andes (Mendoza Province, Argentina). *Cretaceous Research*, 118: 104673. <https://doi.org/10.1016/j.cretres.2020.104673>
- HERRERA, Y., F. SPINDLER and M. BRONZATI. 2026. A complete morphological description of *Dakosaurus maximus* (Crocodyliformes: Thalattosuchia) with further insights into their palaeoecology. *Palaeontologia Electronica*, 29(1): a4. <https://doi.org/10.26879/1577>

- HUA, S. 2020. A new specimen of *Teleidosaurus calvadosii* Eudes-Deslongchamps, 1866 (Crocodylia, Thalattosuchia) from the Middle Jurassic of France. *Annales de Paléontologie*, 106(4): 102423. <https://doi.org/10.1016/j.anpal.2020.102423>
- HUA, S. 2024. First record of aff. *Plesiosuchus* sp. (Mesosuchia, Metriorhynchidae) in the Kimmeridgian of Le Havre (Normandy, north-western France): biometry, profile of locomotion, and paleobiological consequences. *Life*, 14(12): 1595. DOI: 10.3390/life14121595
- HUA, S. and V. BUFFRÉNIL. 1996. Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate Paleontology*, 16(4): 703-717. <https://doi.org/10.1080/02724634.1996.10011359>
- HUENE, F. 1927. Beitrag zur Kenntnis mariner Mesozoischer Wirbeltiere in Argentinien. *Centralblatt für Mineralogie, Geologie und Paläontologie Abteilung B*, 1, 22-29.
- HULKE, J.W. 1888. Contribution to the skeletal anatomy of the Mesosuchia based on fossil remains from the clays near Peterborough in the collection of A. Leeds, Esq. *Proceedings of the Zoological Society of London*, pp. 417-442.
- ITURRALDE-VINENT, M. 2003. The conflicting paleontologic versus stratigraphic record of the formation of the Caribbean Seaway. In: Bartolini, C., Buffler, R.T. and Blickwede, J. (Eds.), *The Circum-Gulf of Mexico and the Caribbean: hydrocarbon habitats, basin formation and plate tectonics*. AAPG Memoir, 79: 75-88.
- ITURRALDE-VINENT, M. 2006. Meso-Cenozoic Caribbean paleogeography: implications for the historical biogeography of the region. *International Geology Review*, 48: 791-827. <https://doi.org/10.2747/0020-6814.48.9.791>
- JOHNSON, M.M., M.T. YOUNG and S.L. BRUSATTE. 2020. The phylogenetics of Teleosauroida (Crocodylomorpha, Thalattosuchia) and implications for their ecology and evolution. *PeerJ*, 8:e9808. <https://doi.org/10.7717/peerj.9808>
- JOHNSON, M.M., M.T. YOUNG, S.L. BRUSATTE, B. THUY and R. WEIS. 2018. A catalogue of teleosauroids (Crocodylomorpha: Thalattosuchia) from the Toarcian and Bajocian (Jurassic) of southern Luxembourg. *Historical Biology*, 31(9): 1179-1194. <https://doi.org/10.1080/08912963.2018.1427090>
- JOUBE, S., M.T. YOUNG, A.K. HASTINGS and K. SALIH. 2026. The systematics and nomenclature of Tethysuchia (Archosauria: Crocodylomorpha) under the International Code of Phylogenetic Nomenclature. *Zoological Journal of the Linnean Society*, 206(4): zlag045. <https://doi.org/10.1093/zoolinnean/zlag045>
