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Fossil Focus: Thalattosuchia

by Mark T. Young[*1], Sven Sachs[2] & Pascal Abel[3]

Introduction:

To most people, crocodilians are large-bodied carnivores that have been unchanged since the age of the dinosaurs. However, during their 230 million-year history, modern crocodilians and their extinct relatives evolved a stunning diversity of body plans, with many looking very different from those alive today (crocodiles, alligators, caimans and gharials).

The first crocodylomorphs (the term used for living crocs and various fossil groups) are known from the Late Triassic Period, approximately 235 million to 237 million years ago. These animals lived on land and looked much more like a greyhound than a crocodile, with long legs and a skull that was deep like that of a meat-eating dinosaur, rather than flattened like that of a living crocodile. In fact, many of the fragmentary fossils of these first crocodylomorphs have been confused with dinosaur fossils. For their first 30 or so million years, crocodylomorphs lived only on land. This didn't change until the mass extinction event that separates the Triassic from the Jurassic Period (approximately 201 million years ago), and which wiped out the terrestrial, semi-aquatic and marine reptiles that had been dominant during the Late Triassic. This extinction event not only radically altered crocodylomorph evolution, but ensured that dinosaurs became the dominant group of terrestrial vertebrates during the Jurassic and Cretaceous Periods.

After the Triassic–Jurassic extinction event, the first semi-aquatic crocodylomorphs, which lived partly on land and partly in water, appeared. These were followed soon after by the first marine crocodylomorphs, the thalattosuchians. Thalattosuchia was the pinnacle of marine specialization among crocodylomorphs. First appearing within 10 million years of the Triassic–Jurassic extinction event, they continued well into the Early Cretaceous, with the most recent known thalattosuchian fossil approximately 125 million years old. The early thalattosuchians looked similar to living Indian gharials: they were semi-aquatic, long-snouted and probably fed on small-bodied fish. These forms would ultimately give rise to species that could swim in the open ocean and looked more like today's dolphins and killer whales. This article provides an introduction to this extraordinary group, including an overview of their diversity, fossil discoveries and what we can infer about their biology.

Thalattosuchian biodiversity:

Thalattosuchians are divided into two groups: Teleosauroidea and Metriorhynchoidea (Figs. 1, 2). We know that these two groups diverged during the Early Jurassic, by at least the early Toarcian age (approximately 182 million years ago). The fossil record reveals a high diversity of teleosauroids (*Steneosaurus bollensis*, *Steneosaurus brevior*, *Steneosaurus gracilirostris* and *Platysuchus multiscrobiculatus*; Fig. 3) and one metriorhynchoid (*Pelagosaurus typus*) from across Europe at this time. Fossils are known from the Holzmaden area of Germany, Normandy in France, and Whitby and

