Exploring Ichthyosaurs in the 21st Century

State of the Art and Future Prospects

Ben Moon, University of Bristol — 5 Nov 2020
bcmoon.uk — @moononthebones

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1. **Introduction**
2. State of the Art
3. Future Prospects
4. Conclusion

As promised by the advert I'll talk about both the state-of-the-art of ichthyosaur research and future prospects, but first here's a brief introduction of what we're dealing with.

larrylustig; H. T. De la Beche; Apple Maps; kateandtoms.com

Like many good stories, we begin on the beach – specifically between Lyme Regis and Charmouth in Dorset – in 1810. This is when Mary and Joseph Anning found the first remains of an unknown animal in the cliffs along the beach. Mary Anning went on to make a huge number of discoveries and became an important, but frequently ignored at the time, contributor to the birth of palaeontology as a science.

Lyme Regis too remains a hotspot for sea-spotters and fossil hunters alike – hosting their annual fossil festival along the parade and with plenty of fossil shops, collecting excursions, and fish and chips.



larrylustig; H. T. De la Beche; Apple Maps; kateandtoms.com

Temnodontosaurus platyodon **(Conybeare, 1822) — Early Jurassic — U.K.**

jemdi

This was the critter that Mary and Joseph found – with a skull over 1 m long, massive eye, and big pointed teeth – no one had seen anything quite like this at the time. It took a little while, and several people, to try to figure out what this thing was, but eventually the name ichthyosaur – meaning ‘fish lizard’ came to be used as this was thought to be an animal somewhere between fish and lizards, This specimen is now in the Natural History Museum in London.

Stenopterygius quadriscissus **(Quenstedt, 1858) — Early Jurassic — Germany**

B. Moon

It wasn’t long before ichthyosaurs were found in other places too – such as this specimen from Germany – and with more specimens came new sights – these spectacularly complete ichthyosaurs showed more of the body than before, including the tail bend and skeletons of embryos that had not yet been born when the mother died…

Temnodontosaurus trigonodon (Theodori, 1843) — Early Jurassic — Germany

B. Moon

… and the variety of sizes increased too – from small skeletons only 1 m long to colossal predatory ichthyosaurs that reached up to 10 m on body length…

***Stenopterygius* sp. — Early Jurassic — Germany**

B. Moon

…and with even more unexpected preservation we finally got to see beyond just the bones and even found soft tissue outlines of some ichthyosaurs' skin showing that these truly were lizard-like reptiles that had the body form of fishes.

Stenopterygius **sp. — Early Jurassic — Germany**

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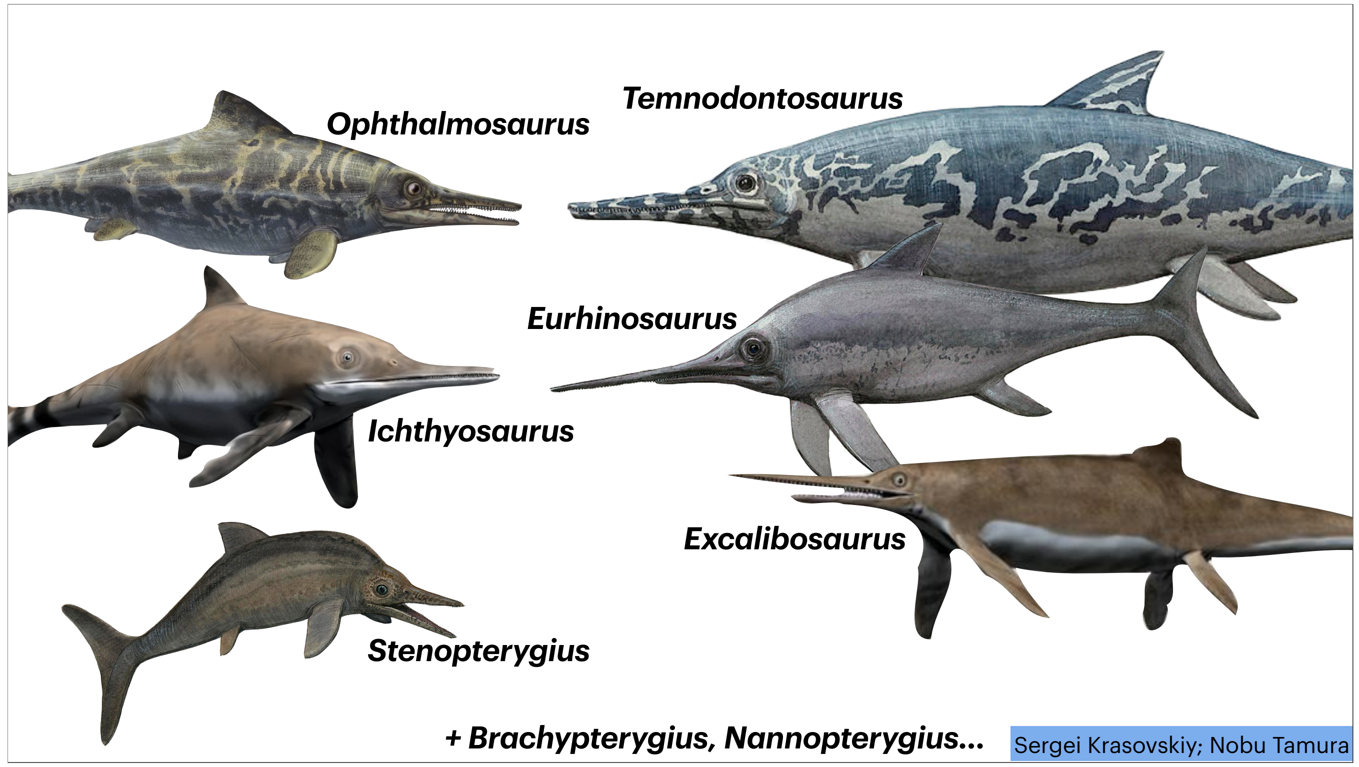
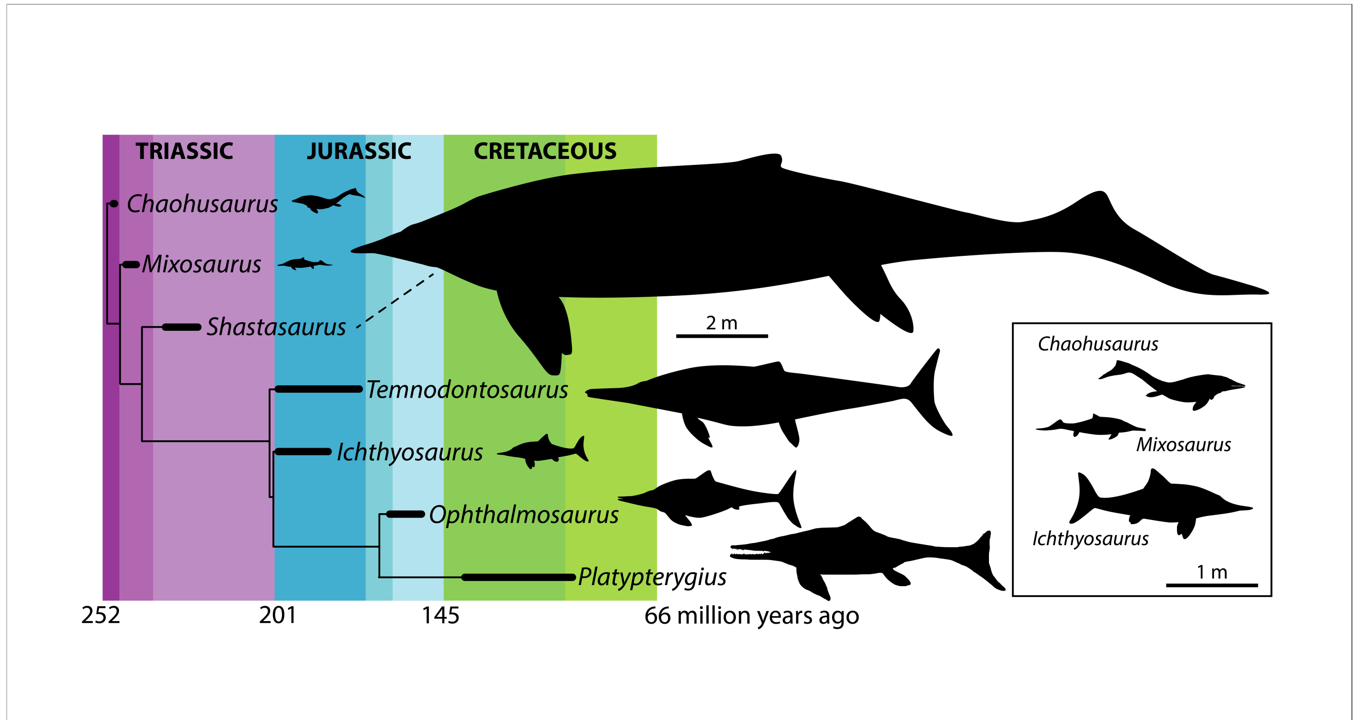
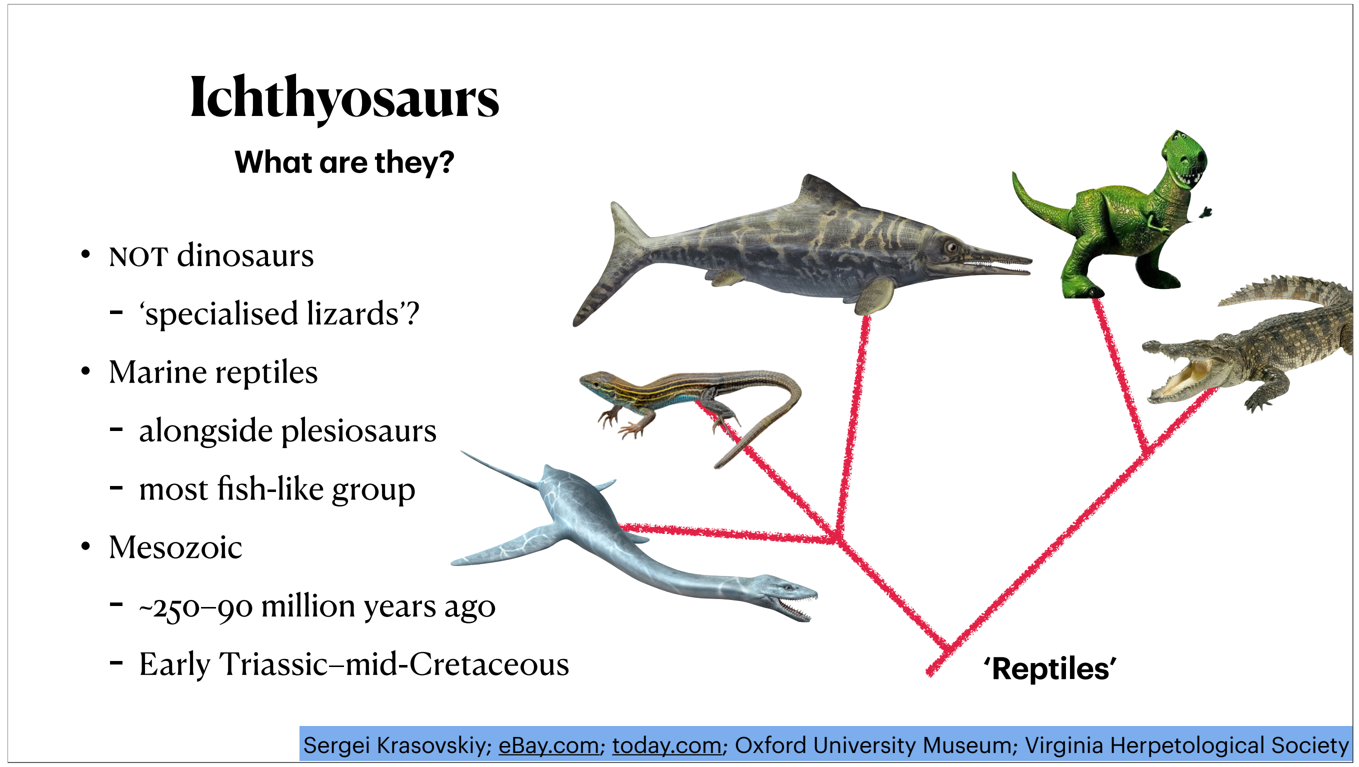


With all these finds it wasn't long before there was a relatively high diversity of species, sizes, and forms known primarily from the Jurassic of Europe – from 1–10 m, fish-eaters to apex predators, and even weird swordfish-like taxa – and this spread even further with finds from across the world.



Now there are over 100 species known from every continent except Antarctica throughout the Mesozoic, with only a few shown here – first appearing about 250 million years ago and going extinct about 90 million years ago – and now ranging from the smallest, *Cartorhycnhus,* only 40 cm to the colossal, whale-sized, *Shastasaurus* and *Shonisaurus* at over 15 and 20 m long.



So where do we stand? First it should be pointed out that ichthyosaurs are *not* dinosaurs – no matter how often the media get this wrong – they are probably a group of specialised marine reptiles on the branch that evolved into lizards; this is with other iconic groups like plesiosaurs that lived alongside ichthyosaurs in the Mesozoic. Ichthyosaurs evolved soon after the end-Permian mass extinction – this is the largest extinction known and wiped out up to 95% of species, depending on the estimate – essentially wiping the slate clean for new creatures to evolve. For 160 million years ichthyosaurs were key components of the marine ecosystem, but became extinct about 25 million years before the asteroid impact and extinction that wiped out the dinosaurs and plesiosaurs and ended the Mesozoic.

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Here I'll pick out three areas that have made huge gains recently in our knowledge of ichthyosaur palaeobiology.

