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Author(s): Jonathan P. Tennant
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Fossil Focus: Mesozoic crocodyliforms

by Jonathan P. Tennant[*1]

Introduction:

Crocodilians are truly iconic creatures, and throughout history have inspired stories of dragons and soul-devouring gods. Modern crocodilians are the crocodiles, alligators, caimans and gharials, all part of the crown group Crocodylia (Fig. 1). There are only 23 recognized species alive today, and of these 10 are considered to be endangered, according to the IUCN red list, due to ongoing environmental disruption and human activity. This relative lack of modern diversity stands out in stark contrast to that of their close relatives, the dinosaurs, whose modern descendants, the birds, have about 10,000 species around today! It isn't obvious from looking at modern birds and crocodiles that they share a common ancestor. For instance, when was the last time you saw a feathered crocodile, or a pigeon sitting on a river bank waiting to ambush an unsuspecting wildebeest?

Figure 1 — Clockwise from top: Saltwater crocodile (*Crocodylus porosus*), American alligator (*Alligator mississippiensis*) and Indian gharial (*Gavialis gangeticus*) (Source, CC BY-SA 3.0, Credit: Bobisbob).

To understand why the two groups are so different, we have to use a time machine: the fossil record. Going back to the Mesozoic era, between 252 million and 66 million years ago, we find the forerunners of living crocodilians, known as crocodyliforms, which were very different to their modern counterparts. They were an incredibly successful group, with a large number of different species characterized by a range of peculiar and unique features. Some were fully equipped for swimming out to sea, while others reached phenomenal sizes, rivalling those of the biggest predatory dinosaurs!

Crocodilians and their forerunners form a group known as Pseudosuchia, literally 'false crocodiles', of which crocodyliforms are a major part. Pseudosuchians are closely related to dinosaurs and pterosaurs, united in a group called Archosauria, and the split between these lineages happened around 250 million years ago, in the early Triassic period (Fig. 2). The only remnants of this ancient divergence are modern birds and crocodilians. The group Crocodylomorpha, which includes Crocodyliformes and a closely related group called Sphenosuchia, were the only major group of pseudosuchians to survive the mass-extinction event at the end of the Triassic period 201 million years ago, and around 120 million years after that, they gave rise to the group containing modern crocodiles and their kin, Crocodylia.

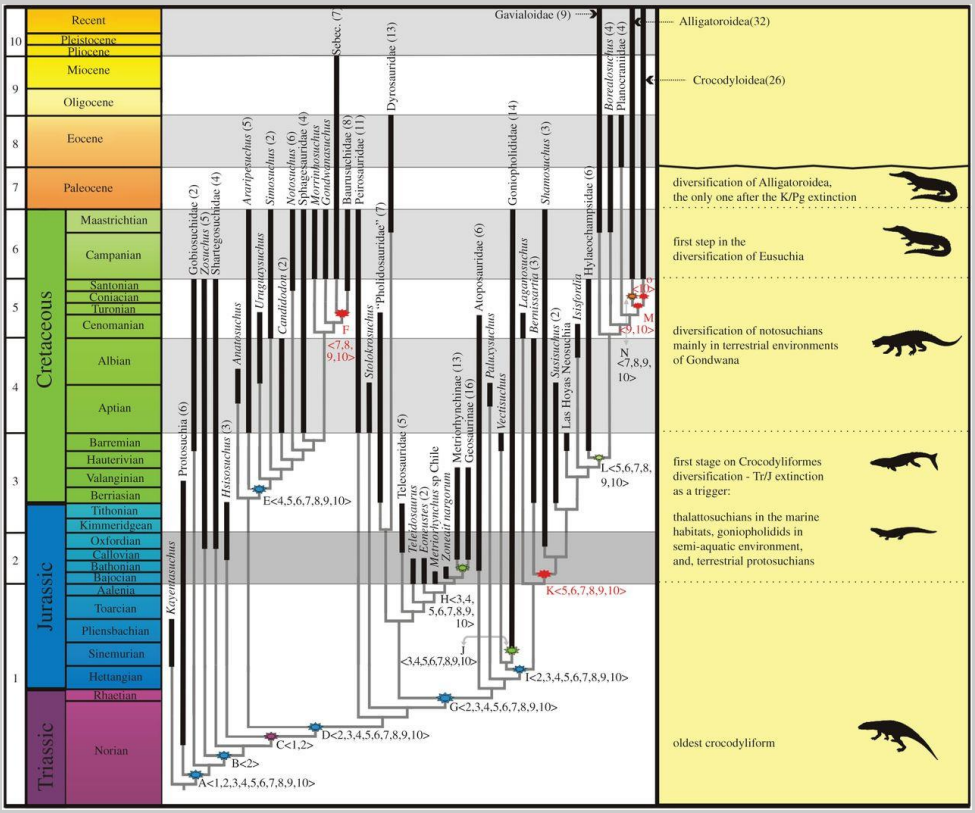

Figure 2 — Diversification events and relationships in the history of Crocodyliforms (Bronzati *et al.*, 2015).

Protosuchians and early crocodyliforms:

The earliest crocodyliforms, comprising the groups Protosuchia, Shartegosuchidae and Sphagesauridae, lived on land. They were small compared to modern species (usually no more than a metre in length), with two rows of osteoderms (a type of bony body armour) along their backs, and an upright limb

posture with a slender body (Fig. 3). They were widely distributed across the globe during the Jurassic period (201 million to 145 million years ago) and the Cretaceous period (145 million to 66 million years ago), and discoveries from South Africa and North America have helped to clarify their evolutionary relationships. Some researchers consider these groups to represent a 'grade' — a group defined by their similar appearance rather than strictly by their evolutionary relationships — because analyses suggest that not all of their descendants share the same common ancestor, which means that they are not a monophyletic group. A diverse array of early crocodyliforms, including *Zosuchus* and *Gobiosuchus*, survived until at least the Early Cretaceous in Central Asia, where they would have lived alongside more 'advanced' crocs before finally going extinct.

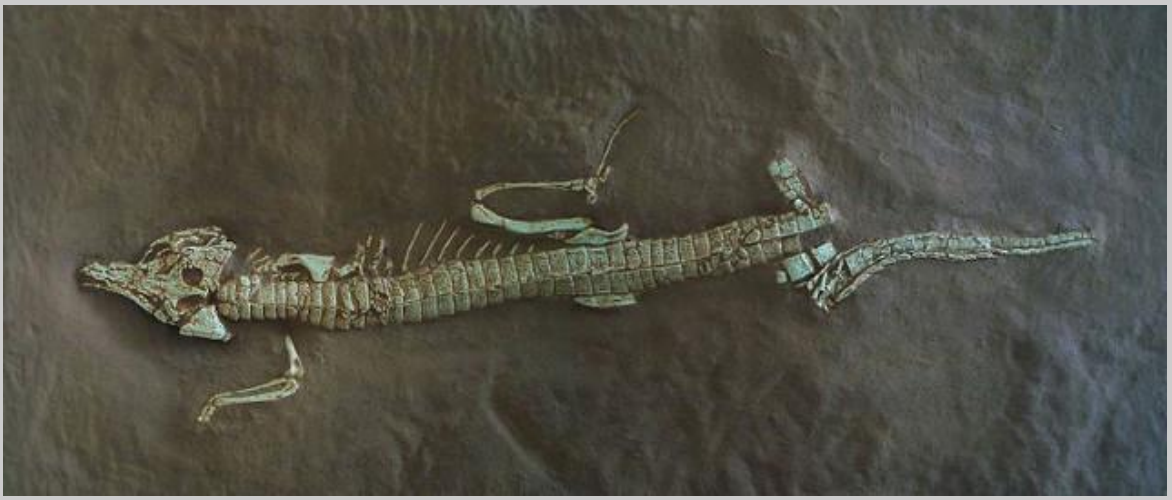

Figure 3 — *Protosuchus richardsoni* from the American Museum of Natural History, New York (cast) (Source, CC BY-SA 3.0, Credit: Smokeybjb).