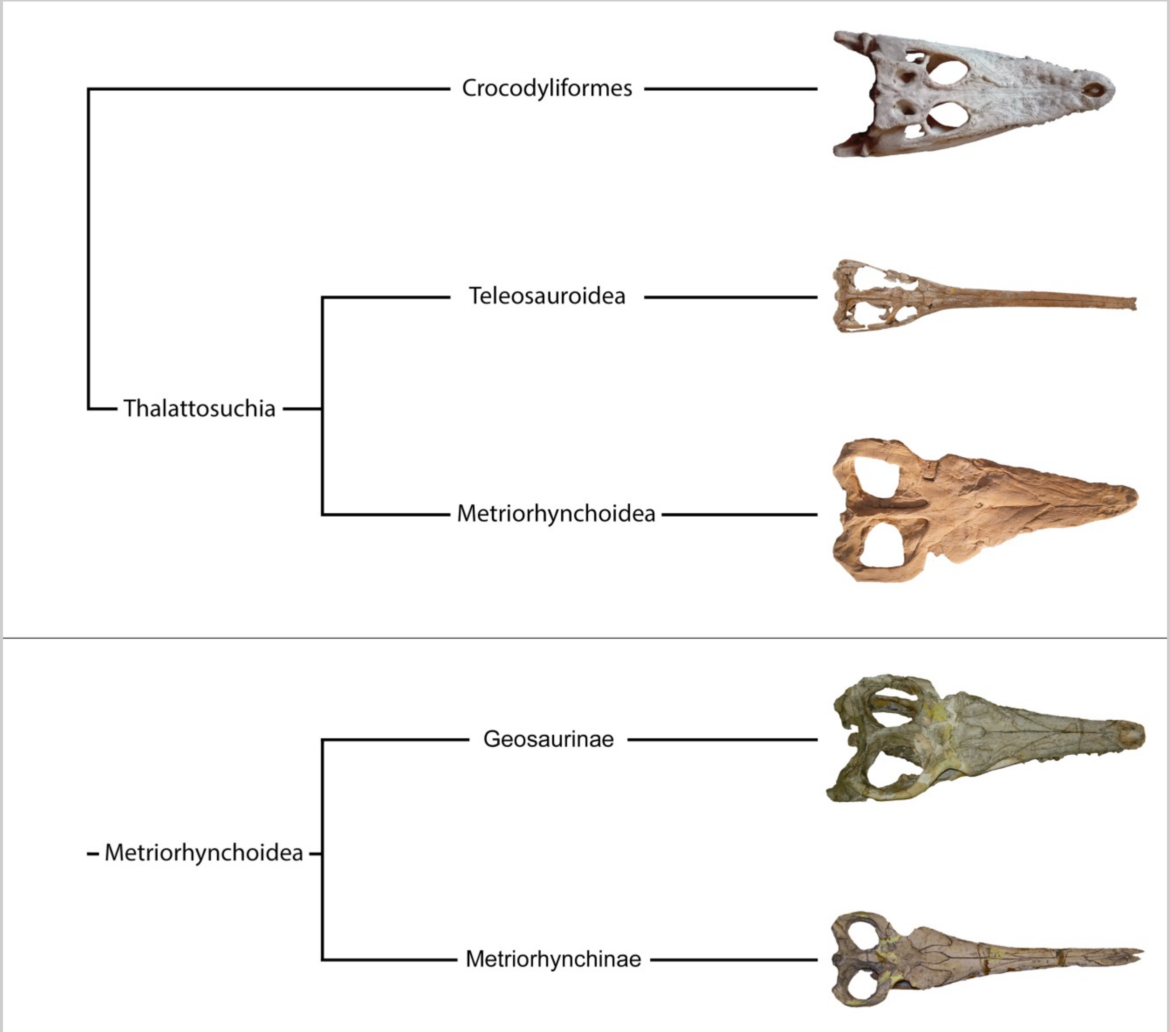

Figure 1 — A simplified look at the evolutionary relationships of Thalattosuchia. Top: how the two major subgroups of thalattosuchians relate to living crocodilians. Bottom: the two subgroups of metriorhynchids. The crocodyliform skull is a Yacare caiman (*Caiman yacare*), the teleosauroid skull is *Steneosaurus leedsi* and the metriorhynchoid skull is *Dakosaurus maximus*. The geosaurine skull is '*Metriorhynchus*' *casamiquelai* and the metriorhynchine skull is *Cricosaurus araucanensis*. Credit: M. Young, S. Sachs, P. Abel and NHM image resources.

Somerset in England. Thus, at least in the group of islands that made up what is now Europe 182 million years ago, the teleosauroids were the largest-bodied and most dominant crocodylomorph group.