- KEAN, K.J., D. FOFFA, M.M. JOHNSON, M.T. YOUNG, G. GREITENS and S.L. BRUSATTE. 2020. First and most northern occurrence of a thalattosuchian crocodylomorph from the Jurassic of the Isle of Skye, Scotland. *Scottish Journal of Geology*, 57(1): sjg2020-013. <https://doi.org/10.1144/sjg2020-013>
- KEAR, B.P. 2012. A revision of Australia's Jurassic plesiosaurs. *Palaeontology*, 55(5): 1125-1138. <https://doi.org/10.1111/j.1475-4983.2012.01183.x>
- KEAR, B.P., V.S. ENGELSCHØN, Ø. HAMMER, A.J. ROBERTS and J.H. HURUM. 2023. Earliest Triassic ichthyosaur fossils push back oceanic reptile origins. *Current Biology*, 33(5): R178-R179. <https://doi.org/10.1016/j.cub.2022.12.053>
- LE MORT, J., J.E. MARTIN, L. PICOT and S. HUA. 2022. First description of the most complete *Metriorhynchus* aff. *superciliosus* (Thalattosuchia) specimen from the Callovian of the Vaches-Noires cliffs (Normandy, France) and limitations in the classification of Metriorhynchidae. *Annales de Paléontologie*, 108: 102539. <https://doi.org/10.1016/j.anpal.2022.102539>
- LE MORT, J., J.E. MARTIN, L. PICOT and S. HUA. 2025. The tailbend of Metriorhynchidae (Crocodylia: Thalattosuchia) measurements, limits and paleoecological implications. *Paläontologische Zeitschrift*, 100: 103-117. <https://doi.org/10.1007/s12542-025-00753-w>
- LIRA, G. 1989. Geología del área pre-Andina de Calama, con énfasis en la estratigrafía y paleogeografía del Mesozoico, 22° a 22°40' latitud Sur, Región de Antofagasta. Tesis, Departamento de Geología, Universidad de Chile. Santiago, 1-211.
- MARTIN, J.E., U. DEESRI, R. LIARD, A. WATTANAPITUKSAKUL, S. SUTEETHORN, K. LAUPRASERT, H. TONG, E. BUFFETAUT, V. SUTEETHORN, G. SUAN, P. TELOUK and V. BALTER. 2016. Strontium isotopes and the long-term residency of thalattosuchians in the freshwater environment. *Paleobiology*, 42(1): 143-156. <https://doi.org/10.1017/pab.2015.42>

- NESBITT, S.J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, 352: 1-292.
- NOVAS, F.E., F.L. AGNOLIN, G.L. LIO, S. ROSADILLA, M. SUÁREZ, R. DE LA CRUZ, I. DE SOUZA CARVALHO, D. RUBILAR-ROGERS and M.P. ISASI. 2021. New transitional fossil from late Jurassic of Chile sheds light on the origin of modern crocodiles. *Scientific Reports*, 11: 14960. <https://doi.org/10.1038/s41598-021-93994-z>
- OTERO, R.A. 2022. Ray-finned fishes (Actinopterygii) from the Upper Jurassic (Oxfordian) of the Atacama Desert, northern Chile. *PeerJ*, 10:e13739. <https://doi.org/10.7717/peerj.13739>
- OTERO, R.A., J. ALARCÓN-MUÑOZ, S. SOTO-ACUÑA, J. ROJAS, O. ROJAS and H. ORTÍZ. 2020a. Cryptoclydid plesiosaurs (Sauropterygia, Plesiosauria) from the Upper Jurassic of the Atacama Desert. *Journal of vertebrate Paleontology*, 40(1): e1764573. <https://doi.org/10.1080/02724634.2020.1764573>
- OTERO, R.A., J. PARDO-PÉREZ, J. ALARCÓN-MUÑOZ, S. SOTO-ACUÑA, J. ROJAS and O. ROJAS. 2023. Ictiosaurios (Diapsida, Ichthyopterygia) del Jurásico Superior de Cerritos Bayos, norte de Chile. *Museo de Historia Natural y Cultural del Desierto de Atacama, Publicación Ocasional* 6.