Thalattosuchians:

What could be more terrifying than a 10-metre-long shark? Well, how about a 10-metre-long shark-croc? Thalattosuchians were a bizarre yet magnificent group of sea-dwelling reptiles, which were diverse during the Jurassic, but went extinct in the Early Cretaceous. They consist of two groups: the metriorhynchoids and the teleosauroids. Both of these groups could reach enormous proportions, and some evolved flipper-like limbs and tails, becoming quite shark-like (Fig. 4). The best discoveries come from South America and Europe, and are quite similar species, suggesting that some species could travel between these two continents in the Late Jurassic. Well-preserved skulls show that metriorhynchids had salt glands, similar to those of modern sharks, turtles, some sea birds and marine iguanas, which means that they were capable of drinking sea water.

The evolutionary relationships of thalattosuchians are poorly understood. Traditionally, they were thought to be closely related to other, more advanced, marine crocodyliforms, including pholidosaurids. However, this result is likely to be due to convergent evolution between the two groups that has made them appear superficially similar, especially in their possession of longer snouts, and in fact they might belong outside of Crocodyliformes, in the broader group of Crocodylomorpha.

In early 2016, a discovery from North Africa of a 12-metre-long teleosaurid known as *Teleosaurus rex* showed that this group survived an extinction event at the end of the Jurassic and start of the Cretaceous, where they were previously thought to have gone extinct, and became isolated in increasingly rare lagoonal environments as the shallow seas of Europe closed off due to a major fall in sea level. The timing of extinction for thalattosuchians is quite contentious; the youngest material interpreted as their fossilized remains might actually belong to a completely different group, the plesiosaurs, instead.

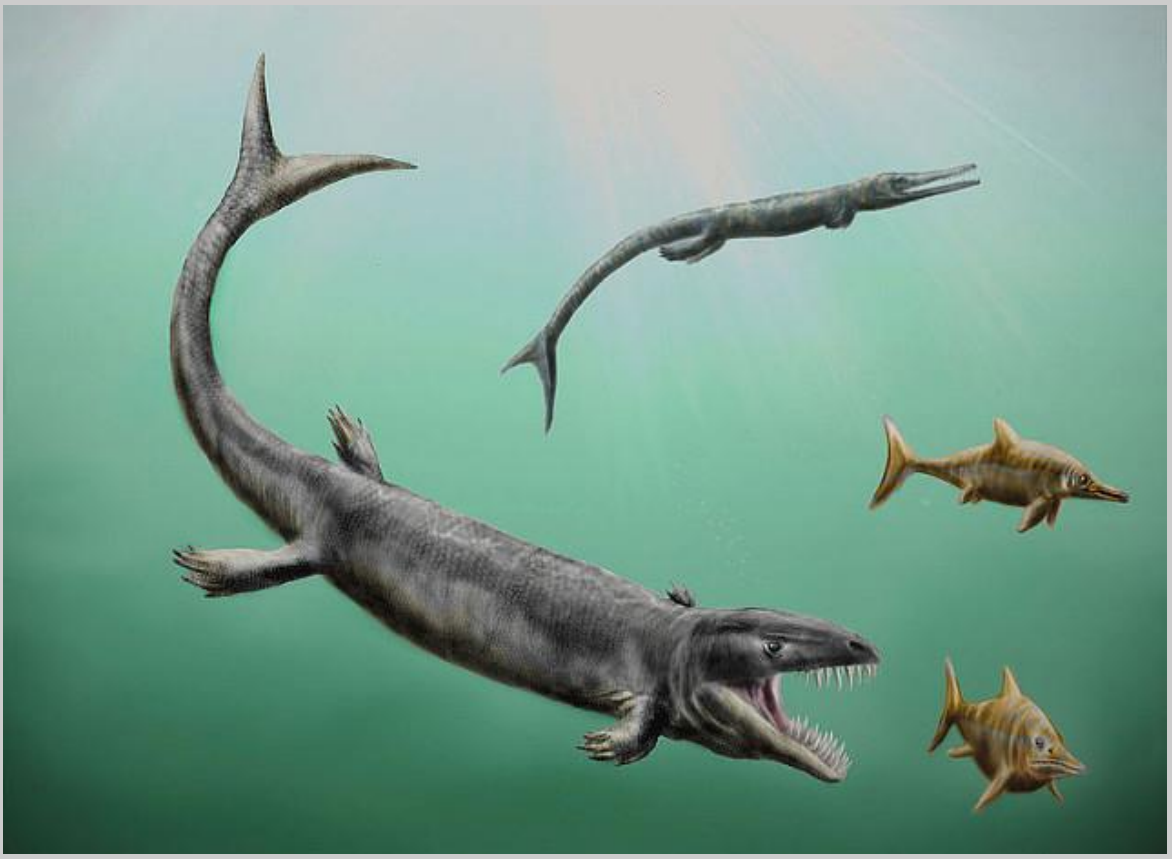

Figure 4 — *Dakosaurus* pursuing ichthyosaurs with *Cricosaurus* in the background (Source, CC BY-SA 3.0, Credit: Durbed).

Goniopholidids:

The goniopholidids were relatively small-bodied at 2–4 metres long, and abundant in freshwater and non-marine brackish environments in the Northern Hemisphere throughout the Jurassic and Cretaceous. The shape of their skulls was much more like that of modern crocodiles, being relatively long and flattened (Fig. 5). They also possessed a dual row of interlocking osteoderms on their backs and the underside of their bellies, giving them armoured protection and also bracing their bodies for movement on land.