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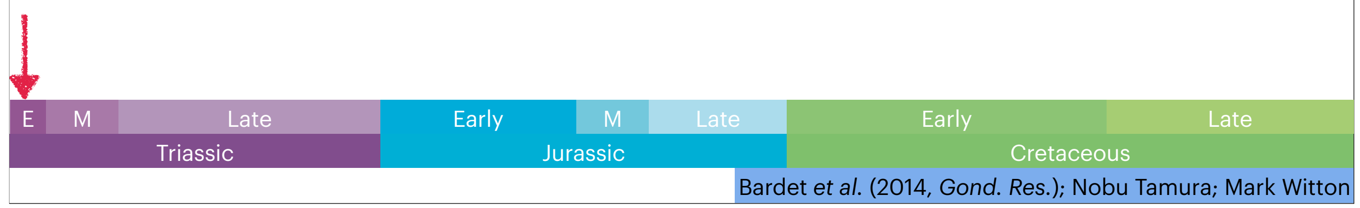
Enter the Oceans

Origins and early forms



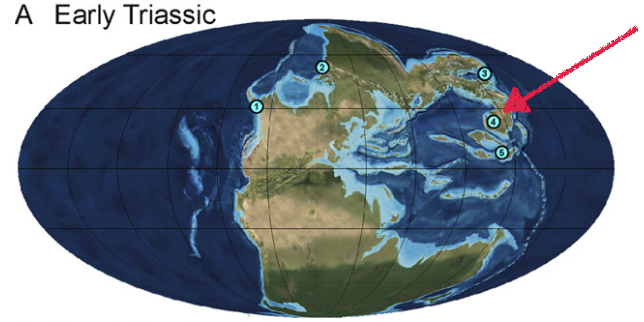
Starting at the very beginning … a very good place to start.

The earliest ichthyosaurs come from China and are dated to about 250 million years ago, and diversified rapidly including these two species – *Chaohusaurus geishanensis* and *Cartorhynchus lenticarpus* – within only a few million years of that: by 247 million years ago 7 species are known from the northern hemisphere. These ichthyosaurs appear already strongly modified: they are often small and lizard-like in appearance – up to 2 m – but have adaptations to the water already.

Enter the Oceans

Origins and early forms

A Early Triassic



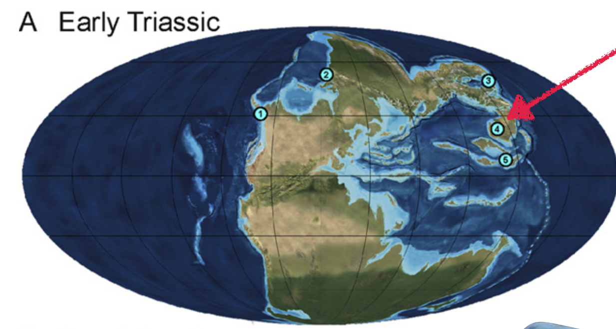
E | M | Late | Early | M | Late | Early | Late

Triassic | Jurassic | Cretaceous

Bardet *et al.* (2014, *Gond. Res.*); Nobu Tamura; Mark Witton

Enter the Oceans

Origins and early forms



Chaohusaurus geishanensis

E	M	Late	Early	M	Late	Early	Late
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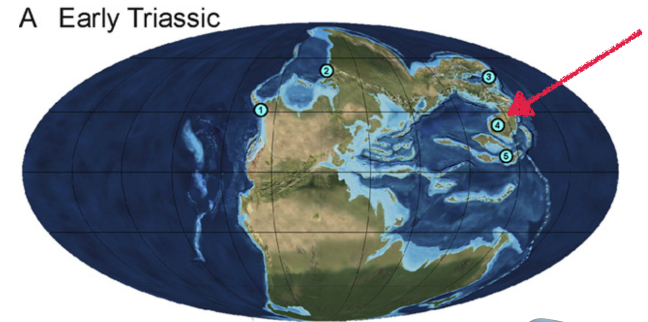

Chaohusaurus geishanensis

Cartorhynchus lenticarpus

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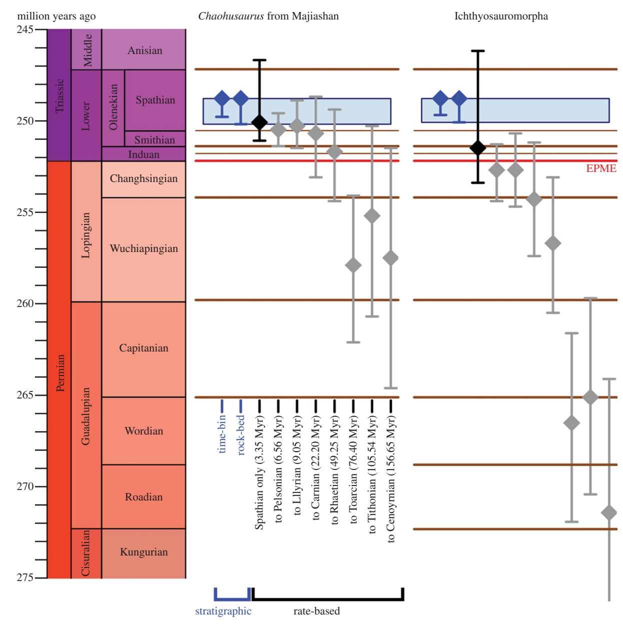
Enter the Oceans

Rapid early evolution



Motani *et al.* (2018, *PRSB*); Moon & Stubbs (2020, *Commun. Biol*)

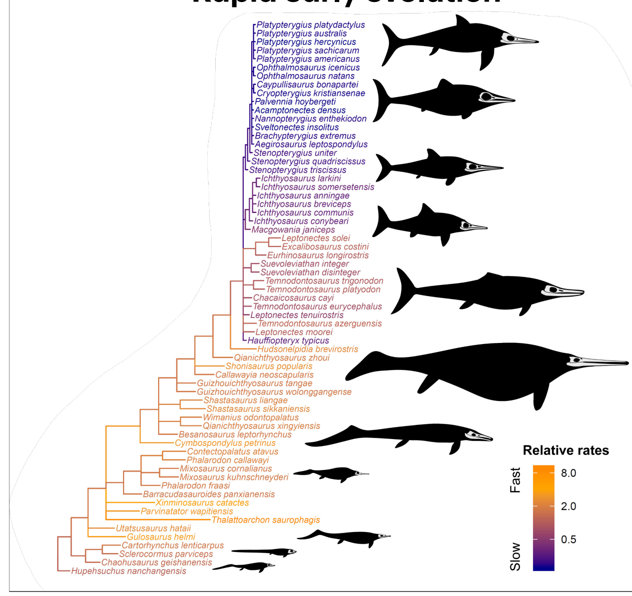
The origin of this early diversity is not entirely certain: ichthyosaurs appear ‘fully formed’ – as it were – in the Early Triassic. Motani et al. (2018) used the fossil record of ichthyosaurs to estimate when they might have originated – suggesting they may well have been well into the Permian – but there are no ichthyosaur fossils anywhere near that old.

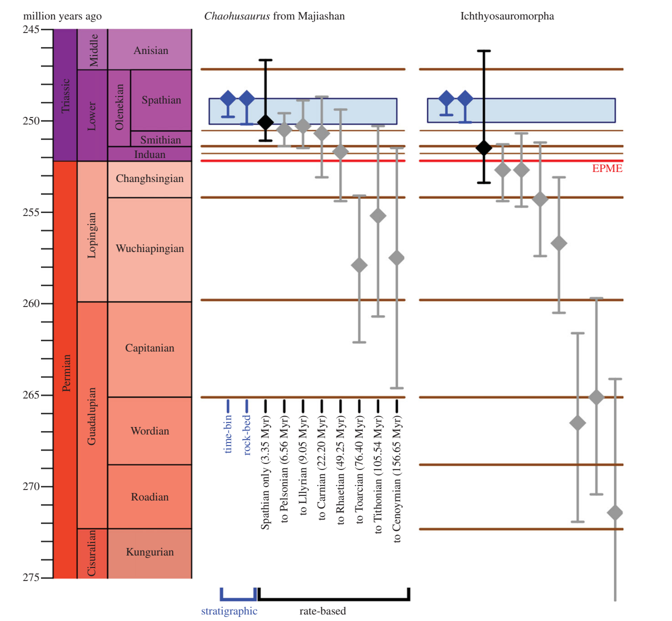
Tom Stubbs – also at Bristol – and I looked at how quickly this diversity arose. We used a phylogeny of ichthyosaurs that I created during my PhD – essentially a family tree of ichthyosaurs created by comparing how similar all these ichthyosaurs look. With this we looked at how quickly new species of ichthyosaurs evolved, but also how quickly their body size and morphology changed through time. We covered a variety of possible origin dates – not quite so far back as the Middle Permian, but including the later Permian – and found high rates of evolution in the earlier ichthyosaurs in all of our analyses, but only in the very earliest ichthyosaurs.

What this suggests is that ichthyosaurs pretty much crashed onto the scene soon after the end-Permian mass extinction. They were able to take advantage of a relatively empty world and become bigger and more variable than anything else around at the time. These high rates in early ichthyosaurs are also associated with substantial changes accompanying their move into water.

Enter the Oceans

Rapid early evolution





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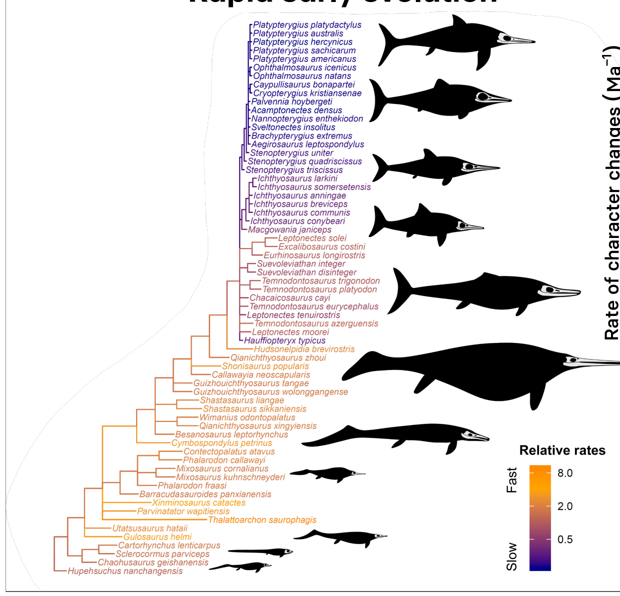

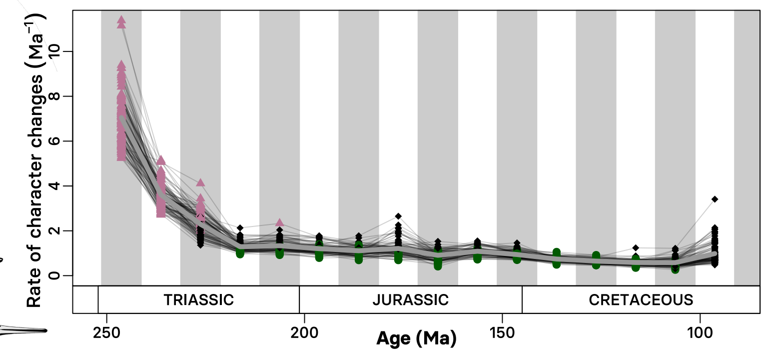

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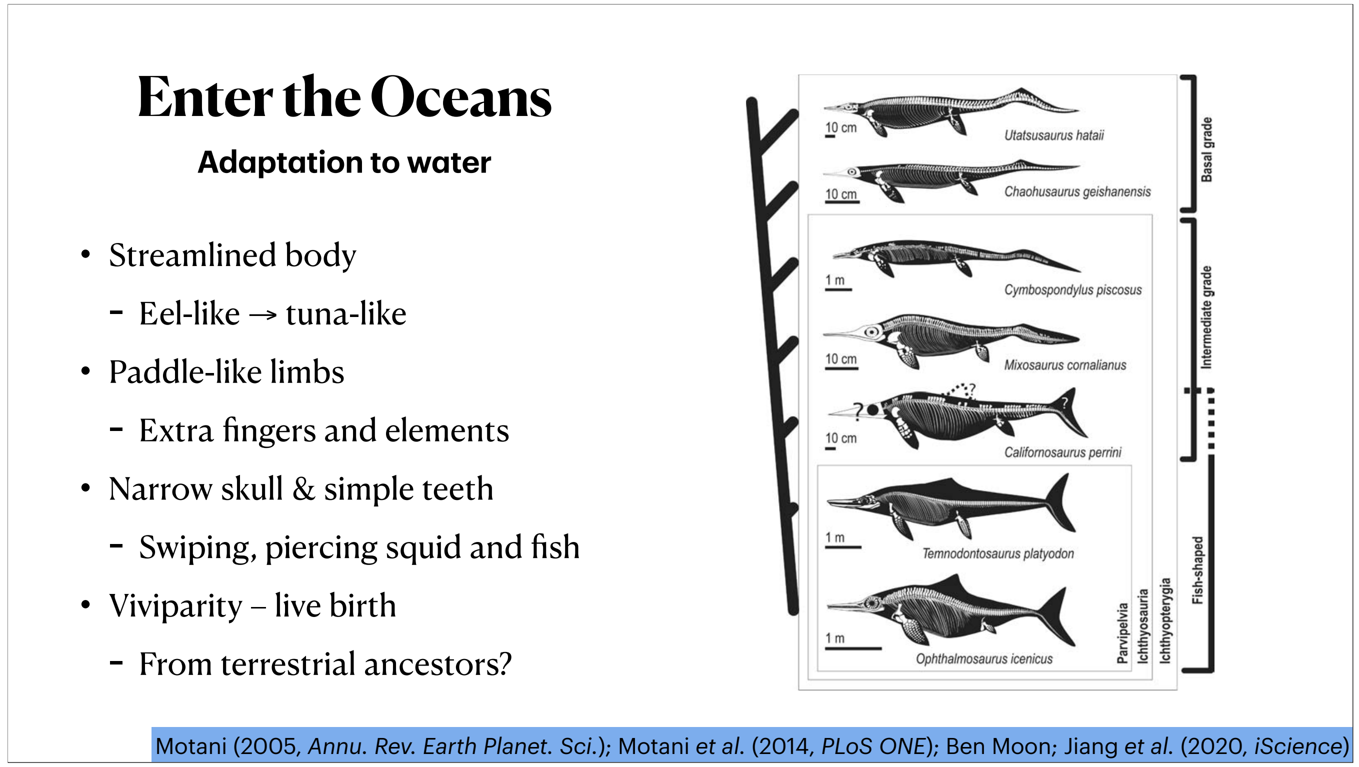


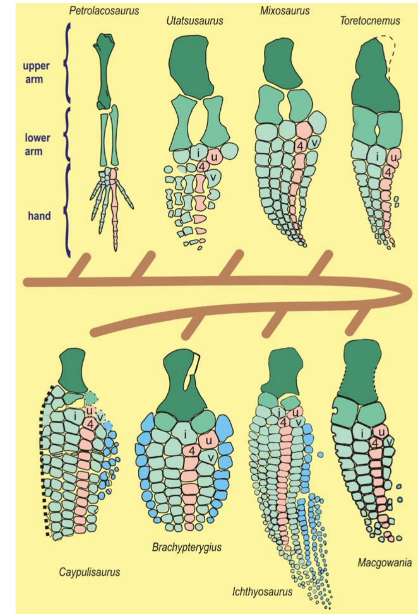
Living in water is quite a different prospect to living on land – it's a much denser and more viscous medium, meaning it's simply much harder to move through it easily. To be able to survive ichthyosaurs – and other marine vertebrates – evolved a suite of features focussed on being able to swim easily and catch their prey. This includes:

- A streamlined body – the tail is the main propulsive organ and while it starts off long, through ichthyosaur evolution their whole body becomes shorter and stockier, and they evolve a fish-like tail fin. The marks a fundamental transition in how ichthyosaurs swim: they go from eel-like swimming in their early forms to more tuna-like motion by the Jurassic. This is a more effective mode of swimming: less energy and movement of the tail is needed to push them forwards.
- Paddle-like limbs – by adding more bones and making them smaller, ichthyosaurs evolved streamlined, rigid limbs that could be used to aid both stability and agility – acting like large rudders.
- Their narrow skulls allowed them to swipe through the water to catch the fast-moving squid and fish that formed the bulk of their diets. Some specimens from Germany preserve the remains of individuals last meals that are full of squid and fish fragments, and sometimes even other reptiles – like in the case of this Triassic ichthyosaur from China announced earlier this year.
- And finally viviparity – giving birth to live young. This is mostly associated with mammals, but is found in several reptile groups. Even the first ichthyosaurs gave birth to live young and specimens with embryos have been found throughout ichthyosaur fossil record. These early ichthyosaurs appear give birth head first, which has been used to suggest this first developed in their terrestrial ancestors, but later ichthyosaurs gave birth tail first – probably to prevent the young drowning.