History of study:

Thalattosuchians were among the first group of fossil reptiles to be named and described in scientific journals. In 1758, two scientific papers were written about the discovery of a partial thalattosuchian skeleton near Whitby. In the first, Captain William Chapman stated that the skeleton had been found in January 1758; the second paper, by Charles Morton and John Wooller, claimed the skeleton had actually been discovered about ten years previously. This skeleton also caused other disagreements among eighteenth-century naturalists and anatomists. Some considered it to be closely related to living

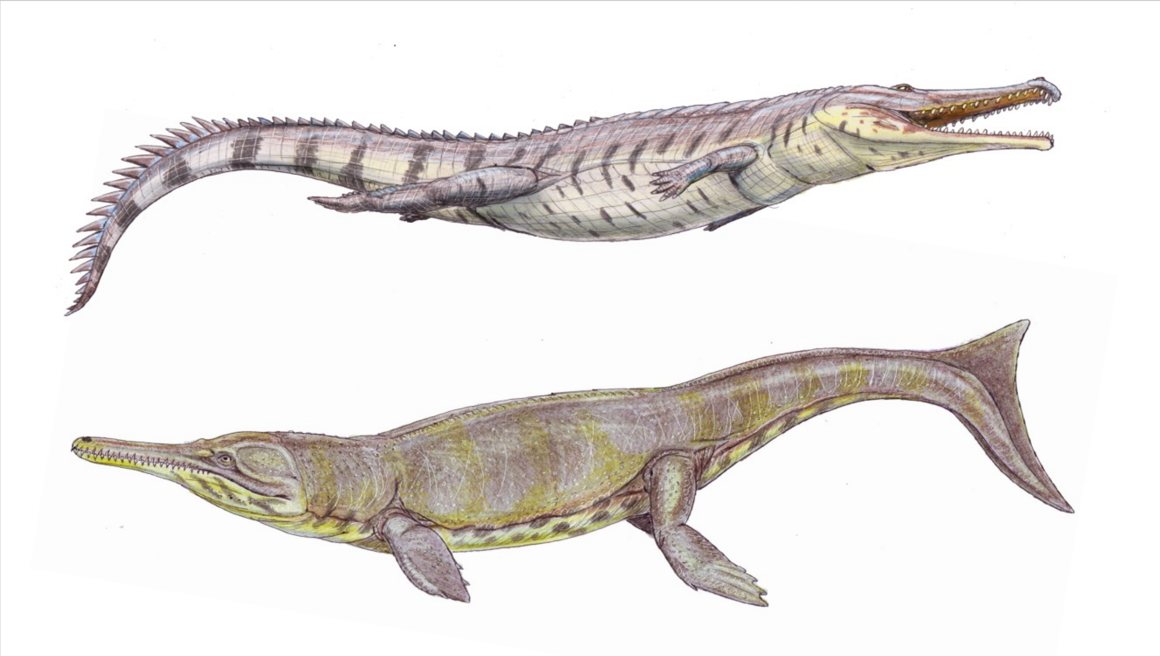

Figure 2 — Life reconstructions of two thalattosuchians. Top: the teleosauroid *Machimosaurus hugii* (by Dmitry Bogdanov). Bottom: the metriorhynchid *Metriorhynchus superciliosus* (by Dmitry Bogdanov).