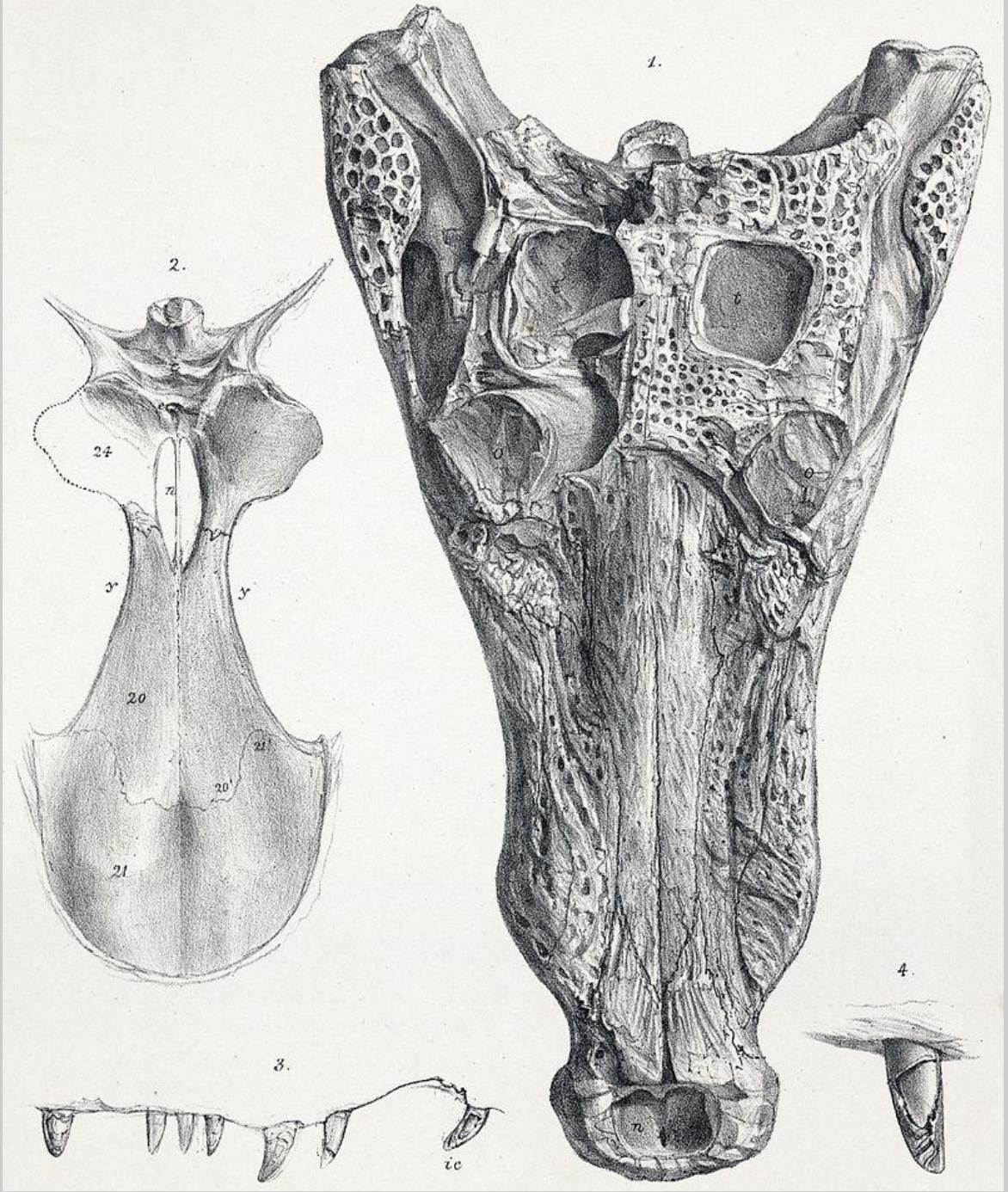

Figure 5 — Skull of *Goniopholis simus* by Richard Owen (half natural size).

As with many crocodyliform groups, which species belong to the group and how they are related remain fairly poorly understood, in spite of numerous discoveries. This is partly due to a failure to differentiate different species of *Goniopholis* based on their anatomy, but work is now showing that there is a hitherto under-appreciated diversity of goniopholidids, particularly in the Early Cretaceous of Europe.

The oldest fossil assigned to this group, *Calsoyasuchus*, comes from the Lower Jurassic of North America. If this species really is a goniopholidid, this has important implications because it means that we would expect other closely related crocodyliform groups to also have a Lower Jurassic record. This

is because lineages ‘split’ from each other instantaneously (geologically speaking), which implies that sister groups originate at the same time. If *Calsoyasuchus* is truly a goniopholidid, this would mean that the radiation of this group into Europe and Asia took place between 10 million and 15 million years after the origin of the group.

Atoposaurids:

Atoposaurids were typically no bigger than half a metre long, and were adapted primarily to near-shore environments such as lagoons or coastal estuaries (Fig. 6). Because of their size, they are relatively rare in the fossil record, which has made understanding their relationships quite difficult. Analyses have found that atoposaurids were actually confined to the Late Jurassic of Europe, with different populations occupying the French and German basins; Europe at the time was like a tropical island archipelago. Weird taxa previously assigned to this group, such as *Montsecosuchus* or *Brillanceausuchus*, probably represent much more advanced groups closer to paralligatorids (see below) than atoposaurids.

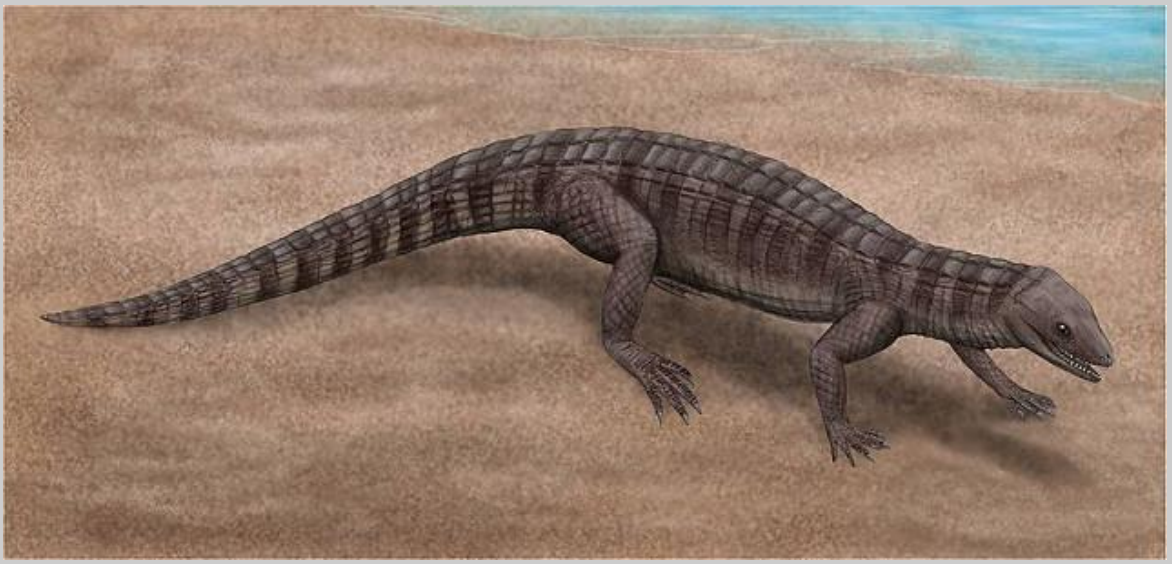

Figure 6 — The possible atoposaurid *Montsecosuchus depereti* from the Early Cretaceous of Spain (Source, CC BY-SA 3.0, Credit: Smokeybjb).