- OTERO, R.A., S. SOTO-ACUÑA, J. ROJAS and O. ROJAS. 2020b. First pliosaur remains (Sauropterygia, Pliosauridae) from the Oxfordian of the Atacama Desert. *Journal of South American Earth Sciences*, 104: 102811. <https://doi.org/10.1016/j.jsames.2020.102811>
- ŐSI, A., M.T. YOUNG, A. GALÁCZ and M. RABI. 2018. A new large-bodied thalattosuchian crocodyliform from the Lower Jurassic (Toarcian) of Hungary, with further evidence of the mosaic acquisition of marine adaptations in Metriorhynchoidea. *PeerJ*, 6:e4668. <https://doi.org/10.7717/peerj.4668>
- PARRILLA-BEL, J. and J.I. CANUDO. 2015. Postcranial elements of *Maledictosuchus riclaensis* (Thalattosuchia) from the Middle Jurassic of Spain. *Journal of Iberian Geology*, 41(1): 31-40. https://doi.org/10.5209/rev_JIGE.2015.v41.n1.48653
- 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(1): e54275. <https://doi.org/10.1371/journal.pone.0054275>
- PIERCE, S.E. and M.J. BENTON. 2006. *Pelagosaurus typus* Bronn, 1841 (Mesoeucrocodylia: Thalattosuchia) from the upper Lias (Toarcian, Lower Jurassic) of Somerset, England. *Journal of Vertebrate Paleontology*, 26(3): 621-635. [https://doi.org/10.1671/0272-4634\(2006\)26\[621:PTBMTF\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2006)26[621:PTBMTF]2.0.CO;2)
- SACHS, S., M.T. 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(2): 343-356. <https://doi.org/10.4202/app.00541.2018>
- SACHS, S., M.T. 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. *Palaeontologica Electronica*, 24(2): a24. <https://doi.org/10.26879/928>
- SCOTSESE, C.R. 2021. An atlas of Phanerozoic paleogeographic maps: the seas come in and the seas go out. *Annual Review of Earth and Planetary Sciences*, 49: 679-728. <https://doi.org/10.1146/annurev-earth-081320-064052>
- SÉON, N., R. AMIOT, J.E. MARTIN, M.T. YOUNG, H. MIDDLETON, F. FOUREL, L. PICOT, X. VALENTIN and C. LÉCUYER 2020. Thermophysiology of Jurassic marine crocodylomorphs inferred from the oxygen isotope composition of their tooth apatite. *Philosophical Transactions of the Royal Society B*, 375(1793): 20190139. <https://doi.org/10.1098/rstb.2019.0139>
- SOTO-ACUÑA, S., E. GONZÁLEZ, D. BAJOR and A. MOURGUES. 2018. Presencia de cocodrilos marinos (Thalattosuchia: Metriorhynchidae) en el Bajociano del Grupo Caracoles, norte de Chile. *Libro de Resúmenes del I. Congreso Chileno de Paleontología*, pp. 364-368.
- SOTO-ACUÑA, S., R.A. OTERO, J. ALARCÓN, L. OSSA-FUENTES and O. ROJAS. 2015. Presencia de cocodrilos marinos (Thalattosuchia: Metriorhynchidae) en la Formación Cerritos Bayos (Oxfordiano), Cuenca de Tarapacá, Región de Antofagasta. *Libro de Resúmenes del XIV. Congreso Geológico Chileno*, pp. 690-693.
- SOTO-ACUÑA, S., R.A. OTERO and D. RUBILAR-ROGERS. 2012. Un nuevo ejemplar de *Metriorhynchus casamiquelai* Gasparini y Chong, 1977 (Crocodylomorpha: Thalattosuchia) del Caloviano de Sierra de Moreno, Región de Antofagasta. *Libro de Resúmenes del XIII. Congreso Geológico Chileno*, pp. 755-757.

- SPINDLER, F., R. LAUER, H. TISCHLINGER and M. MÄUSER. 2021. The integument of pelagic crocodylomorphs (Thalattosuchia: Metriorhynchidae). *Palaeontologica Electronica*, 24(2): a25. <https://doi.org/10.26879/1099>
- TAVERA, J. 1981. *Ichthyosaurus* de la Formación Lautaro, en el área de Manflas, Región de Atacama. *Comunicaciones, Universidad de Chile, Departamento de Geología*, 33: 1-16.
- VIGNAUD, P. and Z. GASPARINI. 1996. New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) in the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences*, 322(2a): 245-250.