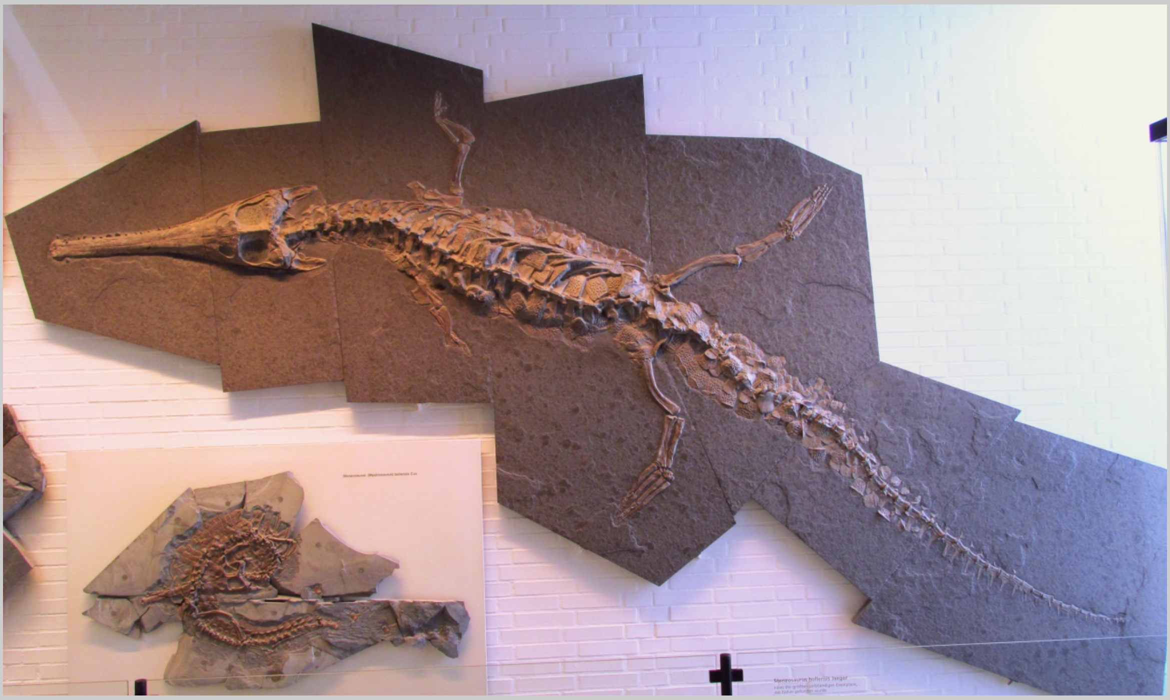

Figure 3 — Skeleton of *Steneosaurus bollensis*, Lower Jurassic (early Toarcian, Posidonienschiefer Formation) of Holzmaden (Germany). Length ~ 4 m. On display at the Urweltmuseum Hauff in Holzmaden (Germany). Credit: S. Sachs.

crocodilians, whereas others thought it was a whale or dolphin. Recent re-study of this materials strongly suggests that the specimen is a large teleosauroid, belonging to the species *Steneosaurus bollensis*. To the best of our knowledge, this specimen was the first fossil crocodylomorph described in a scientific paper. After its discovery, it formed part of the collection of the Royal Society, a scientific society in London, but it was transferred to the British Museum in 1781. Today, the specimen is held in the Natural History Museum in London.

During the latter half of the eighteenth century, more thalattosuchian fossils were discovered across Europe, particularly in England, France, Germany and Italy. The first scientific paper that named a thalattosuchian was by Samuel Thomas von Sömmerring in 1814 (Fig. 4). This was the teleosauroid *Steneosaurus priscus*. The skeleton was discovered in a quarry in Daiting in Bavaria, Southern Germany. The first description of a metriorhynchoid was also by von Sömmerring, two years later, in 1816. This species, *Geosaurus giganteus*, was discovered in the same quarry as *Steneosaurus priscus*, albeit at twice the depth. This means that the first species in both major thalattosuchian subgroups had already been described and named before William Buckland named the first dinosaur in 1824. Thalattosuchians continued to be widely studied during the nineteenth century in Europe: there was something of a 'gold rush' in naming new species, or giving already-described species new names, between the 1820s and the 1850s. It was not until the seminal work of the French father-and-son team Jacques and Eugène Eudes-Deslongchamps (Fig. 4) in the 1860s that the classification of thalattosuchians began to stabilize.

Unfortunately, the study of thalattosuchians largely fell into obscurity during much of the twentieth century in Europe (although there were certain decades in which thalattosuchian research advanced in France, in particular the 1950s and 1990s). The longest and most detailed descriptions of thalattosuchians were written between 1901 and 1913, including seminal papers on German specimens by Eberhard Fraas (Figs. 4, 5) in 1901 and 1902 (where the term Thalattosuchia was first coined and defined) and the descriptive catalogue of the British Oxford Clay marine reptiles held in the

Figure 4 — Photographs of famous naturalists and scientists who have conducted research into thalattosuchians. Left: The German anatomist Samuel Thomas von Sömmerring (28 January 1755 – 2 March 1830). Source: Wikimedia Commons. Middle: The French naturalist Eugène Eudes-Deslongchamps (10 March 1830 – 21 December 1889). Source: Wikimedia Commons. Right: The German scientist Eberhard Fraas (26 June 1862 – 6 March 1915). Source: Wikimedia Commons.