Notosuchians:

Notosuchians are often described as bizarre, and you only need to take a look at some of the nicknames given to them to understand why. They were a Cretaceous group of terrestrial species primarily from the Southern Hemisphere (Gondwana), some of which looked more like an armadillo than a crocodile, while others are known informally by names like ‘boar-croc’. They were generally small-bodied and quite slender, with characteristic short and deep skulls (Fig. 7). One genus is called *Simosuchus*, which translates as ‘pug-nosed crocodile’, due to its blunt snout (Fig. 8). Another, *Anatosuchus*, has been dubbed a crocoduck after its wide, flattened, pancake-shaped snout.

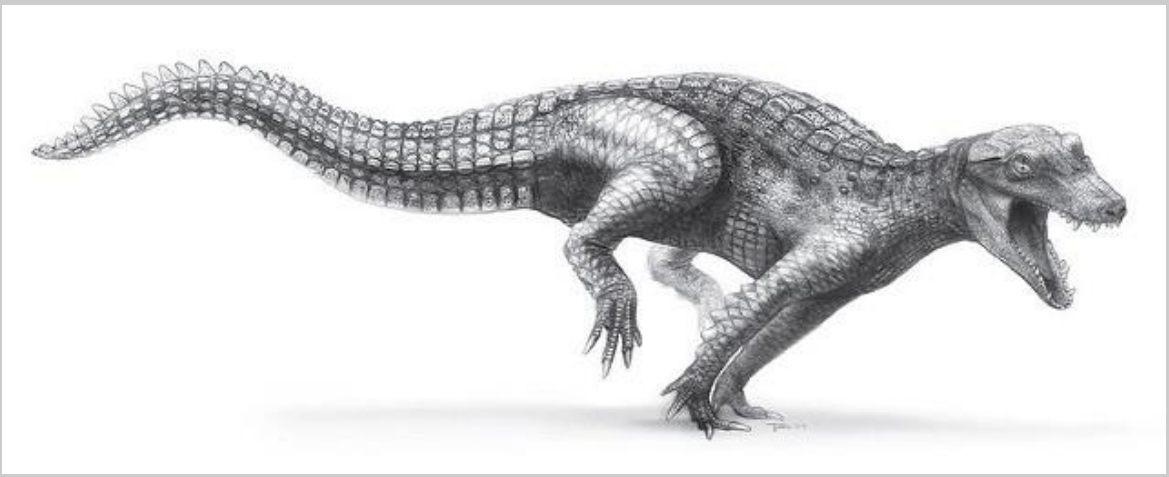

Figure 7 — Life restoration of the notosuchian *Araripesuchus wegeneri* (Sereno & Larsson 2009).

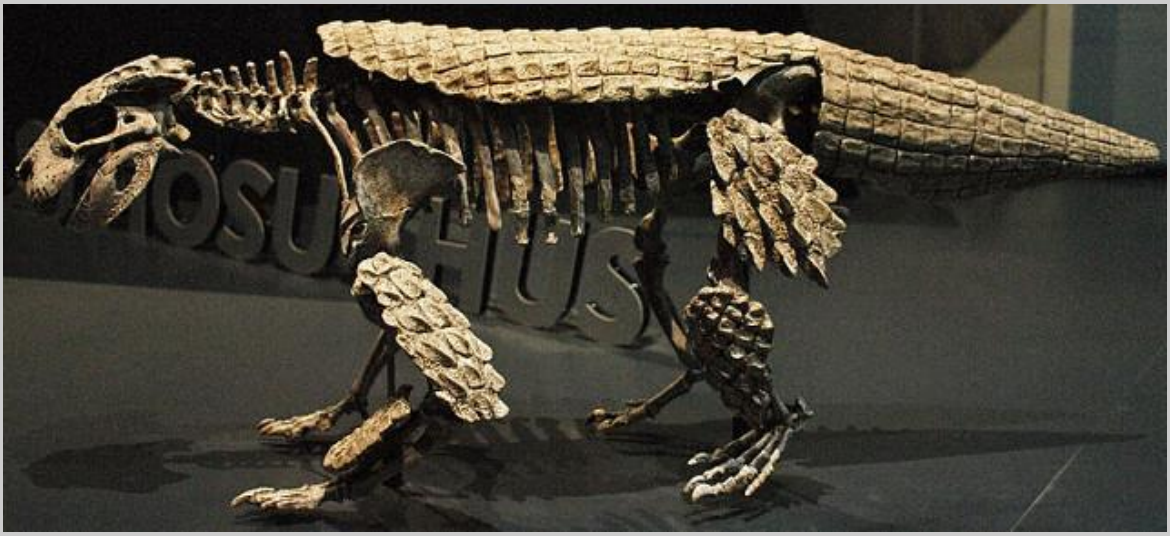

Figure 8 — Mounted skeleton of the notosuchian *Simosuchus* at the Royal Ontario Museum in Canada (Source, CC BY-SA 3.0, Credit: CaptMondo).

Some taxa, such as *Armadillosuchus*, had features that indicate that they were good at digging, possibly to build nests or burrows. Other groups, like sphagesaurids, had complex teeth similar to those of ornithischian dinosaurs such as *Iguanodon*, and this has led to them sometimes being misidentified as dinosaurs. Some genera, such as *Chimaerasuchus*, were adapted to consuming plant matter, and others were even tusked, which suggests that they might have foraged for different food items, including molluscs, arthropods and roots (Fig. 9). Not exactly the behaviour we associate with modern crocodiles! Others, such as baurusuchids, were well-adapted to a carnivorous lifestyle, and some such as *Yacarerani* even had teeth similar to what we see in mammals with complex and multi-cusped molars.

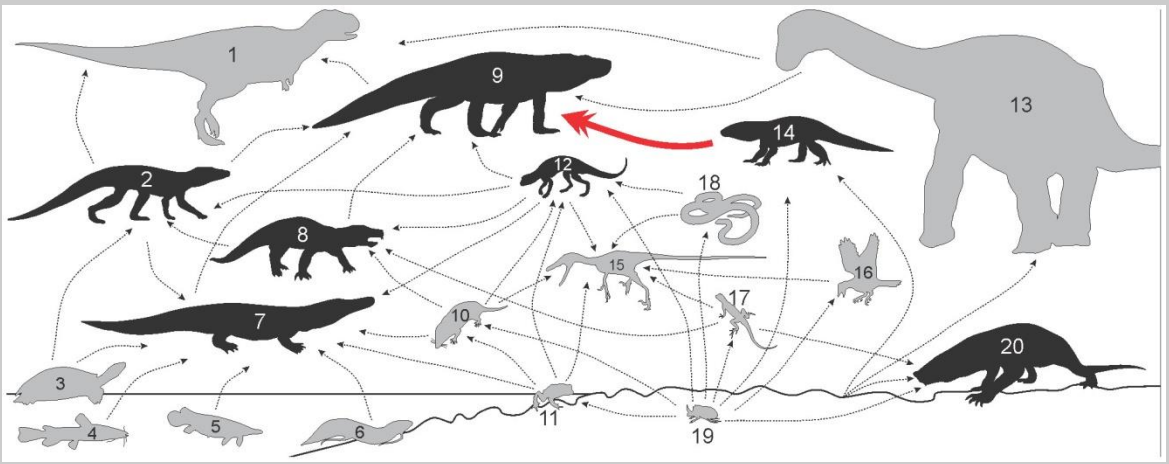

Figure 9 — Food-web reconstruction comprising notosuchians in the Late Cretaceous of Brazil (Godoy *et al*., 2014).