Enter the Oceans

Adaptation to water

- Streamlined body
  - Eel-like → tuna-like
- Paddle-like limbs
  - Extra fingers and elements
- Narrow skull & simple teeth
  - Swiping, piercing squid and fish
- Viviparity – live birth
  - From terrestrial ancestors?



Motani (2005, *Annu. Rev. Earth Planet. Sci.*); Motani *et al.* (2014, *PLoS ONE*); Ben Moon; Jiang *et al.* (2020, *iScience*)

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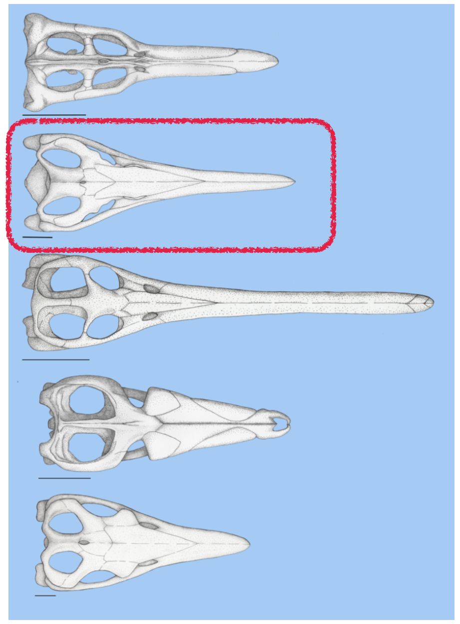

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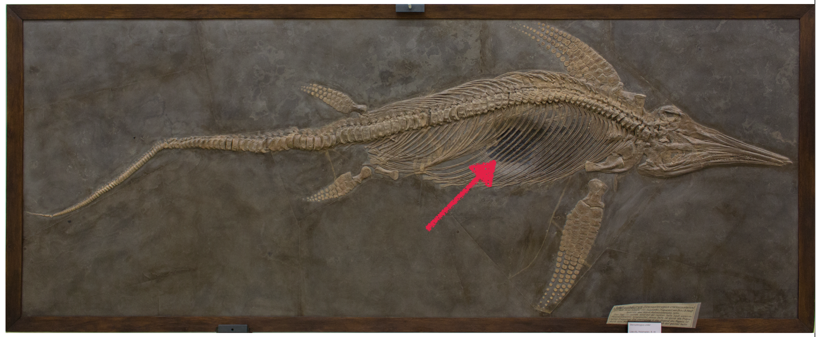

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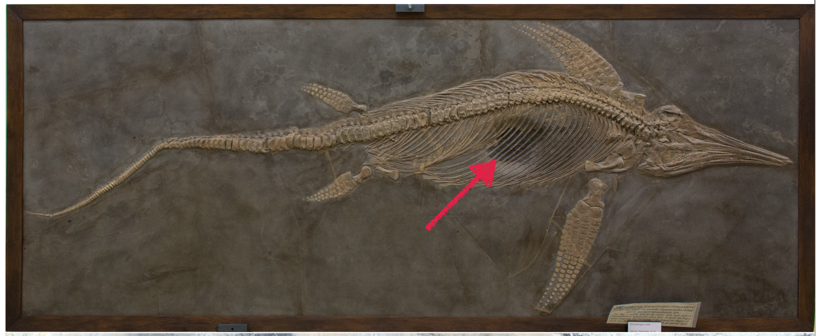

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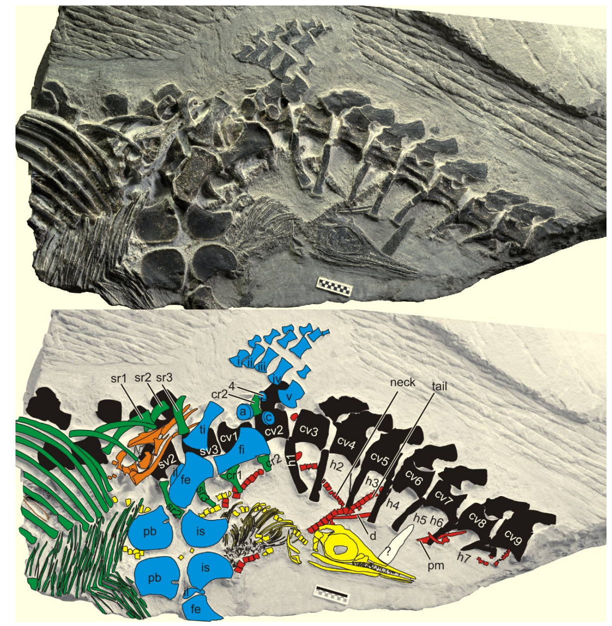

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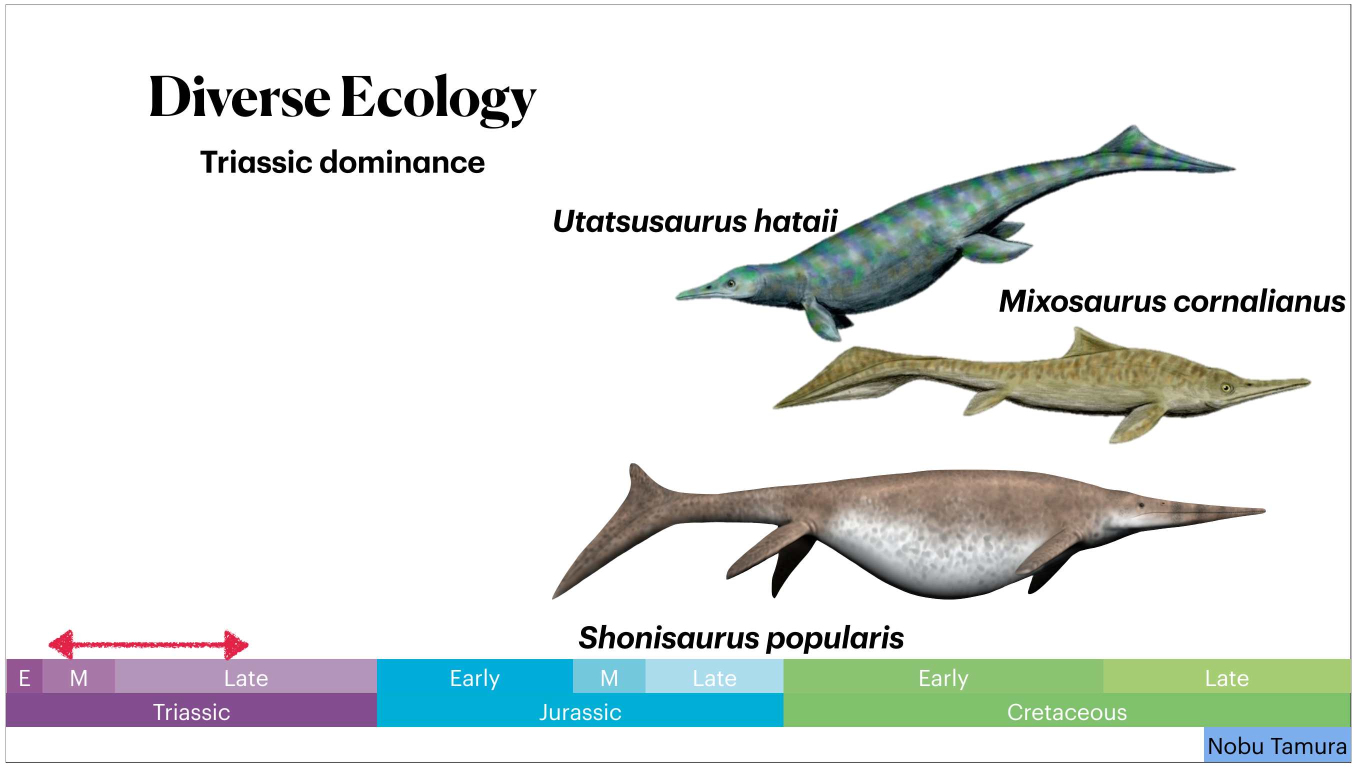
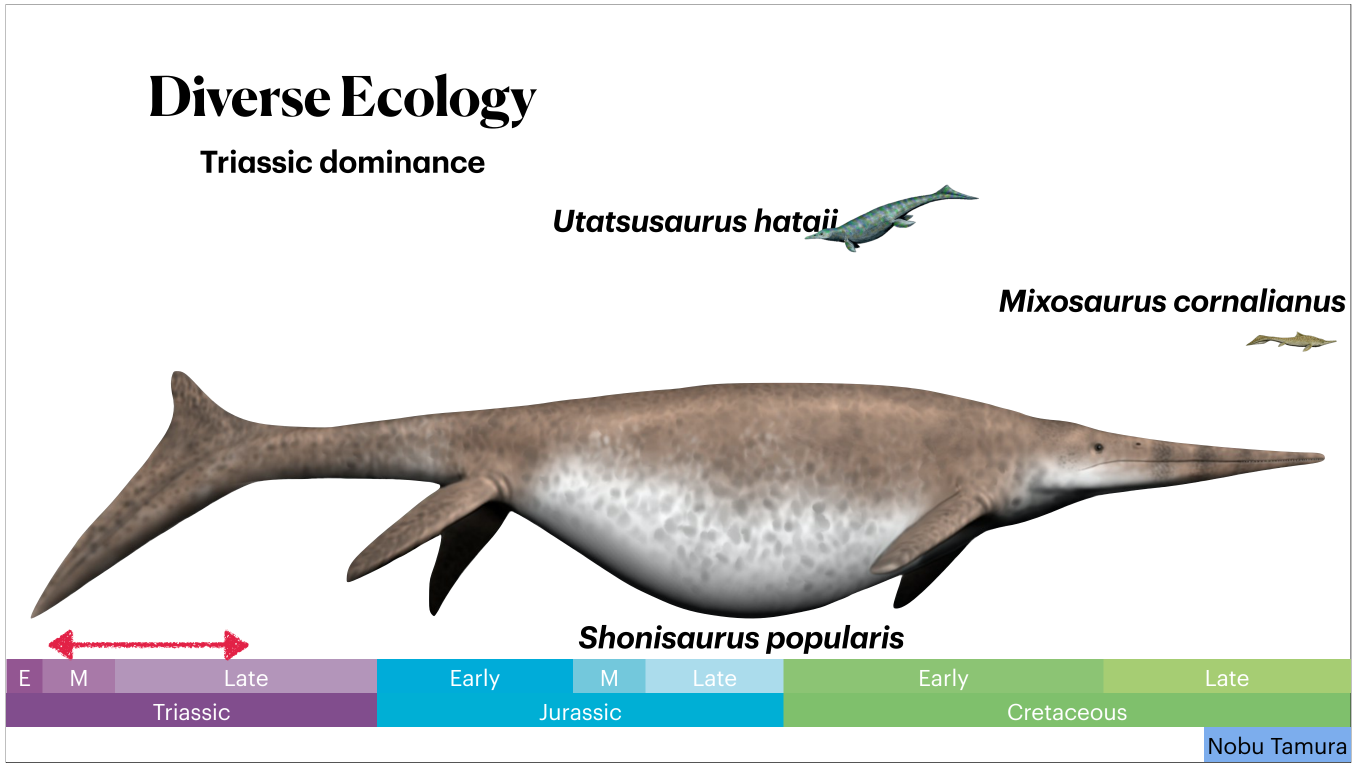
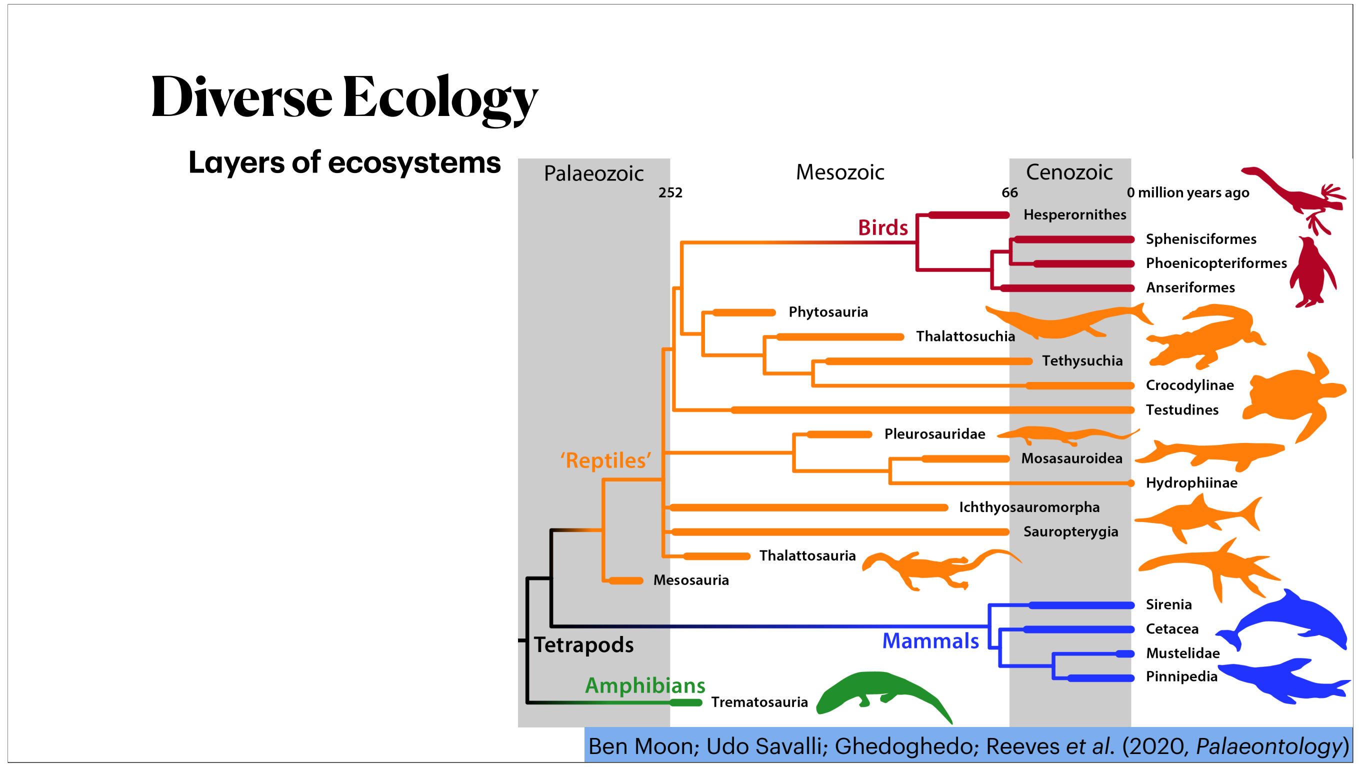