Figure 5 — *Cricosaurus suevicus* from the Upper Jurassic (late Kimmeridgian) of Nusplingen (Germany). Length ~ 2 m. Top: Photograph of the skeleton described by Eberhard Fraas in 1901, 1902. Middle: The life reconstruction appearing in Fraas' work. Bottom: A modern life reconstruction by Joschua Knüppe. Skeleton on display in the Staatliches Museum für Naturkunde Stuttgart. Credit: M. B. Andrade.

Natural History Museum, London, by Charles Andrews in 1913. However, there was extensive research into thalattosuchians in South America, starting during the 1970s and continuing to the present day. New species were described from beautifully preserved 3D skulls (Fig. 6). These exquisite specimens helped show just how diverse thalattosuchians were becoming during the Jurassic.

Figure 6 — Skulls of the South American metriorhynchids (seen in dorsal view). a, *Cricosaurus araucanensis* from the Upper Jurassic (early Tithonian) of Argentina. b, ‘*Metriorhynchus*’ *casamiquelai* from the Middle Jurassic (middle Callovian) of Chile. c, *Dakosaurus andiniensis* from the Upper Jurassic (late Tithonian) of Argentina. d, *Purranisaurus potens* from the Upper Jurassic (late Tithonian) of Argentina. Credit: Z. Gasparini and S. Sachs.

Since the turn of the millennium, there has been a renaissance in thalattosuchian research. More new species have been named in the past 18 years than in the previous 100. Moreover, their evolutionary relationships are being investigated, and insights are being made into how they fed, moved and reproduced. Today, research into thalattosuchians is at the cutting edge of science, with CT scanning being used to peer inside their skulls to investigate what happened to their brains and sensory systems during the land-to-sea transition.

Teleosauroidea:

During the Jurassic, teleosauroids spread out across the world, and today fossils are found in Africa (Ethiopia, Madagascar, Morocco and Tunisia), Asia (China, India and Thailand) and Europe (France, Germany, Luxembourg, Poland, Portugal, Spain, Slovakia, Switzerland and the United Kingdom). Their fossils are mostly known from lagoons and coastal marine environments, but some fossils are also known from estuaries and freshwater ecosystems. At the same time as they spread out, they became highly diverse. In most ecosystems, there were three ‘ecomorphotypes’: (1) long-snouted forms that looked like a living Indian gharial, with many small, pointed teeth well suited to grasping small fish; (2) long-snouted forms that had a shorter snout and fewer teeth than ‘ecomorphoype’ 1, although the teeth were bigger and would have helped tackle larger prey; and (3) short-snouted forms that had even fewer teeth, but in which the teeth were very robust, with numerous ridges on the enamel. These three ecomorphotypes occurred in several ecosystems where multiple species of teleosauroids are known, and it seems that teleosauroids maintained their high species diversity by feeding on different types of prey.

By the end of the Middle Jurassic, a new type of teleosauroid had evolved: the Machimosaurini. This group includes the genera *Lemmysuchus* and *Machimosaurus* (Fig. 7). These were the giants of the

Figure 7 — Skulls of machimosaurin teleosauroids in dorsal view. Top: *Machimosaurus buffetauti*, Upper Jurassic (early Kimmeridgian, Lacunosamergel Formation) of Neuffen (Germany). Bottom: *Lemmysuchus obtusidens*, Middle Jurassic (middle Callovian, Oxford Clay Formation) of Peterborough (England). Credit: R. Schoch and NHM image resources.

teleosauroid group, reaching between 5 metres and 7.2 metres in length, and they were the largest crocodylomorphs of the Jurassic. Machimosaurins started out similar to the third ecomorphotype described in the previous paragraph, with short snouts and robust teeth. During the Late Jurassic and Early Cretaceous, they evolved blunt teeth with serrated edges, even shorter snouts and huge jaw-closing muscles, and they are thought to have fed on sea turtles. Marine turtle shells from the Late Jurassic and Early Cretaceous of Europe and Africa are frequently found with *Machimosaurus* teeth stuck in their shells, or with deep circular bite-marks matching *Machimosaurus* teeth (Fig. 8).