This diversity of forms might have contributed to the group's explosive diversification in the Late Cretaceous of Gondwana (Fig. 10).

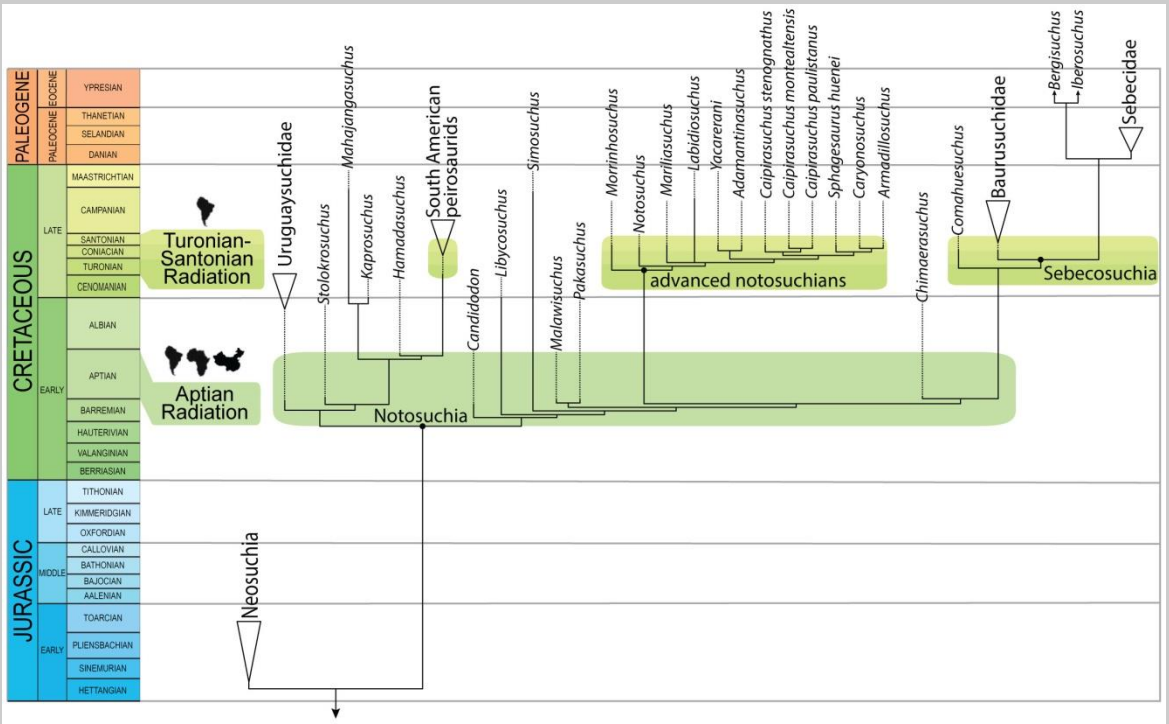

Figure 10 — Time-calibrated relationships of Notosuchia (Pol *et al*., 2014).

Paralligatorids:

This group (Fig. 11) was generally small to medium-sized at no more than 1–1.5 metres in length, and was widely geographically distributed during the Cretaceous of North America, Asia and Europe, as well as the late Jurassic of Brazil. Some genera, such as *Shamosuchus*, had teeth well adapted to crushing

shells, feeding predominantly on molluscs. The oldest genus, *Batrachomimus*, was originally identified as an early amphibian, hence the name, which refers to the Batrachia (frogs, salamanders and toads). The identification of *Wannchampsus* in 2014 from the Lower Cretaceous of Texas was important in showing that paralligatorids were very closely related to the group that includes modern crocodilians, Eusuchia.

Figure 11 — Life restoration of *Batrachomimus* from the Late Jurassic of Brazil (Source, CC BY-SA 3.0, Credit: Smokeybjb).

Hylaeochampsids:

Hylaeochampsids are a relatively poorly understood group, and the identity of the species that belong to this group is unclear. The group was defined on the basis of a skull from the Early Cretaceous of the United Kingdom, given the genus name *Hylaeochampsus*, but its evolutionary relationships, and which species belong to this group, have remained problems for crocodyliform researchers. Some studies have found that enigmatic taxa such as *Pachycheilosuchus* from the Early Cretaceous of Texas and *Pietraroiasuchus* from the Early Cretaceous of Italy might belong to this group. All of these taxa are characterized by short snouts, and might have possessed several different types of teeth. For example, *Iharkutosuchus* from the Late Cretaceous of Hungary had teeth adapted for crushing, similar to some notosuchians.

Pholidosaurids:

Pholidosaurids were known from semi-aquatic and marine environments throughout Europe, Africa and North and South America during the Cretaceous. They all had long, slender snouts, similar to the modern gharial (Fig. 12). Some were absolute monsters — *Sarcosuchus* from the middle Cretaceous of the Sahara reached up to 12 metres in length (twice as long as a modern saltwater crocodile) and weighed around 8 tonnes! It probably even preyed on dinosaurs, ambushing them at the edges of river systems, in a hunting style similar to that of the modern Nile crocodile. The evolutionary relationships of pholidosaurids are currently poorly understood, although the group might be closely related to the marine dyrosaurids.