It seems that this combination of traits – and being able to evolve rapidly early on – was a prime reason for the early success of ichthyosaurs in the Triassic: they soon came to dominate the oceans and had huge variety of size and ecology. Here are three Triassic taxa – and now shown at their relative sizes.



Small *Mixosaurus* were about 1 m long and had rounded teeth and robust skulls for crushing shellfish; larger predators between 5–8 m long ate the smaller reptiles; and in the Late Triassic the huge *Shonisaurus* grew over 20 m long – the largest marine reptile known. This was the zenith of ichthyosaur diversity.



And so were many other marine reptiles at the time – it was during the Triassic that the modern structure of marine ecosystems first becomes established, with large tetrapod-dominated upper tiers. Sharks had been around for a while by this point, but in the Triassic reptiles began taking up positions similar to modern whales, dolphins, seals, and sea lions as the top predators.

And the variety of different marine reptiles is shown perhaps best by their feeding methods – this *Neusticosaurus* from the Middle Triassic of Switzerland had long, pointed teeth for catching fish.

Whereas *Henodus* from the Late Triassic of Germany was heavily built with a bony carapace and big, rounded teeth that would have been perfect for crushing shellfish.

Recently I've been involved in a study led by Jane Reeves – a former MSc student at Bristol – where we've been able to study the ecology of all marine tetrapods from the Mesozoic. This includes ichthyosaurs, plesiosaurs and their relatives, marine crocodiles, mosasaurs, and even early birds. By categorising them according to various features – such as their diet, swimming ability, habitat, armour and other things, here shown by different colour points: one for each genus – we've been able to reconstruct the diversity of ecologies throughout the Mesozoic.

What's perhaps most striking is that ichthyosaurs quickly become an important component of marine ecosystems and stay that for almost all of their 160 million year existence – here shown by their relative contribution to the variety of ecologies at the time. Numerous other clades came and went – placodonts marine crocodiles are two prominent cases – but ichthyosaurs managed to outlast them until their demise in the middle of the Cretaceous.

Diverse Ecology

Layers of ecosystems

Ben Moon; Udo Savalli; Ghedoghedo; Reeves *et al.* (2020, *Palaeontology*)

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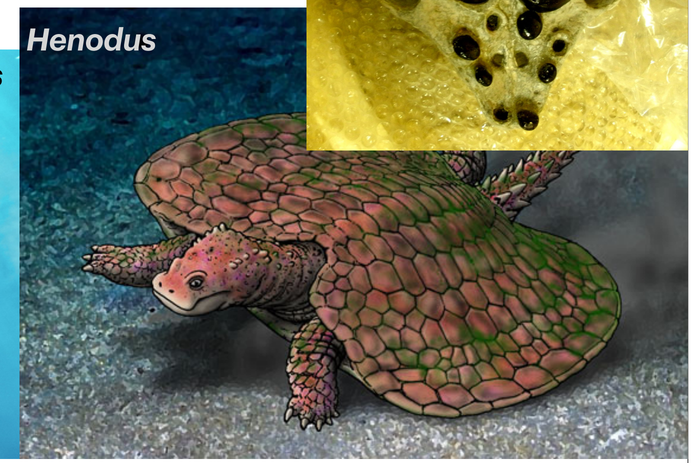

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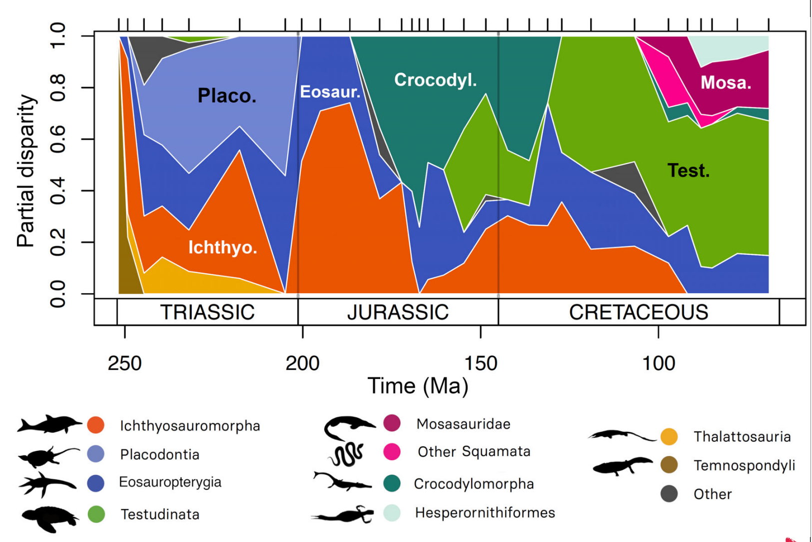

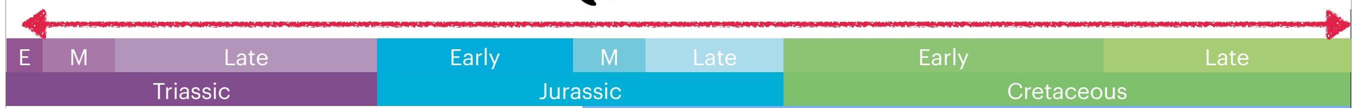

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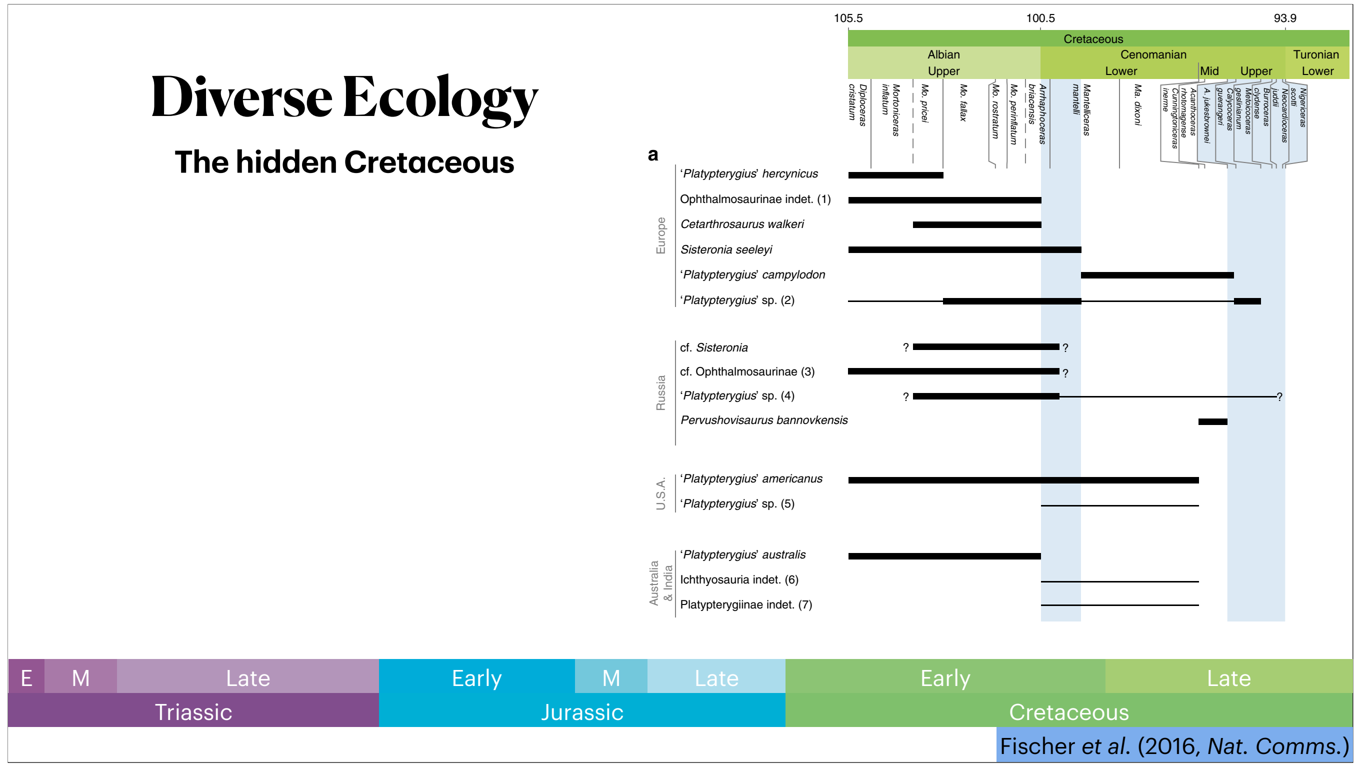


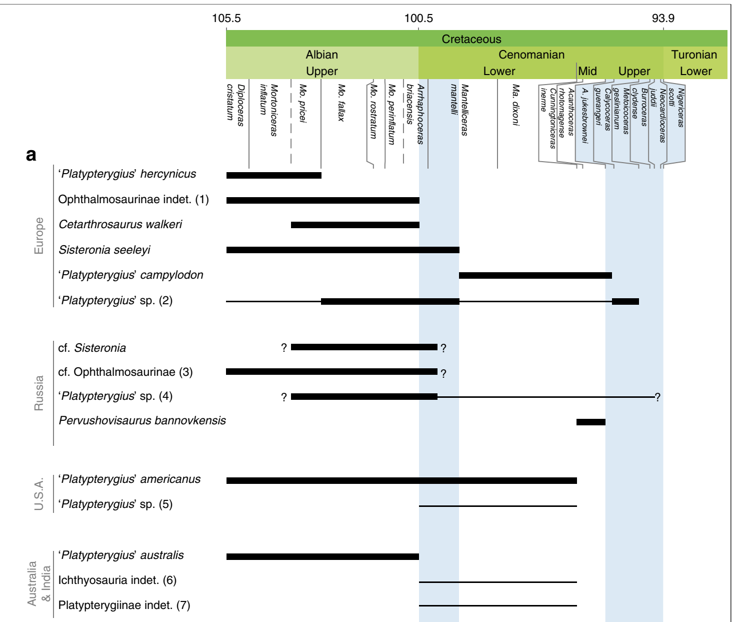
Sometimes this diversity isn't quite so obvious. It's been a long-standing mystery why ichthyosaurs became extinct in the middle of the Cretaceous when other marine reptile groups – plesiosaurs particularly – lasted to the end of the Mesozoic. From being relatively diverse in the Late Albian ichthyosaurs rapidly disappeared over about 10 Ma.

This is even more striking as these late ichthyosaurs were still globally-distributed and had many different ecological niches – the different roles they play in the ecosystem. Perhaps surprisingly this diversity was unknown, despite the long history of finding ichthyosaurs from the Cretaceous – the remains were often poorly preserved and incomplete so few people had taken the time to look at the systematically.

Fischer et al. took the time and have managed to bring the Cretaceous ichthyosaur record to everyone's attention, however, they showed that ichthyosaurs had a rather lengthy slow decline in diversity associated with increased environmental volatility as sea levels rose then the oceans suffered a major anoxic event during the Cenomanian. Despite their early success, ichthyosaurs could not evolve fast enough to escape these events.