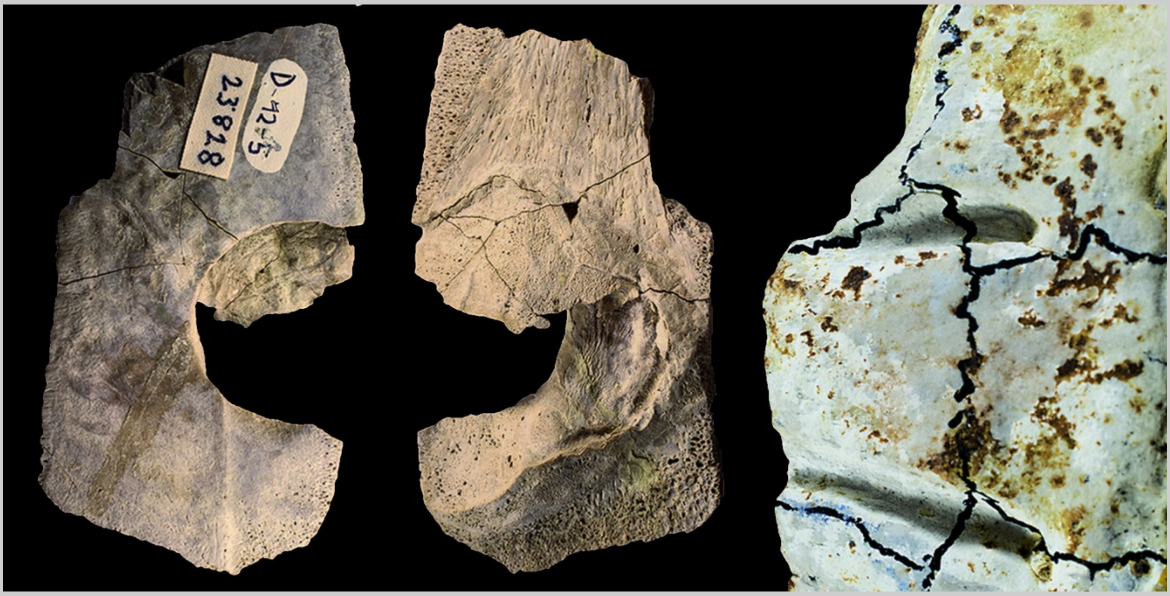

Figure 8 — Marine turtle shell fragments from the Solothurn Turtle Limestone of Switzerland (Upper Jurassic, late Kimmeridgian). Left and middle: Unidentified turtle shell with round *Machimosaurus* bite marks. Right: Grooves on a *Plesiochelys* carapace caused by the back teeth of *Machimosaurus*. Credit: S. Thüring.

Metriorhynchoidea:

The second group of thalattosuchians, metriorhynchoids, can be split into two subgroups: (1) true metriorhynchids that evolved into dolphin-like forms with a tail fin, flippers and loss of bony armour; and (2) 'basal metriorhynchoids' that are intermediate between the gharial-like teleosauroids and the dolphin-like metriorhynchids (Fig. 9). These basal metriorhynchoids are a poorly understood series of species that are largely known from broken fossils, mostly incomplete skulls. However, they must have been successful, because from a 15-million-year span of time in the Early and Middle Jurassic they are known from the United Kingdom, France, Germany, Portugal, Hungary, China, Chile and Oregon in the United States. Each of these species can provide some insights into how the metriorhynchid body plan evolved. Unfortunately, because all but one of these species are known only from fragmentary fossils, it's not clear what skeletal changes occurred as thalattosuchians evolved from gharial-like to dolphin-like forms.