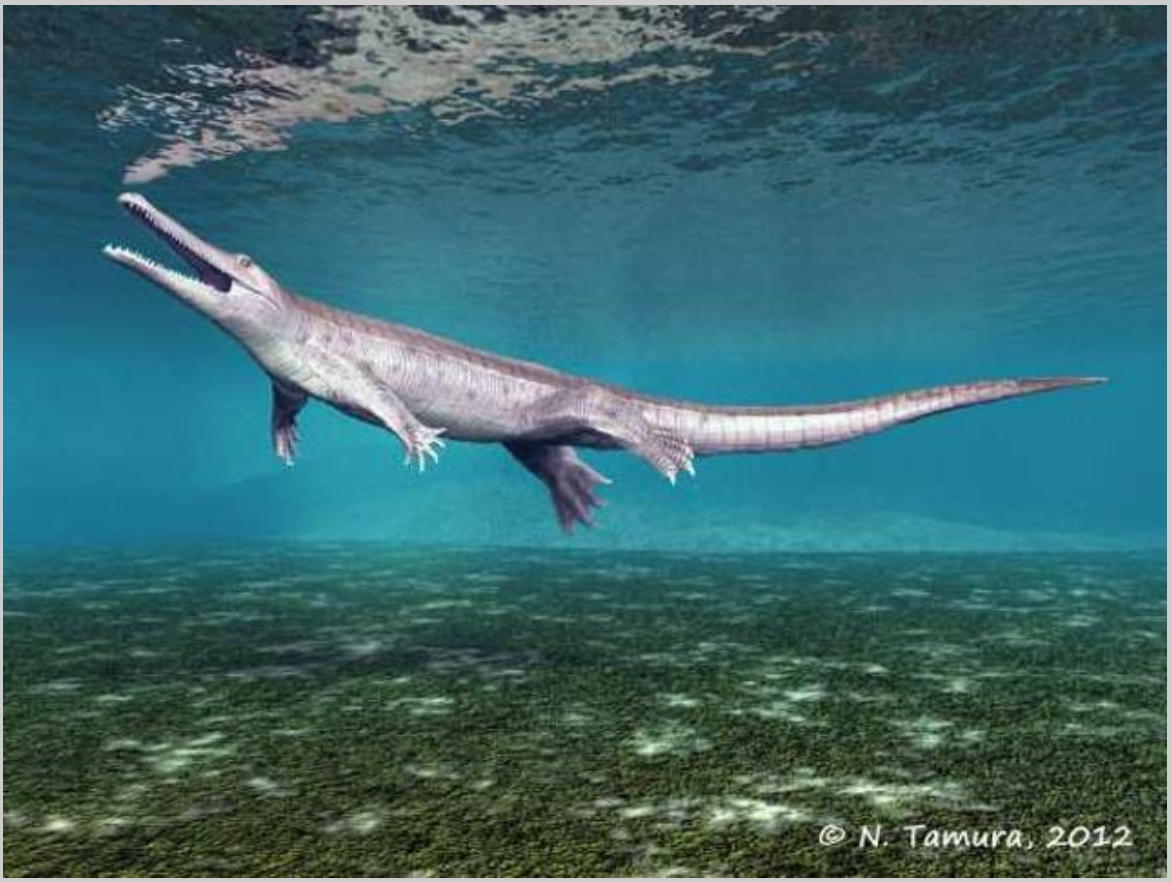

Figure 12 — Life restoration of *Pholidosaurus meyeri* (Source, CC BY 3.0, Credit: Nobu Tamura).

Dyrosaurids:

Dyrosaurids were a group of marine crocodyliforms (Fig. 13) that along with crocodylians were the only group to pass through the end-Cretaceous mass extinction. They are known from multiple places around the globe, and being geographically widespread might have made them more resilient to extinction. They were particularly common in the Trans-Saharan seaway, an epicontinental sea (a shallow sea on top of a continent) that existed when South America and Africa began to break apart. After the Cretaceous, some genera, such as *Acherontisuchus*, lived in shallow inland habitats in tropical environments of South America. Some, such as *Rhabdognathus*, had an extremely long snout, around

75% of the total skull length, indicating a strong adaptation to hunting fish (a piscivorous diet). They would have been ferocious and dangerous hunters, with mouths packed full of strong, sharp teeth. Some genera, such as *Arambourgisuchus*, had a skull that was around one metre long — definitely not something you'd want to encounter when out for a swim! Of note for its cool name is the Colombian species *Anthracosuchus balrogus*, named after the Balrog in *The Lord of the Rings* because it was found deep in a mine.

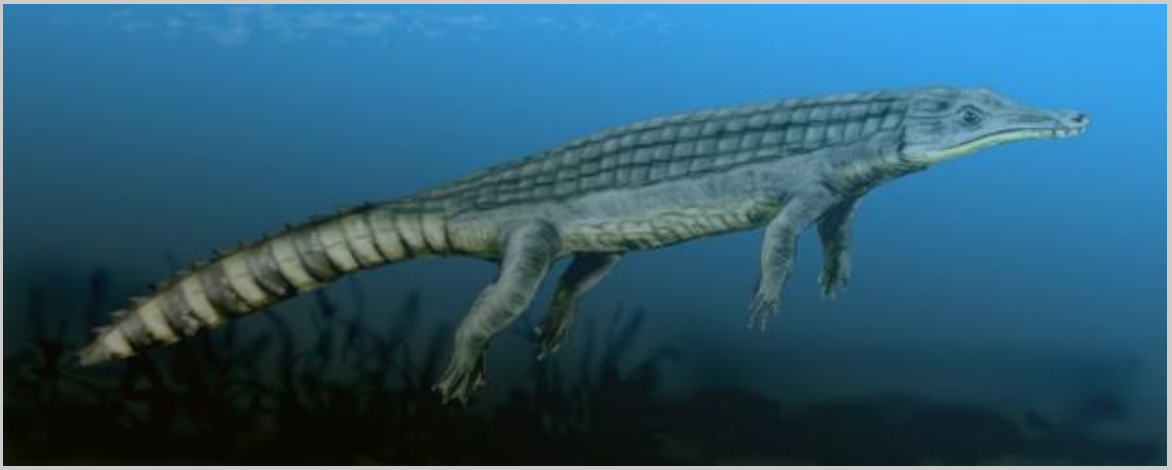

Figure 13 — Reconstruction of *Chenaninasuchus lateroculi* from the Late Palaeocene (66 million to 56 million years ago) of Morocco (Source, CC BY 3.0, Credit: Nobu Tamura).

The earliest crocodylians:

The origin of crocodylians is widely debated by palaeontologists. In the 1990s, taxa such as the Late Cretaceous *Brachychampsa* were established as being the earliest representatives of Crocodylia and all modern crocodilians. It is highly unlikely or even impossible that we'll ever find *the* ancestral crocodylian that gave rise to all others, but we do know that modern crocodilians come from a stock of relatively advanced crocodyliforms called eusuchians. Many recent analyses consider hylaeochampsids and paralligatorids to be eusuchians, meaning that they could be early forerunners of modern species, but this remains hotly contested.

Part of the problem stems from what we define as a eusuchian — should we define it on the basis of features that members of the group share, or on the species that are included in the group? These questions are fairly difficult to resolve, for two reasons:

1. Palaeontologists can interpret different features in different ways
2. The fossil record will never document a perfect 'transition' between two groups

In 2015, hylaeochampsids and paralligatorids were moved from their former positions as possible sister groups to Crocodylia. A new group, Allodaposuchidae, was found to have 'filled the gap' between Early Cretaceous hylaeochampsids and Crocodylia, providing a possible solution to some of the contention (Fig. 14). As such, new discoveries are challenging traditional relationships between eusuchians, and casting controversy over which taxa are most closely related to modern species.