Diverse Ecology

The hidden Cretaceous



Fischer *et al.* (2016, *Nat. Comms.*)

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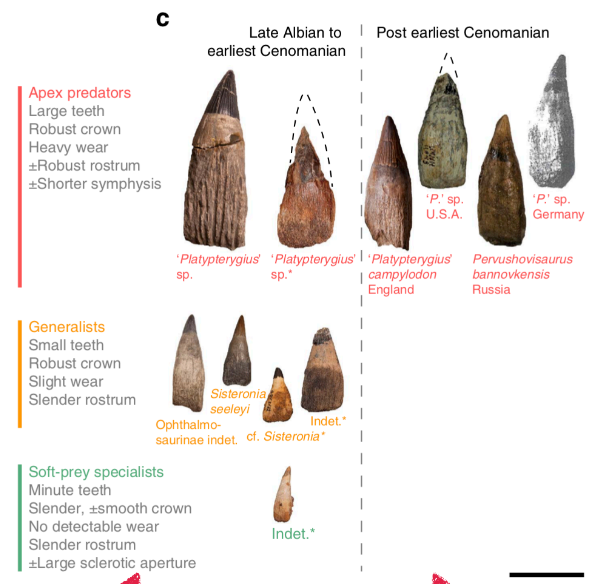

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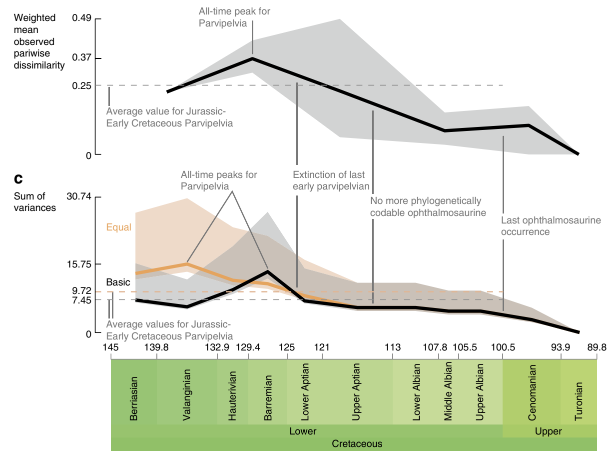

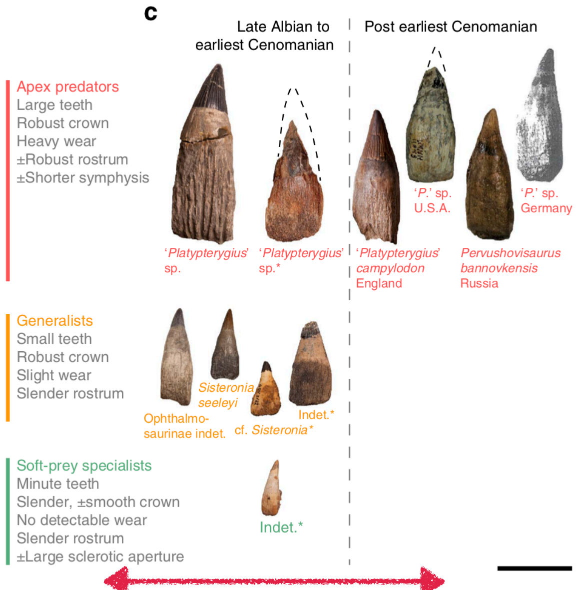

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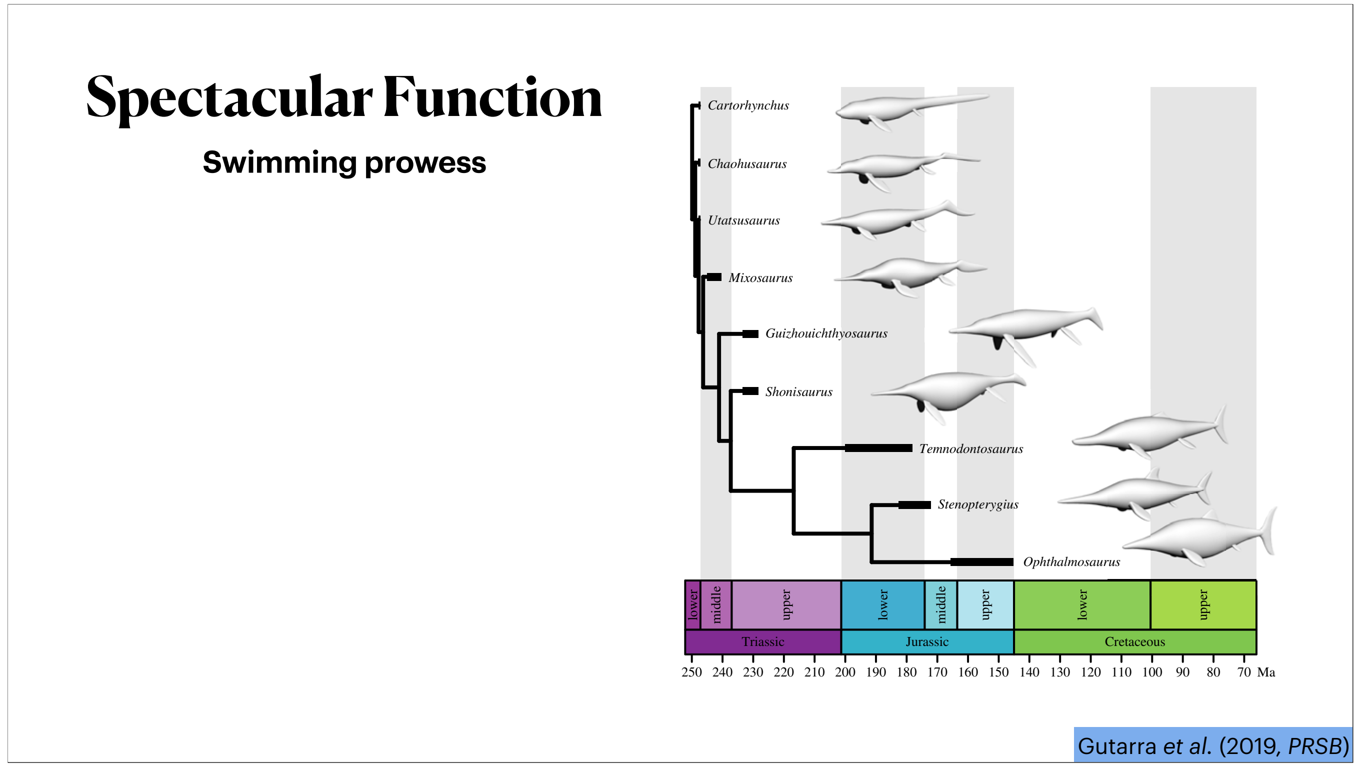


There still remains the question of how ichthyosaurs maintained their success between first evolving and their eventually extinction – 160 million years of Earth history – and through a combination of re-analysing specimens and using modern reconstruction techniques we're staying to get a better picture of how ichthyosaurs worked.

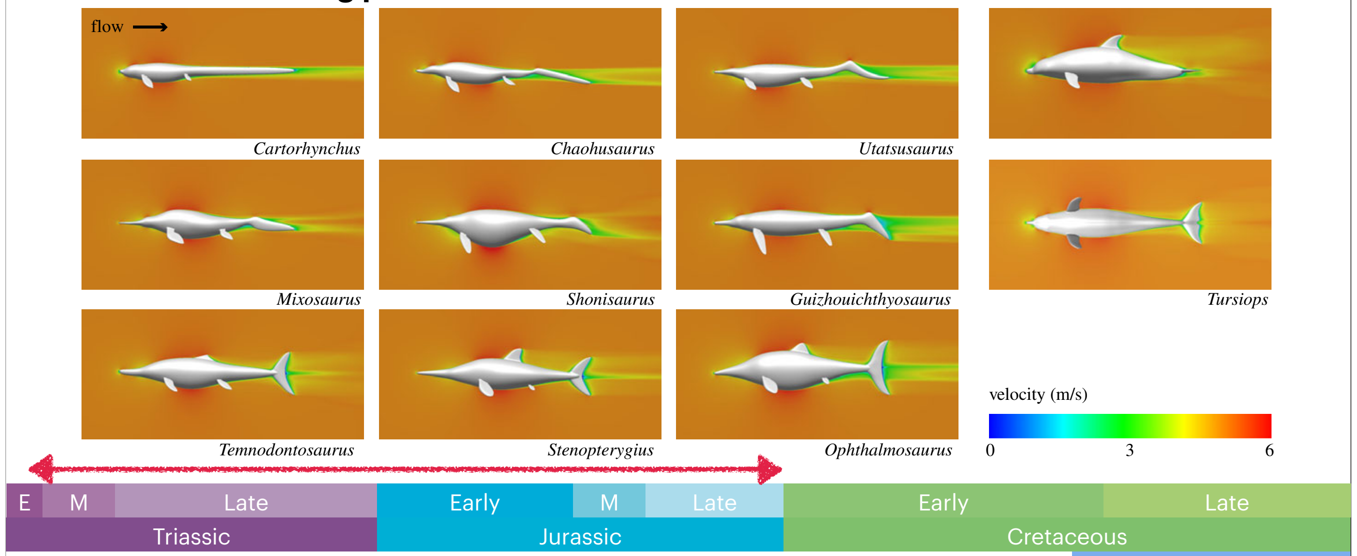
Ichthyosaurs have a glut of exceptionally complete and well preserved specimens, from which Susana Gutarra and our collaborators have managed to build accurate 3D models covering the majority of ichthyosaur evolution – a remarkable feat on its own.

With these we've used a modern engineering technique to simulate the flow of water around the bodies of these ichthyosaurs to compare how streamlined they were – and so how much effort each animal needed to swim.

We had hoped to see a change from earlier to later ichthyosaurs – that they became more streamlined through their evolution – but this isn't quite what we found. Instead we saw that all the different shapes were fairly similar, but that how the body was used to swim mattered more – mackerel- and tuna-like swimming uses only a small part of the body and is more efficient than eel-like swimming that uses the whole body.

Spectacular Function

Swimming prowess



Gutarra *et al.* (2019, *PRSB*)

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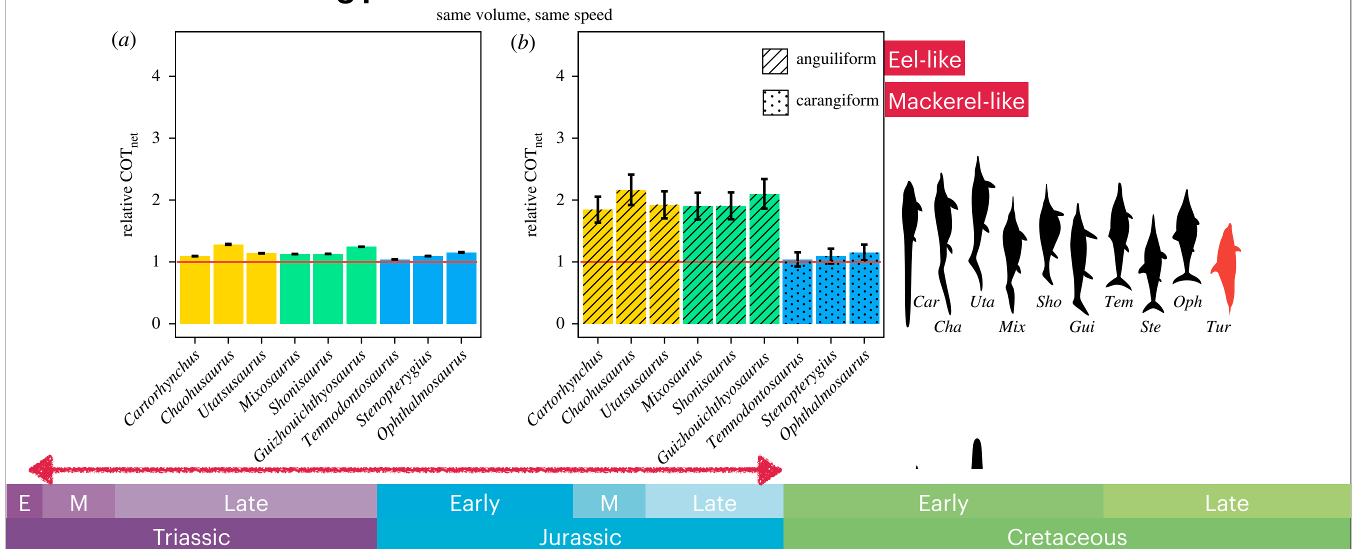

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Those were a few snapshots of where ichthyosaur – and marine reptile – research is at the moment, but of course there are still outstanding problems that I and many others are interested in and currently working on.

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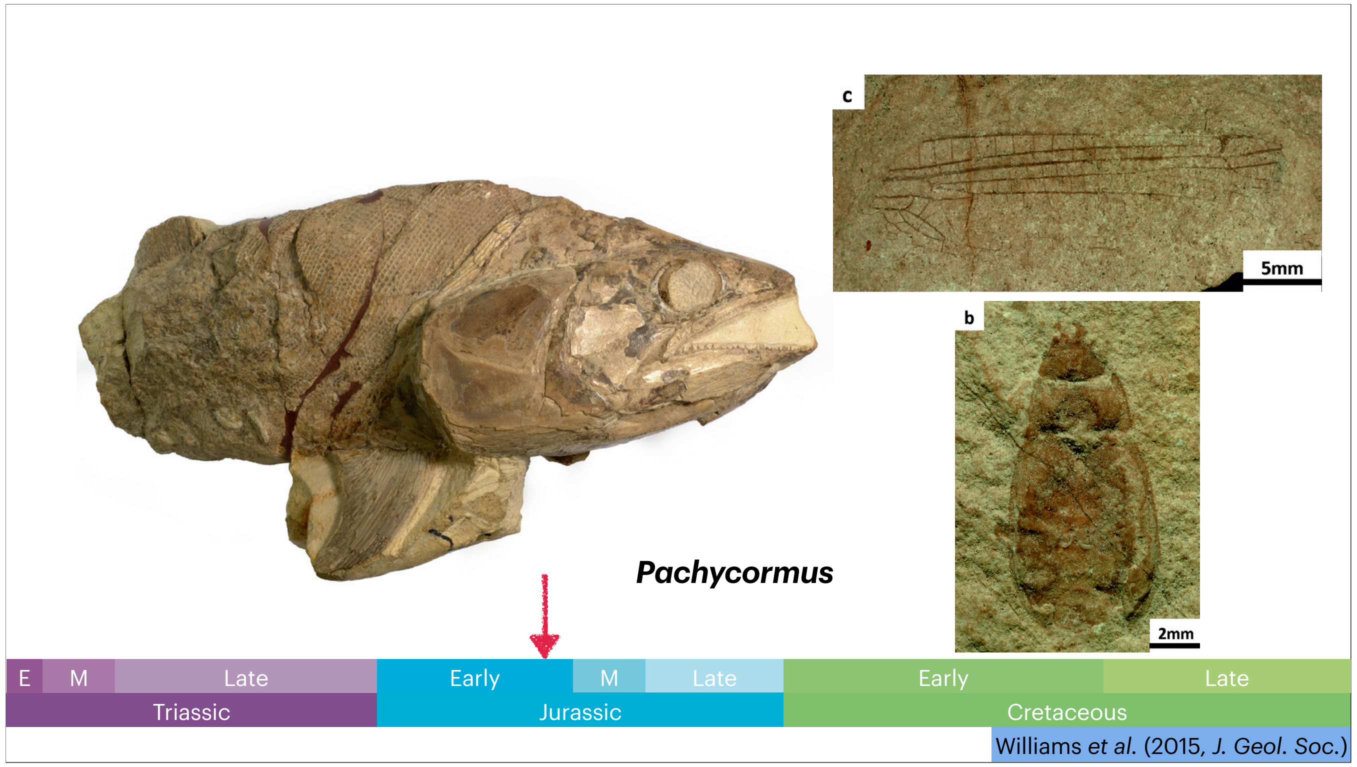
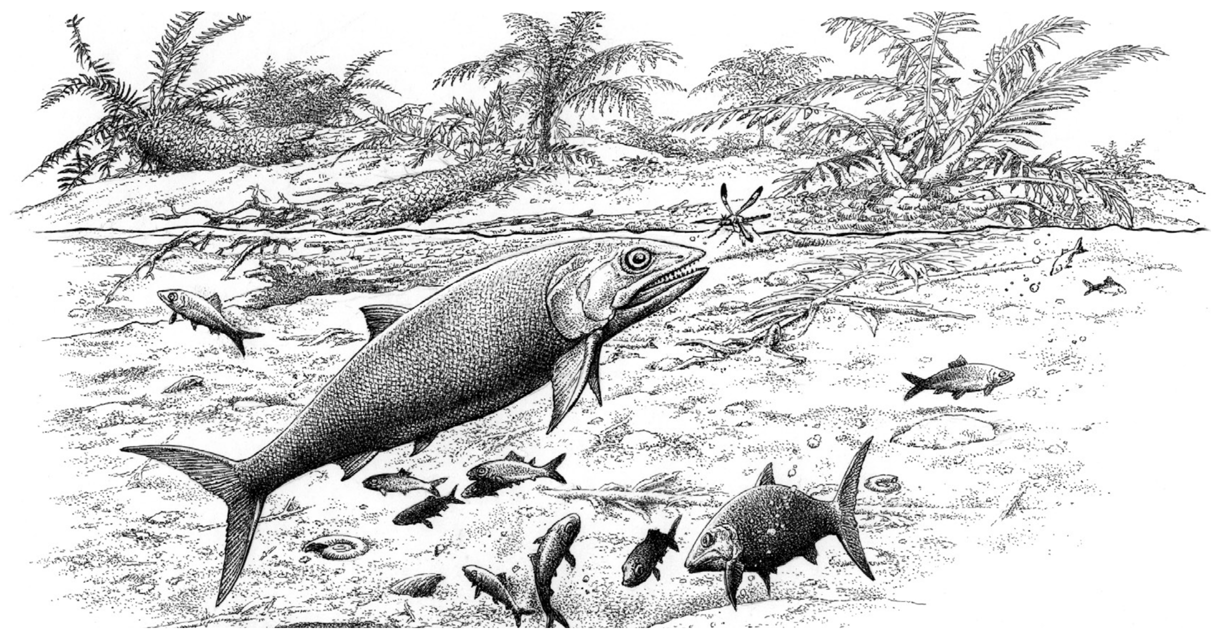