- WILBERG, E.W. 2015A. A new metriorhynchoid (Crocodylomorpha, Thalattosuchia) from the Middle Jurassic of Oregon and the evolutionary timing of marine adaptations in thalattosuchian crocodylomorphs. *Journal of Vertebrate Paleontology*, 35(2): e902846. <https://doi.org/10.1080/02724634.2014.902846>
- WILBERG, E.W. 2015B. What's in an outgroup? The impact of outgroup choice on the phylogenetic position of Thalattosuchia (Crocodylomorpha) and the origin of Crocodyliformes. *Systematic Biology*, 64(4): 621-637. <https://doi.org/10.1093/sysbio/syv020>
- WILBERG, E.W., P.L. GODOY, E.F. GRIFFITHS, A.H. TURNER and R.B.J. BENSON. 2022. A new early diverging thalattosuchian (Crocodylomorpha) from the Early Jurassic (Pliensbachian) of Dorset, U.K. and implications for the origin and evolution of the group. *Journal of Vertebrate Paleontology*, 42(3): e2161909. <https://doi.org/10.1080/02724634.2022.2161909>
- WILBERG, E.W., A.H. TURNER and C.A. BROCHU. 2019. Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. *Scientific Reports*, 9: 514. <https://doi.org/10.1038/s41598-018-36795-1>
- WILKINSON, L.E., M.T. YOUNG and M.J. BENTON. 2008. A new metriorhynchid crocodilian (Mesoeucrocodylia: Thalattosuchia) from the Kimmeridgian (Upper Jurassic) of Wiltshire, UK. *Palaeontology*, 51(6): 1307-1333. <https://doi.org/10.1111/j.1475-4983.2008.00818.x>
- WINTRICH, T., S. HAYASHI, A. HOUSSAYE, Y. NAKAJIMA and P.M. SANDER. 2017. A Triassic plesiosaurian skeleton and bone histology inform on evolution of a unique body plan. *Science Advances*, 3(12): e1701144. DOI: 10.1126/sciadv.1701144
- YOUNG, C.C. 1948. Fossil crocodiles in China, with notes on dinosaurian remains associated with the Kansu crocodiles. *Bulletin of the Geological Society of China*, 28(3-4): 255-288.
- 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(3): 551-585. <https://doi.org/10.1111/j.1096-3642.2009.00536.x>
- YOUNG, M.T., M.B. ANDRADE, S.L. BRUSATTE, M. SAKAMOTO and J. LISTON. 2013. The oldest known metriorhynchid super-predator: a new genus and species from the Middle Jurassic of England, with implications for serration and mandibular evolution in predacious clades. *Journal of Systematic Palaeontology*, 11(4): 475-513. <https://doi.org/10.1080/14772019.2012.704948>
- 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(2): 510-553. <https://doi.org/10.1093/zoolinnean/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-OMENACA 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(9): e44985. <https://doi.org/10.1371/journal.pone.0044985>
- 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(4): 801-859. <https://doi.org/10.1111/j.1096-3642.2009.00571.x>
- YOUNG, M.T., D. DUFEAU, C. BOWMAN, T. COWGILL, J.A. SCHWAB, L.M. WITMER, Y. HERRERA, O.L. KATSAMENIS, L. STEEL, M. RIGBY and S.L. BRUSATTE. 2024B. Thalattosuchian crocodylomorphs from the Sinemurian (Early Jurassic) of the UK. *Zoological Journal of the Linnean Society*, 201(3): zlae079. <https://doi.org/10.1093/zoolinnean/zlae079>
- YOUNG, M.T., E.W. WILBERG, M.M. JOHNSON, Y. HERRERA, M.B. ANDRADE, A. BRIGNON, S. SACHS, P. ABEL, D. FOFFA, M.S. FERNÁNDEZ, P. VIGNAUD, T. COWGILL and S.L. BRUSATTE. 2024A. The history, systematics, and nomenclature of Thalattosuchia (Archosauria: Crocodylomorpha). *Zoological Journal of the Linnean Society*, 200(2): 547-617. <https://doi.org/10.1093/zoolinnean/zlad165>

ZAMMIT, M. 2011. Australasia's first Jurassic ichthyosaur fossil: an isolated vertebra from the Lower Jurassic Arataura Formation of North Island, New Zealand. *Alcheringa*, 35(3): 341-343. <https://doi.org/10.1080/03115518.2010.497056>

ZVERKOV, N.G., D.V. GRIGORIEV and I.G. DANILOV. 2020. Early Jurassic paleopolar marine reptiles of Siberia. *Geological Magazine*, 158: 1305-1322. <https://doi.org/10.1017/S0016756820001351>