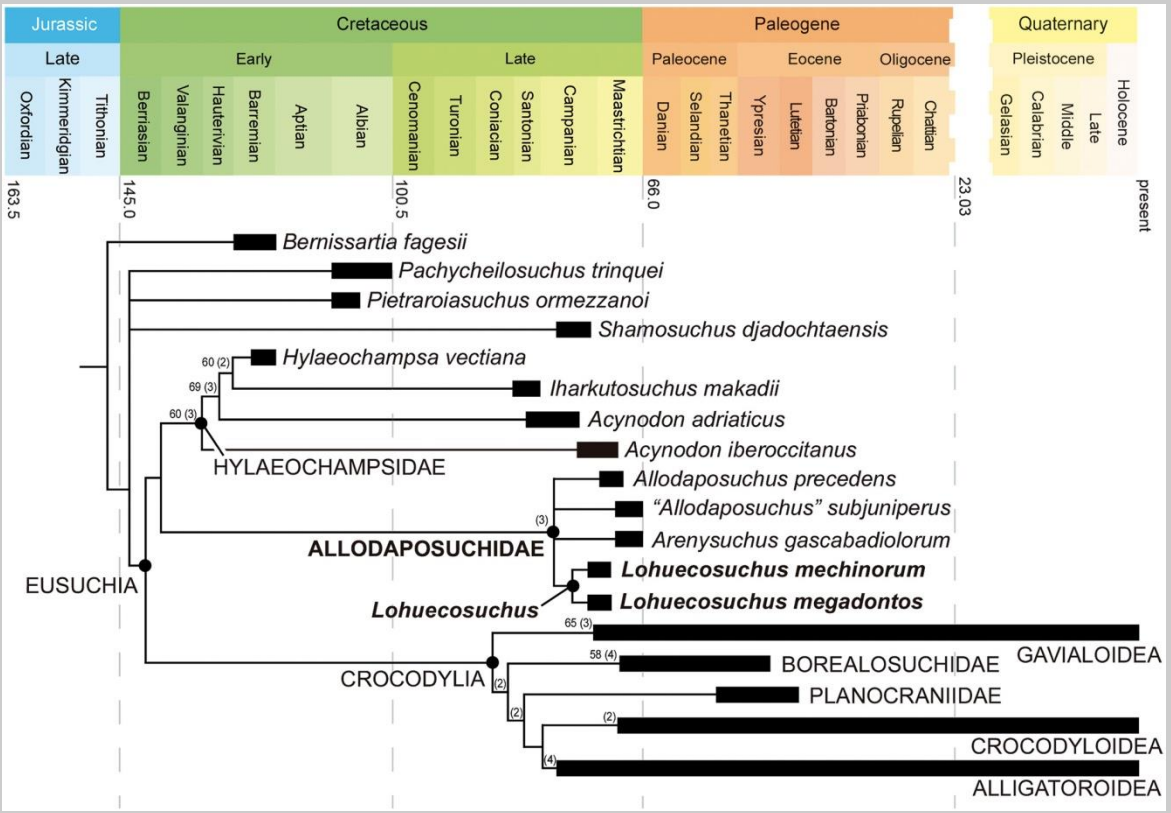

Figure 14 — Time-calibrated relationships of eusuchians and the origin of Crocodylia (Narváez *et al.*, 2015).

What controlled their diversity patterns?

Many studies have investigated the environmental factors responsible for changes in crocodyliform diversity through time (Figs 15, 16). A large-scale study of the history of pseudosuchians found that decreasing temperature over millions of years were responsible for the decline of species in the Northern Hemisphere. However, it was found that changes in sea level were more important for changes in the diversity of marine groups such as thalattosuchians and dyrosaurids; these changes controlled the availability of the shallow marine environments which the groups inhabited. Changes in sea level also seem to have been responsible for a major extinction in both marine and non-marine groups around 145 million years ago at the Jurassic–Cretaceous boundary, which might have acted as the trigger for the ecological release of new groups of marine reptiles, including turtles and plesiosaurs. Other studies have found that the diversity of marine groups seems to be correlated with changes in sea surface temperature. As a result, the exact controls on crocodyliform diversity in the geological past remain contentious.

The future of crocodiles:

Is it possible to predict the future of crocodiles based on what we know about their geological past? This is a difficult question to answer. Palaeontological studies focus on changes that occur over time

periods of around 10 million years or longer. Translating this information to the modern scale of environmental change is very difficult, and it is hard to justify conservation projects using predictions for 10 million years in the future.

However, the fossil record does provide us with clues to modern and future diversity, by showing us the factors that crocodiles and their ancestors seem to have been most sensitive to over time. We might expect that as sea levels change in the future, which they will undoubtedly continue to do, this will control the habitable ranges of different populations. We might even see increasing contact between crocodiles and humans, and this probably wouldn't end well for the iconic archosaurs.

Crocodiles and their predecessors have had their ups and downs over 250 million years of evolution, adopting a number of strange and wonderful lifestyles, behaviours and forms. It remains our responsibility to ensure that human actions do not put an end to their journey in the blink of a geological eye through a lack of respect for Earth and her ecosystems.

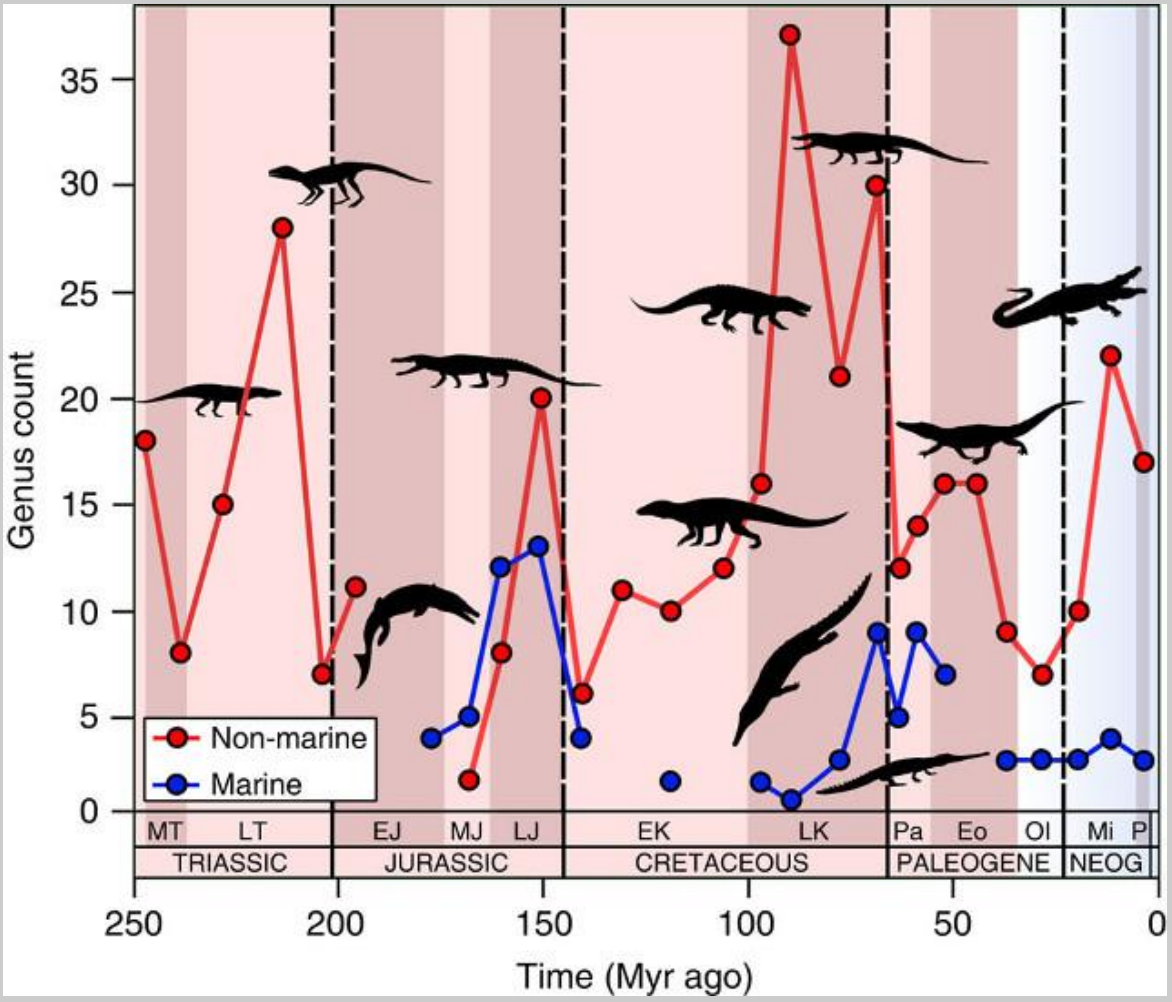

Figure 15 — Raw pseudosuchian diversity through time. Red lines are non-marine and blue lines are marine taxa (Mannion *et al.* 2015).