There has been a good amount of research on quantifying the diversity of ecologies in various ancient reptile groups, but how these different species interact to build the ecosystem itself is still uncertain. Fortunately we have a good instance of increase our understanding of this in Somerset itself.

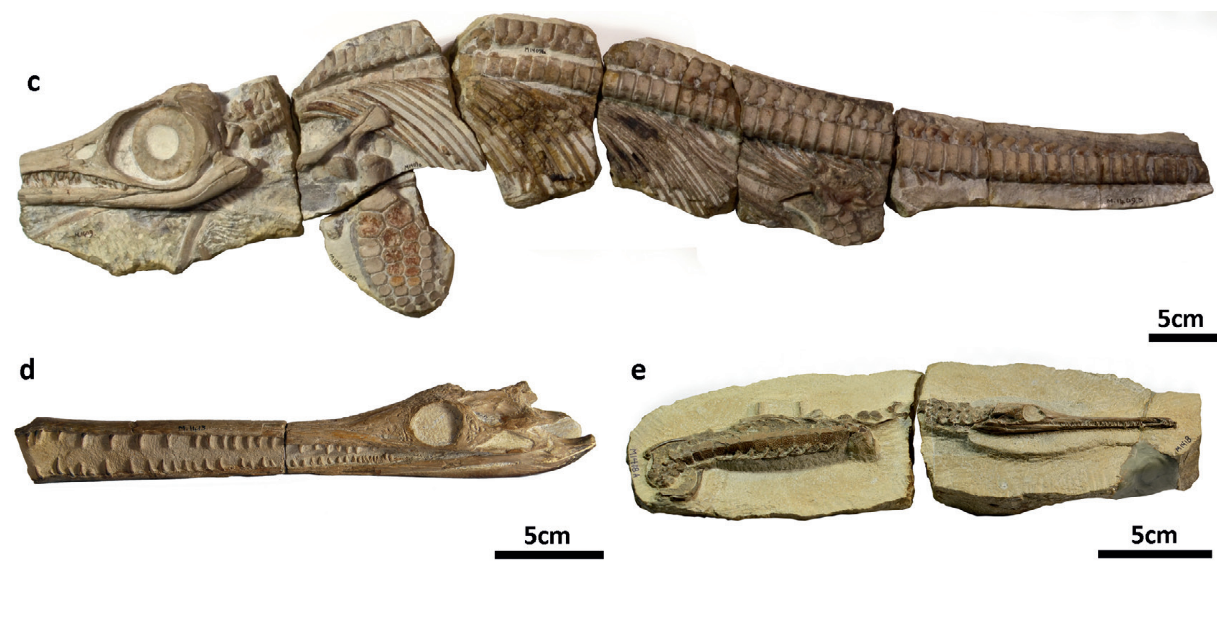
The Strawberry Bank deposits – from the Early Jurassic of Ilminster – produced numerous remains of insects, squid, and fish – such as this specimen of *Pachycormus* – when they were collected by Charles Moore in the mid-19th Century.



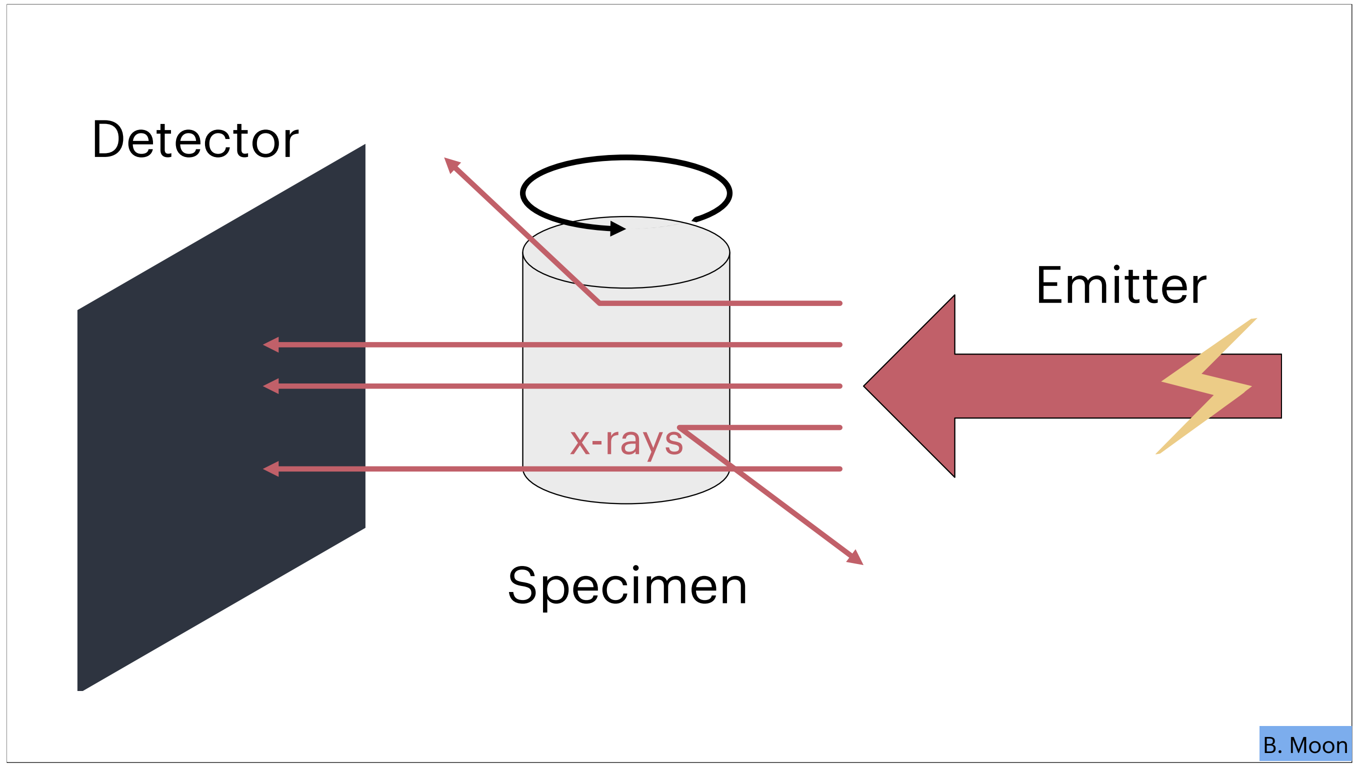
John Sibbick; Williams *et al.* (2015, *J. Geol. Soc.*)

And the completeness and extensiveness of this deposit enabled John Sibbick to create this excellent reconstruction showing the most common fauna – looking back in time to this shallow lagoon on the edge of the Tethys Ocean 182 million years ago.

But among these were also a series of complete infant and juvenile ichthyosaurs and marine crocodiles; this collection is now housed in the BRLSI – which is where I would be presenting this if I wasn't in my house. Remarkably many of the vertebrates there are three-dimensionally preserved – which is exciting by itself – but we've been able to use CT scanning to go even further with these specimens.



John Sibbick; Williams *et al.* (2015, *J. Geol. Soc.*)



As a quick introduction – CT scanning uses x-rays to see through objects – like in hospitals looking for broken bones. These x-rays are generated by an emitter when a high voltage is applied, pass through the specimen where some are scattered away, then are picked up by a detector. If you rotate the specimen and take lots of images at different angles a computer can use this to reconstruct all of those images back into a virtual 3D object.

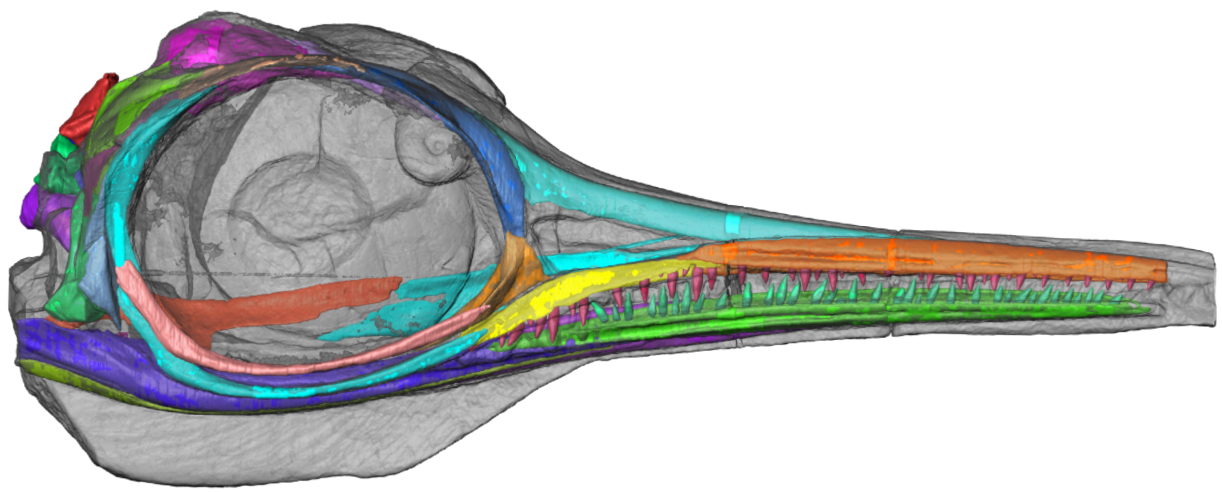
***Hauffiopteryx typicus* (von Huene, 1931) — Early Jurassic — U.K.**

Marek *et al.* (2015, *Palaeontology*); Allemand *et al.* (in rev.)

Which means that we can go from seeing the outside of the specimen – as great as this looks on its own – and pull out the bones from inside that would otherwise go unstudied. This particular specimen is from Strawberry Bank, and is an unusual ichthyosaur called *Hauffiopteryx* – unusual because of its very narrow snout.

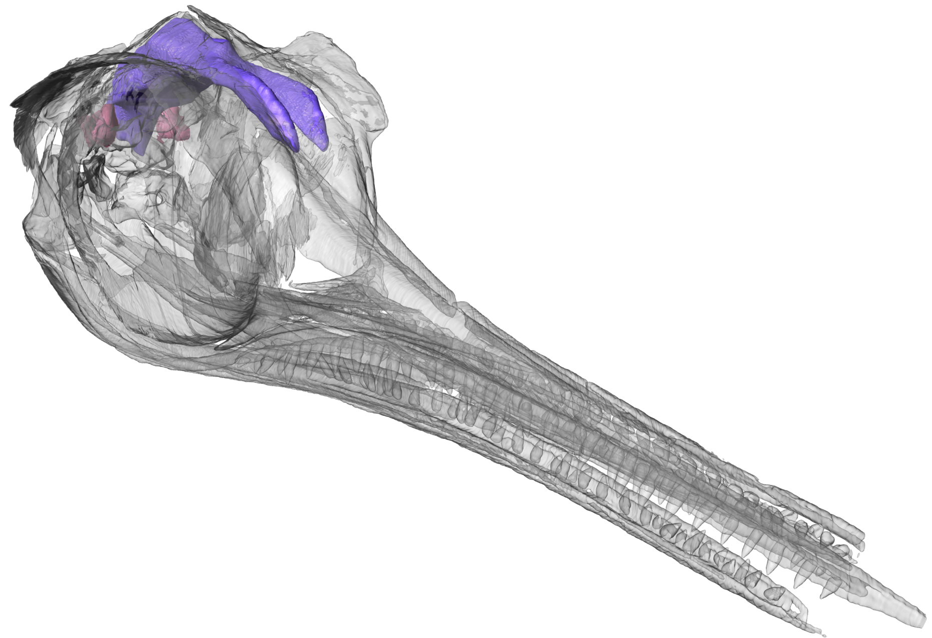
With Ryan Marek, a student from a few years ago, we were able to reconstruct the entire skull of this ichthyosaur, but even more, we could also then fill in the space inside the skull to recreate the shape of the ichthyosaur brain. This had been done in the 1970s by Chris McGowan using latex moulding on a broken skull, but here using CT scans we kept the skull intact and were also able to show the curved shaped of the brain endocast itself and from the shape of this identify the different regions associated with smell – olfactory bulb – or sight – optic lobe.