The oldest known basal metriorhynchoid is *Pelagosaurus typus* (Fig. 10). *Pelagosaurus* is well known and lived across Europe during the Early Jurassic (approximately 182 million years ago), alongside other species of teleosauroids. It looked similar to teleosauroids, but had numerous features that show it is more metriorhynchid-like: eyes facing outwards and slightly forwards (not upwards as in living crocodilians and teleosauroids); a bony ring to support the eyeball; enlarged openings for carotid arteries at the back of the skull; and long foot bones (metatarsals), making the feet more paddle-like. The fossil record shows that the species of basal metriorhynchoids known from fragmentary fossils became increasingly metriorhynchid-like through time.

True metriorhynchids are known from the Middle Jurassic to the Early Cretaceous (approximately 168 million to 125 million years ago; Fig. 11). They evolved numerous adaptations to living in a marine environment, including flippers and a tail fin (Fig. 12). Oddly, however, the oldest known

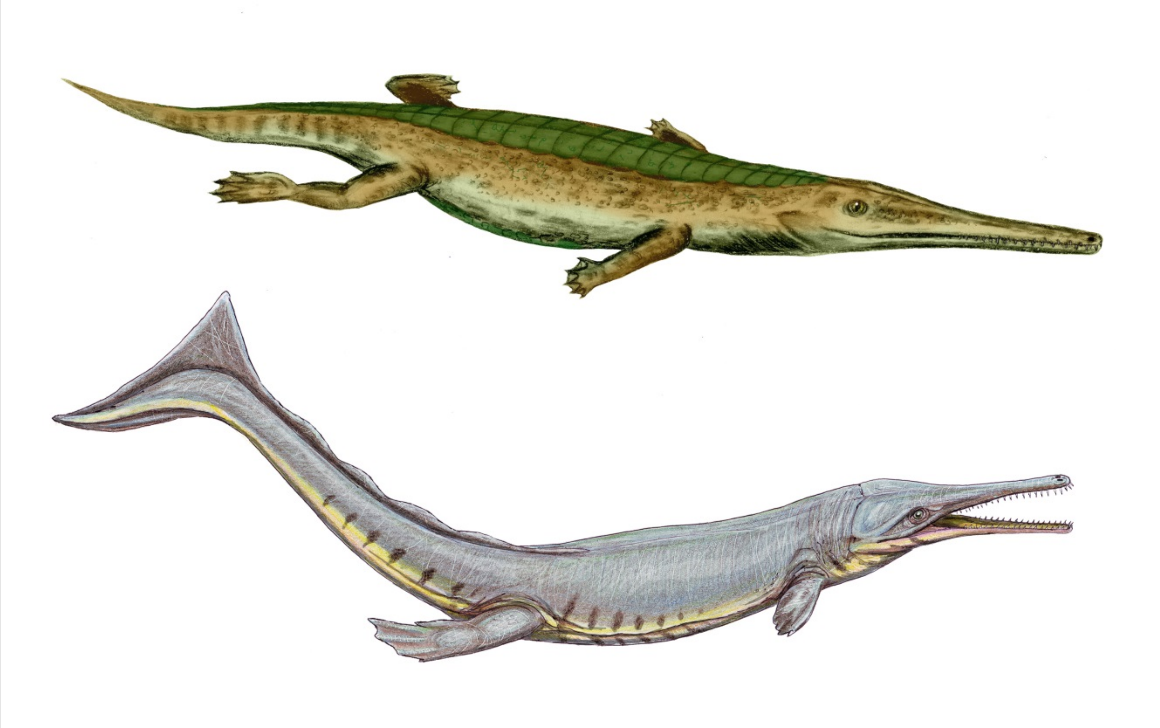

Figure 9 — Life reconstructions of two metriorhynchoids. Top: The 'basal metriorhynchoid' *Pelagosaurus typus* (by Nobu Tamora). Bottom: The metriorhynchid *Cricosaurus suevicus* (by Dmitry Bogdanov).