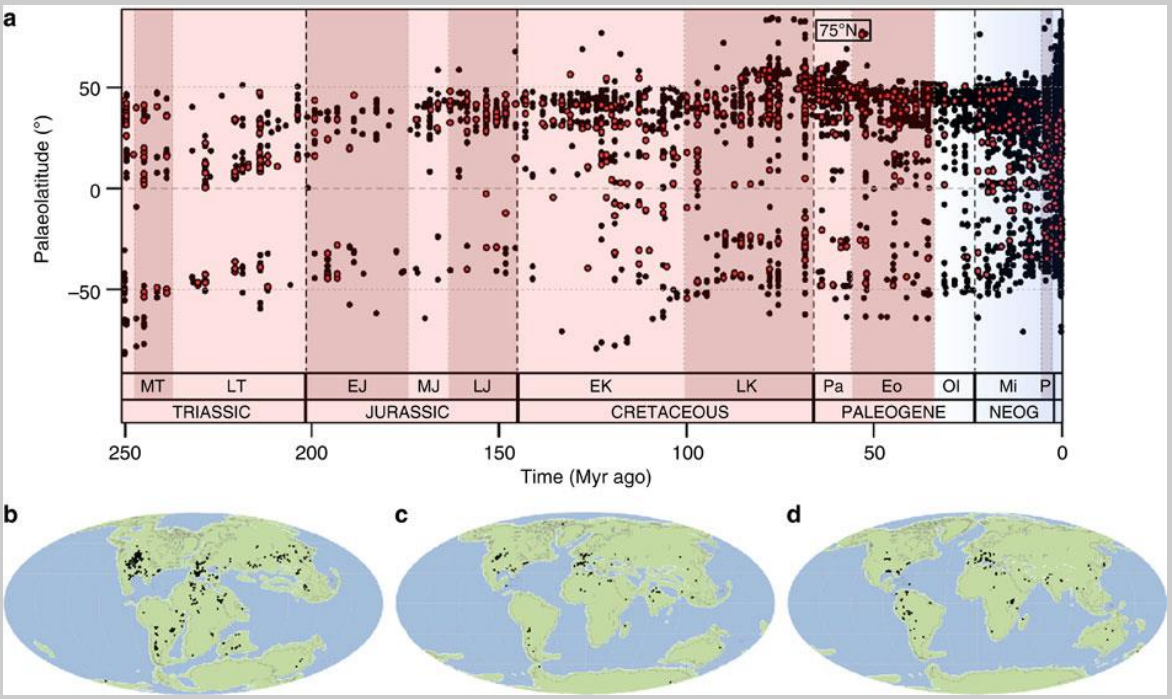

Figure 16 — Occurrences of pseudosuchian fossils through space and time based on palaeolatitude (a) and during the Cretaceous period (145 million to 66 million years ago, b), Eocene epoch (56 million to 33.9 million years ago, c) and Miocene epoch (23 million to 5.3 million years ago, d) (Mannion *et al.*, 2015).

Suggestions for further reading:

Bronzati, M., Montefeltro, F. C. & Langer, M. C. Diversification and the effects of mass extinctions on Crocodyliformes evolutionary history. *Royal Society Open Science* **2,** 140385 (2015). DOI: 10.1098/rsos.140385

Godoy, P. L., Montefeltro, F. C., Norell, M. A. & Langer, M. C. An additional baurusuchid from the Cretaceous of Brazil with evidence of interspecific predation among crocodyliformes. *PLOS ONE* **9,** e97138 (2014). DOI: 10.1371/journal.pone.0097138

Holliday, C. M. & Gardner, N. M. A new eusuchian crocodyliform with novel cranial integument and its significance for the origin and evolution of Crocodylia. *PLOS ONE* **7,** e30471 (2012). DOI: 10.1371/journal.pone.0030471

Mannion, P. D., Benson, R. B. J., Carrano, M. T., Tennant, J. P., Judd, J. & Butler, R. J. Climate constrains the evolutionary history and biodiversity of crocodylians. *Nature Communications* **6,** 8438 (2015). DOI: 10.1038/ncomms9438

Narváez, I., Brochu, C. A., Escaso, F., Pérez-García, A. & Ortega, F. New crocodyliforms from Southwestern Europe and definition of a diverse clade of European Late Cretaceous basal eusuchians. *PLOS ONE* **10,** e0140679 (2015). DOI: 10.1371/journal.pone.0140679

Parrilla-Bel, J., Young, M. T., Moreno-Azanza, M. & Canudo, J. I. The first metriorhynchid crocodylomorph from the Middle Jurassic of Spain, with implications for evolution of the subclade Rhacheosaurini. *PLOS ONE* **8,** e54275 (2013). DOI: 10.1371/journal.pone.0054275

Pol, D., Nascimento, P. M., Carvalho, A. B., Riccomini, C., Pires-Domingues, R. A. & Zaher, H. A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLOS ONE* **9,** e93105 (2014). DOI: 10.1371/journal.pone.0093105

Pol, D. & Leardi, J. L. Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. In: Fernández, M. & Herrera, Y. (Eds.) *Reptiles Extintos - Volumen en Homenaje a Zulma Gasparini. Publicación Electrónica de la Asociación Paleontológica Argentina* **15,** 172–186 (2015). DOI: 10.5710/PEAPA.10.06.2015.108

Stubbs, T. L., Pierce, S. E., Rayfield, E. J. & Anderson, P. S. L. Morphological and biomechanical disparity of crocodile-line archosaurs following the end-Triassic extinction. *Proceedings of the Royal Society B* **280,** 20131940 (2013). DOI: 10.1098/rspb.2013.1940

Toljagic, O. & Butler, R. J. Triassic–Jurassic mass extinction as trigger for the Mesozoic radiation of crocodylomorphs. *Biology Letters* **9,** 20130095 (2013). DOI: 10.1098/rsbl.2013.0095

Turner, A. H. A review of *Shamosuchus* and *Paralligator* (Crocodyliformes, Neosuchia) from the Cretaceous of Asia. *PLOS ONE* **10,** e0118116 (2015). DOI: 10.1371/journal.pone.0118116

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[1]Department of Earth Science and Engineering, Imperial College London, London, SW7 2AZ, UK.