These features are exciting, both because they would be virtually unknowable without such exquisite fossils, but also because they start to tell us mode detail about the ecology of ichthyosaurs – that they have a good senses of smell and sight compared to some other marine reptiles.



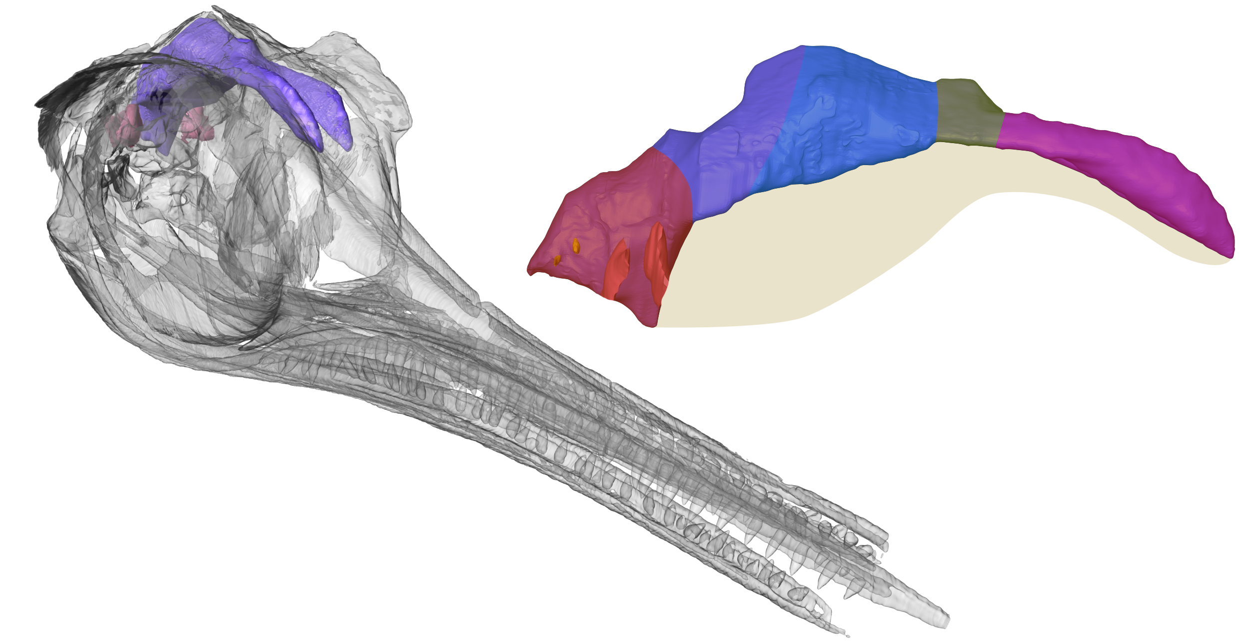
Hauffiopteryx typicus **(von Huene, 1931) — Early Jurassic — U.K.**

Marek *et al*. (2015, *Palaeontology*); Allemand *et al*. (in rev.)



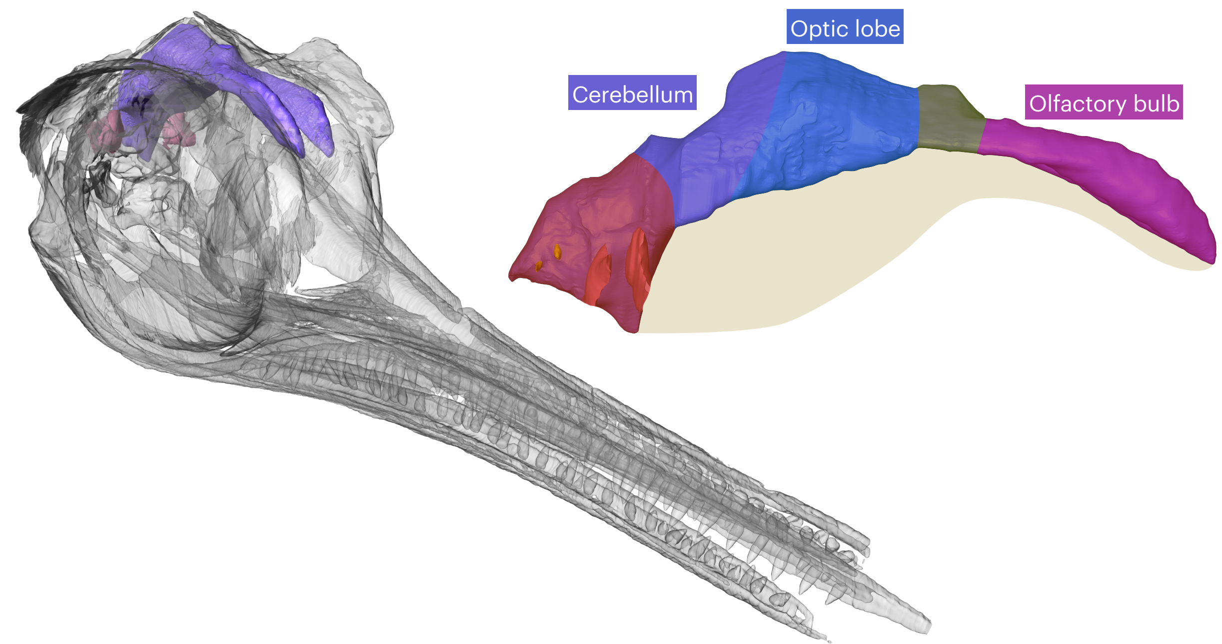
***Hauffiopteryx typicus* (von Huene, 1931) — Early Jurassic — U.K.**

Marek *et al.* (2015, *Palaeontology*); Allemand *et al.* (in rev.)



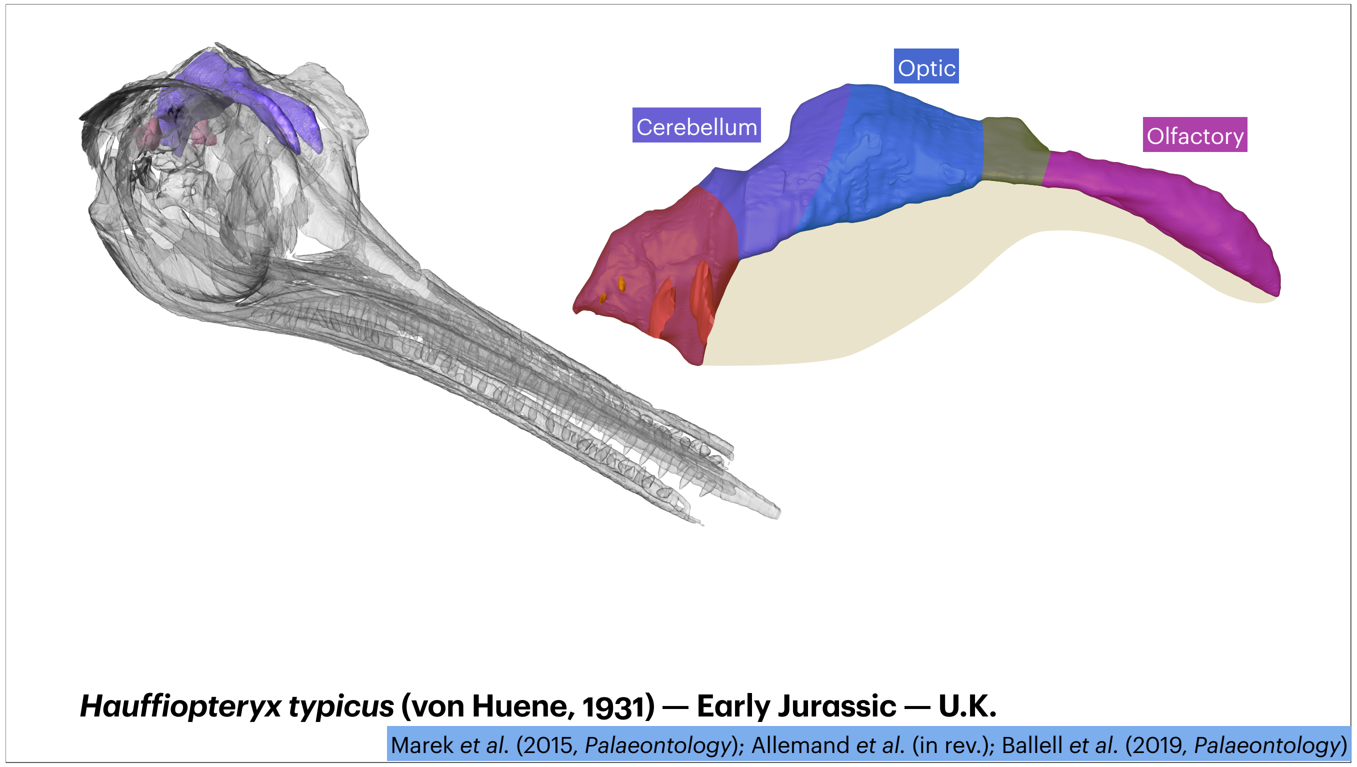
Hauffiopteryx typicus **(von Huene, 1931) — Early Jurassic — U.K.**

Marek *et al.* (2015, *Palaeontology*); Allemand *et al.* (in rev.)



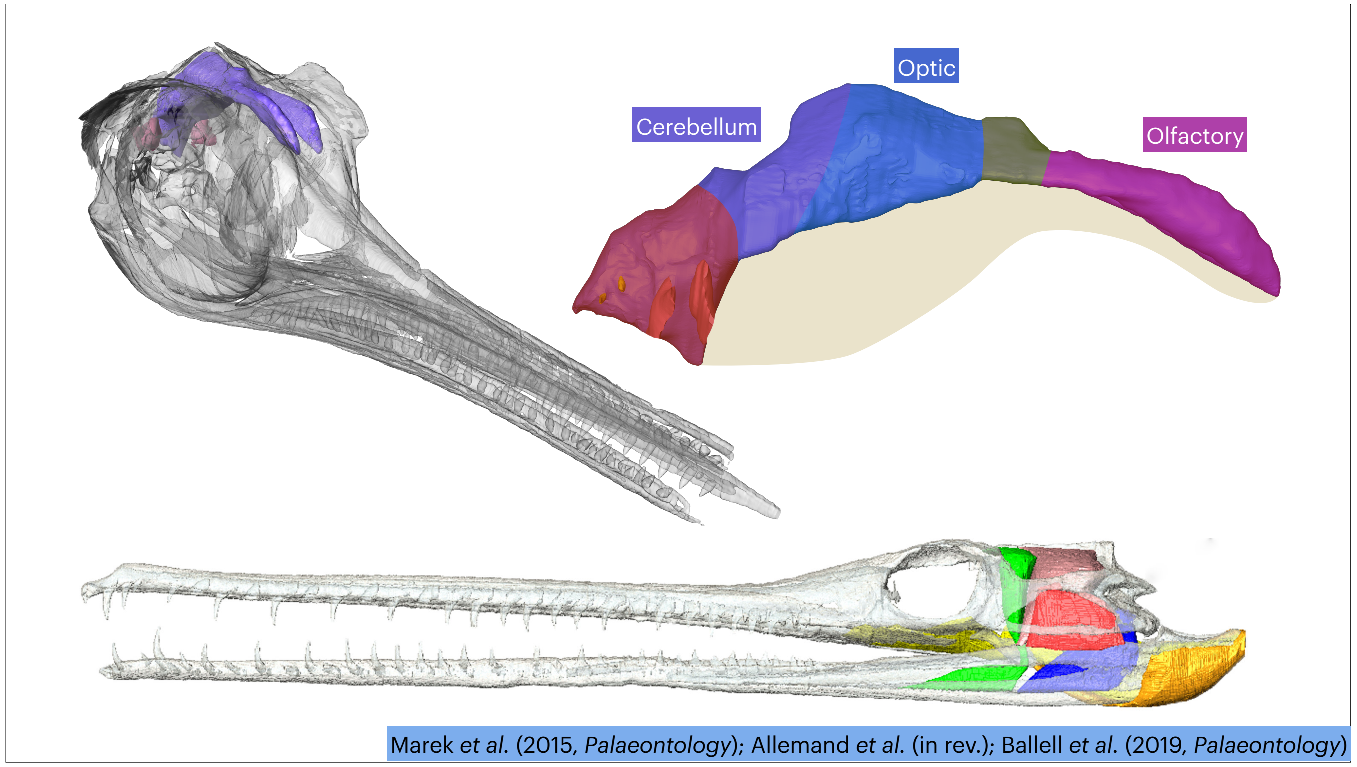
Hauffiopteryx typicus **(von Huene, 1931) — Early Jurassic — U.K.**

Marek *et al.* (2015, *Palaeontology*); Allemand *et al.* (in rev.)