Figure 10 — Skeleton of *Pelagosaurus typus*, Lower Jurassic (early Toarcian, Posidonienschiefer Formation) of Dotternhausen (Germany) with a pathological lower jaw. Length ~ 2 m. On display at the Werksforum Dotternhausen in Dotternhausen (Germany). Credit: S. Sachs.

Figure 11 — Skeleton of *Metriorhynchus superciliosus*, Middle Jurassic (middle Callovian, Oxford Clay Formation) of Peterborough (England). Length ~ 3 m. On display in the Paläontologische Sammlung der Universität Tübingen (Germany). Credit: S. Sachs.

metriorhynchids are too advanced to have been the ancestors of this unique group. Analyses of the evolutionary relationships of thalattosuchians place the oldest known metriorhynchid, *Neptunidraco ammoniticus* from the Middle Jurassic of Italy, as a member of the group Geosaurinae. This confirms that metriorhynchids can be split into two major subgroups: (1) the metriorhynchines, which include the forms that were best adapted to a marine existence (large tail fins and nostrils that were not on the tip of the snout, but closer to the eyes) and are largely long-snouted species that probably fed on small fish or squid; and (2) the geosaurines, which include the largest-bodied metriorhynchids (*Plesiosuchus* and the species closely related to it), forms such as *Dakosaurus* that were similar to living false killer whales, and *Geosaurus*, which was similar to living barracudas. However, no one has yet found any fossil relatives of these two groups, which would represent the earliest metriorhynchids, and therefore we still have no answers to key questions such as when metriorhynchids evolved, where they evolved and what underpinned their sudden marine diversification.

Another important question related to the biology of metriorhynchids is whether they gave birth to live young (like some sea snakes), or came back onto land to lay eggs (like marine turtles). Unfortunately, no fossilized eggs or embryos have been discovered yet. However, the unusual shape of their pelvis could be informative: it has a large diameter, which could be a sign that they gave birth to live young. Only the discovery of new fossils will answer this tantalizing question.

Extinction:

Exactly when the thalattosuchians became extinct is currently unclear. New discoveries from closer to the equator are pushing the fossil record of teleosauroids and metriorhynchoids deeper into the Cretaceous. The 7-metre giant *Machimosaurus rex* from Tunisia is currently the most recent known teleosauroid (from around 130 million years ago), and the most recent known metriorhynchid fossil is

Figure 12 — Modifications of the limbs and tail in Thalattosuchia, showing the evolution of flippers and a tail fin, and loss of bony armour. Top: The forelimb (left) and hindlimb (right) of the teleosauroid *Platysuchus multiscrobiculatus*, Lower Jurassic (early Tithonian, Posidonienschiefer Formation) of Holzmaden (Germany). Middle: The forelimb (left) and hindlimb (right) of the metriorhynchid *Dakosaurus maximus*, Upper Jurassic (late Kimmeridgian, Torleite Formation) of Painten (Germany). Bottom: End of the tail of the teleosauroid *Steneosaurus bollensis* (left) and the metriorhynchid *Cricosaurus* sp. (right). Credit: M. Young and S. Sachs.

an isolated tooth crown from the Aptian Age (about 125 million years ago) of Sicily. This tooth crown has a unique shape, cutting edge and serration, which suggests that it belonged to a close relative of the largest known metriorhynchid, *Plesiosuchus* (and not a plesiosaur, as suggested by some researchers).

Future work:

The biggest obstacle to our understanding of thalattosuchian evolution comes from finding and describing new fossils, in particular those from outside Western Europe. The amazing Argentinean and Chilean fossils have transformed our understanding of thalattosuchian diversity (in particular that of *Dakosaurus andiniensis*; Fig. 6). New discoveries of teleosauroid fossils from Thailand hint that some thalattosuchians might have lived in freshwater ecosystems, and the recent discovery of the giant *Machimosaurus rex* from the Early Cretaceous of Tunisia has overturned our ideas that teleosauroids went extinct at the end of the Jurassic. These findings suggest there is still plenty left to discover and learn.

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Suggestions for further reading:

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