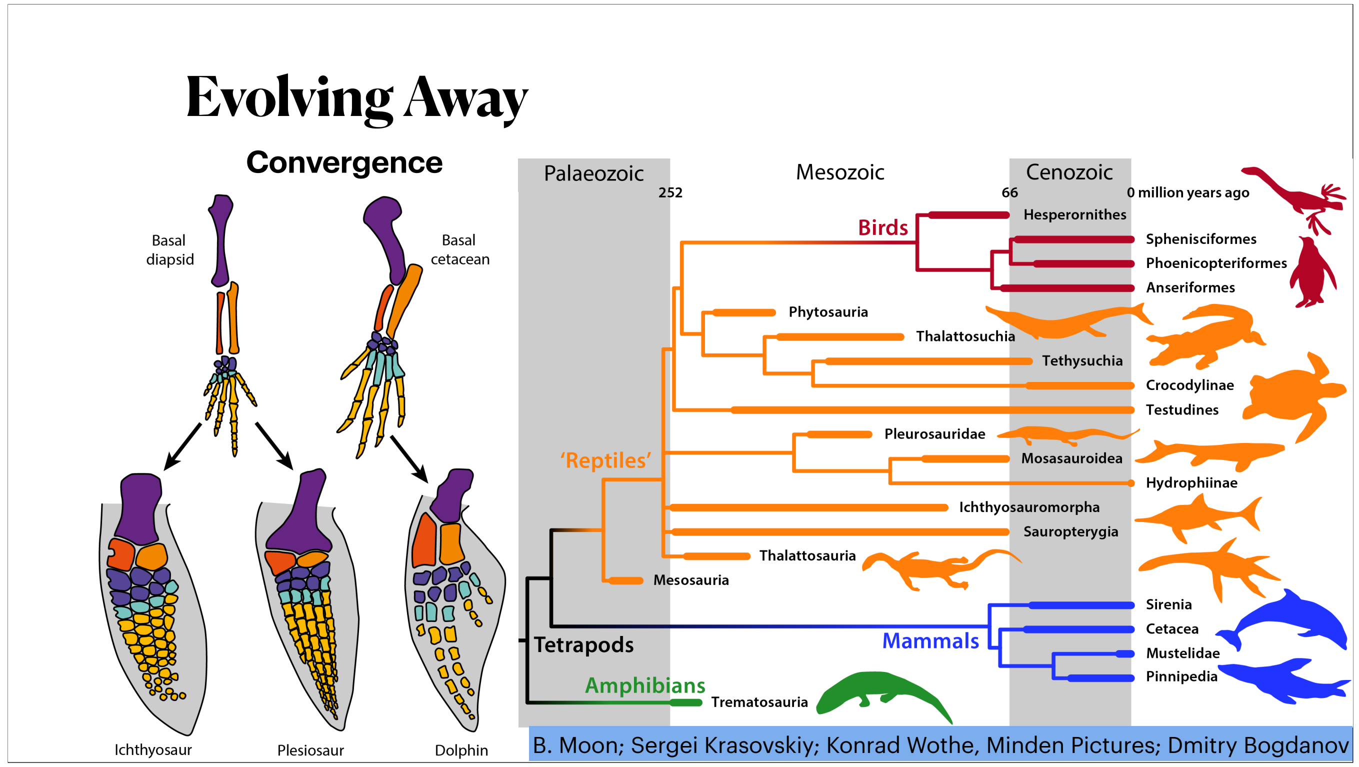


CT scanning specimens offers other opportunities for studying the palaeobiology – beyond just reconstructing the brain, one can also use the skull bones and the space between to reconstruct the muscles that close the jaw. This is work we did with Antonio Ballell reconstructing a marine crocodile from Strawberry Bank, fitting in all of the muscles, and then comparing it to a modern day gharial. It turns out that – while this crocodile skull may look similar to a gharial – they don't work in quite the same way, and the differences may be due to their different prey or hunting methods.

With these data I'm in the process of completing this work for *Hauffiopteryx* and the other Strawberry Bank ichthyosaur species too – *Stenopterygius triscissus* – so that we can compare and contrast these different taxa within this ecosystem.


Cerebellum
Optic
Olfactory
Marek *et al.* (2015, *Palaeontology*); Allemand *et al.* (in rev.); Ballell *et al.* (2019, *Palaeontology*)

Strawberry Bank isn't the only deposit from around this time – there also extensive finds from Yorkshire and especially from southwestern Germany. Together these preserve a comprehensive view into a small period of ichthyosaur evolution – and the evolution of marine ecosystems – with a high diversity of different animals representing all levels of the food chain – how do so many different species live alongside each other without competing? how do they separate their ecological niches? It's records like this – taken alongside the cooccurring climatic shifts – that could give more insight into how ecosystems are affected by rapid global changes.



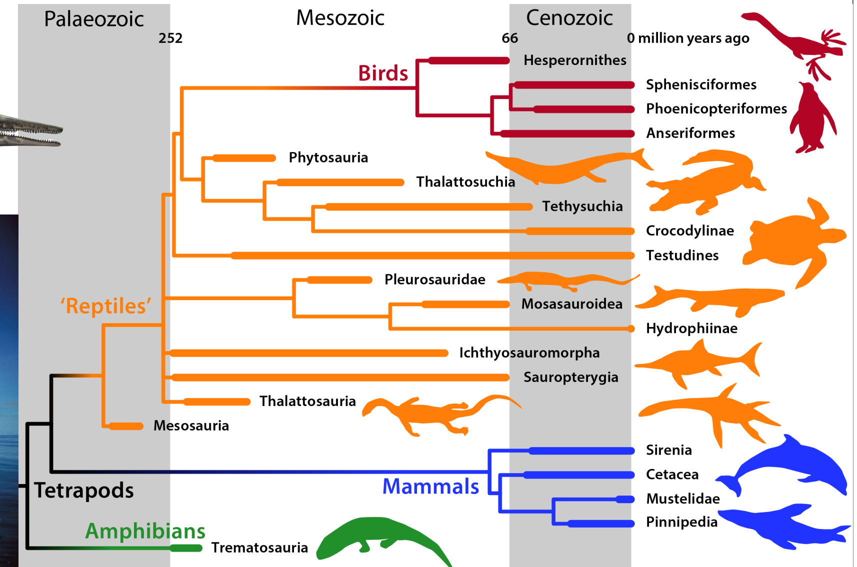
Of course these snapshots are only single points in a much larger story. The final are that is of great interest to me is the evolution of ichthyosaur among the many other groups of marine reptiles. I've shown this image before, but wanted to bring it back just to reiterate how many different vertebrate groups have moved from land back into the oceans over the last 280 million years or so – each of the thicker coloured bars represents one of 21 separate incursions. In many instances these groups have re-evolved similar solutions to the problem of living in water – such as adding bones to the limbs to make them more rigid and hydrodynamic.

The streamlined, fish-shaped body plan of ichthyosaurs, whales, and dolphins are an excellent example of this – but it's also found in the Cretaceous mosasaurs – like *Platecarpus* from about 83 million years ago…

And the Jurassic marine crocodile *Metriorhynchus* from Europe. All three of these groups have independently evolved paddle-like limbs, a tail fin for propulsion, and elongate bodies and skulls from very different ancestries and in slightly different. The question remains: in what way and how quickly does the physical medium of living in water versus the biological limits of evolution come together to drive these similar solutions?

Evolving Away

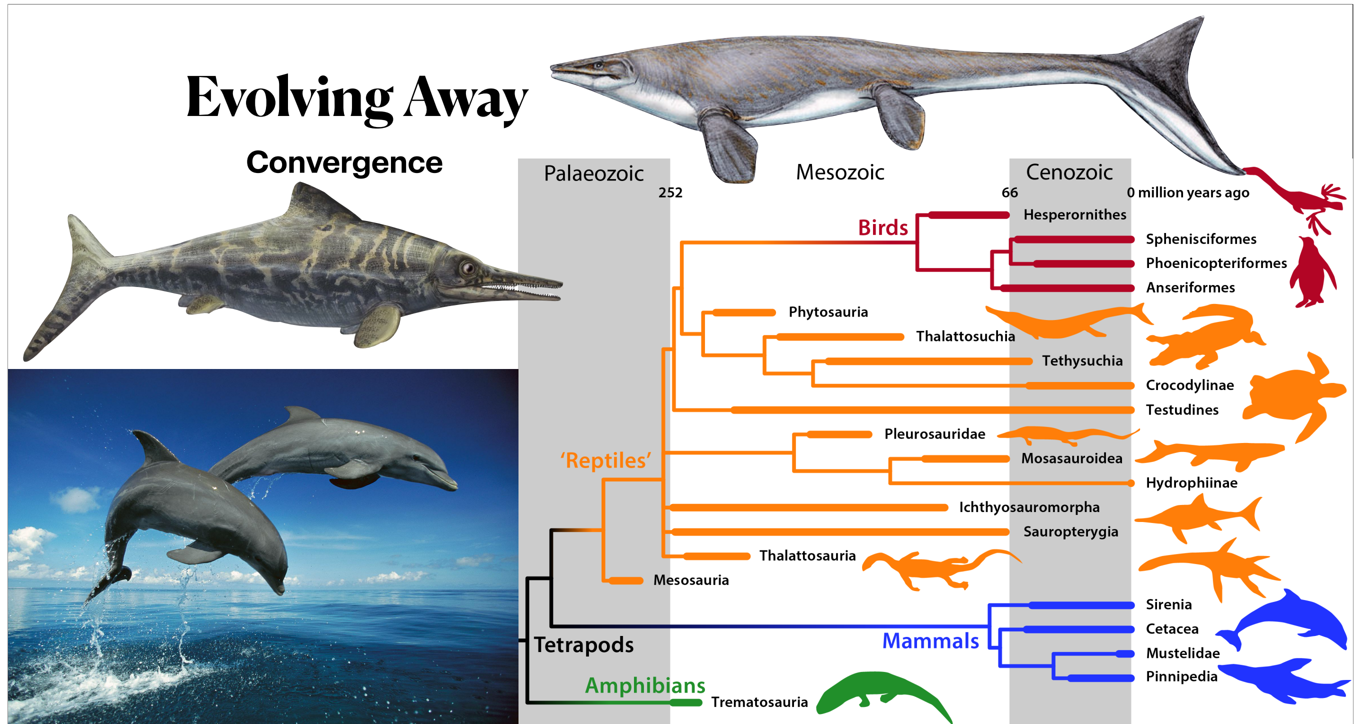
Convergence



B. Moon; Sergei Krasovskiy; Konrad Wothe, Minden Pictures; Dmitry Bogdanov

Evolving Away

Convergence



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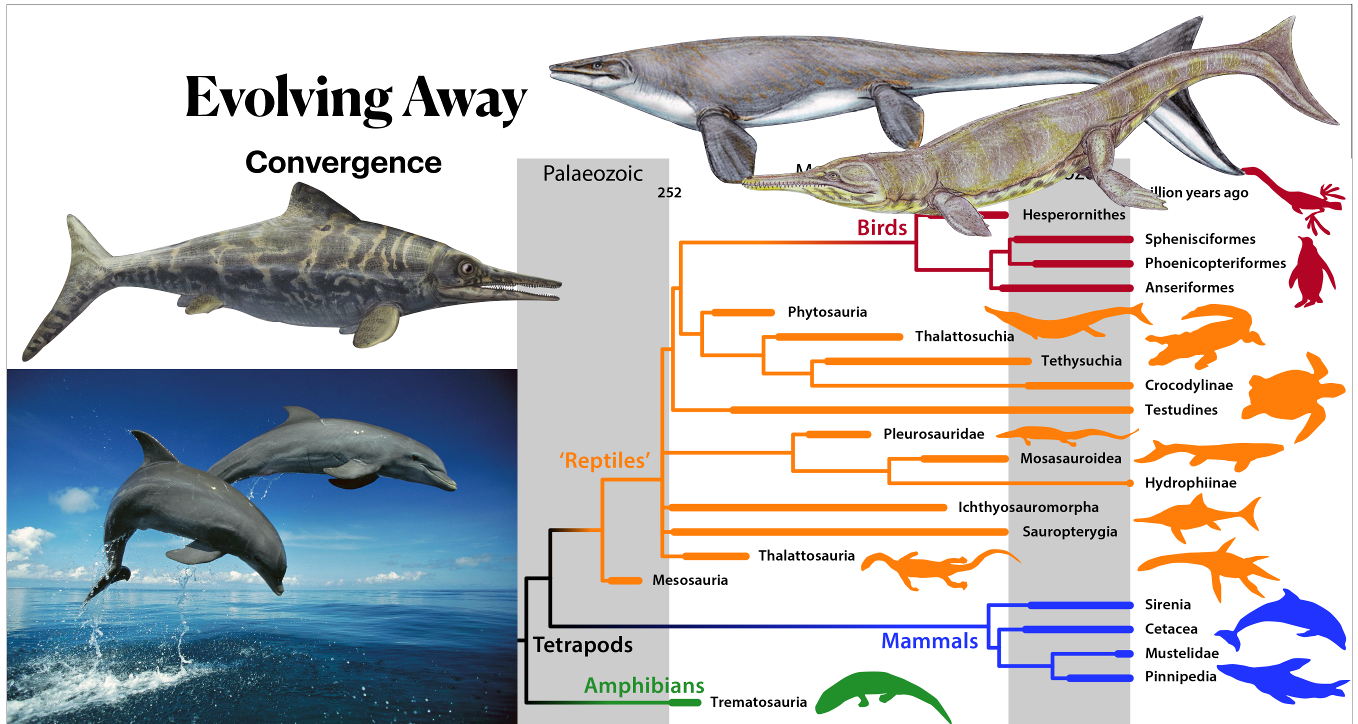
Evolving Away

Convergence



B. Moon; Sergei Krasovskiy; Konrad Wothe, Minden Pictures; Dmitry Bogdanov

1. Introduction
2. State of the Art
3. **Future Prospects**
4. Conclusion

1. Introduction
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4. **Conclusion**

Natural History Museum, London

T. Green

I'd like to finish with some images of museum collections: while we may not be able to visit them right now there are a huge number of ichthyosaurs specimens at major national museums – like the Natural History Museum in London with their famous marine reptile gallery…

Etches Collection, Kimmeridge, Dorset

T. Wren

… and smaller local museums such as the Etches Collection in Kimmeridge – dedicated to the efforts of just one man – Steve shown here – over about 40 years now. These collections doubtless contain new ichthyosaur species that have yet be be described – and there are many other unexplored places around the world.

Hupehsuchus nanchangensis **Young & Dong, 1972 — Early Triassic — China**

China has been particularly productive over the last 30 years – producing a huge number of new but relatively understudied ichthyosaurs and also ichthyosaur relatives. I've been able to collaborate with Long Cheng at the China Geological Survey in Wuhan … incidentally visiting there just last December. We are looking at what is probably the oldest Mesozoic marine reptile fauna known – the closest to the end-Permian mass extinction – and are finding out what was happening in what was still a very stressed environment.

Attenborough and the Sea Dragon, BBC

BBC

I'd also like to add that ichthyosaurs can still capture the public's imagination – as they did 200 years ago when they were first found and 170 years ago when the Crystal Palace models were first shown. I was privileged to work on this documentary shown a few years ago with David Attenborough and Chris Moore – a descendant of Charles Moore – on a new ichthyosaur specimen. From just one specimen we were able to create reconstructions, determine how it died, reconstruct the colour patterning of this ichthyosaur, and explore what bigger critter may have killed it.

Ichthyosaurs have had a long history, but there's plenty more where tat came from

bcmoon.uk — benjamin.moon@bristol.ac.uk — @moononthebones

***Temnodontosaurus trigonodon* (Theodori, 1843) — Early Jurassic — Germany**

B. Moon

Thank you for coming tonight; I'll be happy to make any questions now or feel free to contact me if you think of anything later.