

THE EVOLUTION OF CROCODILES - Curated Transcript of BBC In Our Time podcast  
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In Our Time is hosted by Melvyn Bragg. Melvyn's guests on this podcast are:

Anjali Goswami  
Research Leader in Life Sciences and Dean of Postgraduate Education at the Natural History Museum

Philip Mannion  
Lecturer in the Department of Earth Sciences at University College London

And

Steve Brusatte  
Professor of Palaeontology and Evolution at the University of Edinburgh

Producer Simon Tillotson

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Transcript:

[Melvyn Bragg] Hello. Before the rise of the dinosaurs, the dominant land animals were "crocs", the academic catchall name for ancestors of the alligators and crocodiles that lurk by the water's edge today, among the reeds. That was truly the age of the croc. There were once crocs as large as t-rex, some 10 meters long, some running upright on two legs, some with hooves, some in the oceans as big as a whale. And their prominence was long overlooked by those who treated crocodiles on Earth now as living fossils, less intriguing than dinosaurs, with little left to reveal. With me to discuss the evolution of crocodiles are

Anjali Goswami, Research Leader in Life Sciences and Dean of Postgraduate Education at the Natural History Museum,

Philip Mannion, Lecturer in the Department of Earth Sciences at University College London  
and

Steve Brusatte, Professor of Palaeontology and Evolution at the University of Edinburgh.

[Melvyn Bragg] Steve Brusatte, we've used the word "croc", a rather jaunty word here that hints at a wider group. What does it cover?

[Steve Brusatte] Well, we'll have to start out with a bit of terminology, and I don't like spending too much time on jargon, but we're going to be talking here today about 250 million years of evolution and a huge diversity of species. So to set the stage, today we have crocodiles, the Nile crocodiles, for example, and along with alligators and another group called the gharials - these are ones with really long snouts - these are the only living "crocodilians". There's just about 25 species today spread around the tropics and the subtropics, but the crocodilians have a lot of extinct cousins. And around 250 million years ago, the reptile family tree split into two groups. There was crocs on one side and then dinosaurs and birds and pterodactyls on the other. And technically, that croc group is called the pseudosuchia, but to me, that's really an unwieldy tongue-twister name. It does not suit well for crisply pronouncing here on the radio. So I'll just use the informal term "croc" to cover that entire group on the family tree. And again, that's everything more closely related to today's crocodiles than to dinosaurs, birds, pterodactyls, snakes, lizards, any other reptiles. And the important thing for us is that there was an enormous diversity of these croc species during prehistory.

[Melvyn Bragg] What do you mean by prehistory?

[2:49]

[Steve Brusatte] Well, I'm going back to the Triassic period, and that's about 250 million years ago. And then the Triassic was followed by the Jurassic and the Cretaceous. That's what we often talk about, is the age of dinosaurs before the present day. But as we'll see, quite a lot of that time at the beginning in the Triassic period was really the age of crocs.

[Melvyn Bragg] Could we say they were at that peak then?

[Steve Brusatte] I think so.

[Melvyn Bragg] So what did the peak look like?

[Steve Brusatte] They were at their peak then, really, because there were many species living all over the world doing a whole bunch of different things in terms of their diets and behaviors. And so in the Triassic period, this was the span from about 250 to 200 million years ago. It was the crocs, much more than the dinosaurs, that were dominant on the land. Really, the dinosaurs were the supporting actors at that time. And it was a croc drama that was playing out on the supercontinent of Pangaea. This

was the time when all of the world was gathered together at once. And these Triassic crocs really make a mockery of the few, the pittance of crocs that are still around today. Today's crocs are all really similar. Let's face it - a crocodile an alligator, a garrial. These are all subtropical or tropical animals. They're basically semiaquatic. They move a bit between water and land. They're predators. But in the Triassic, there was so much more. There were crocs that were nearly the length of buses. There were crocs that were at the top of the food chain, but in a different way than today. These crocs back then had heads that were nearly the sizes of bathtubs and filled with steak-knife teeth, almost like mini t-rexes. But there were other crocs that were covered in spikes and horns. Others ate plants. Some even ate insects, probably. Some had sails on their backs. Some lost all of their teeth and had beaks, if you can imagine that. A croc with a head that kind of looked like a turtle. And some of them even sprinted on their hind legs. They walked upright on two legs, kind of like we do, and they together - during the Triassic period - these crocs, they were the dominant animals, much more than dinosaurs. And by that, what I mean is: there were more croc species; they lived in more places; they had a greater variety of diets and behaviors and lifestyles. And really, they were keeping the first dinosaurs in check for several tens of millions of years across the entire Triassic period until about 200 million years ago, when the Triassic period ended.

[Melvyn Bragg] What did they prey on? What was their food?

[5:30]

[Steve Brusatte] They ate a variety of different things. Some of them would have looked and behaved like some of the crocs that live today, and they would have lived in and near the water. They would have eaten fish. They would have eaten small prey. Some were the top predators on land. They were filling those niches that were later filled by big, scary, meat-eating dinosaurs like t-rex. They didn't quite get to the size of t-rex, but there were things that looked kind of like mini t-rexes, and they were crocs. And then there were these ones that ate plants. They had teeth, kind of like mortar and pestle type teeth for eating plants, grinding up plants. And then these ones with beaks... I don't really know what these were eating, but they probably were eating things maybe similar to turtles and other animals that have beaks today, whether that's insects or whether it's small prey. What's important, really, is that diversity of diet was so much greater than what we see Crocs doing today.

[Melvyn Bragg] Thank you very much. Phil Mannion, what was this world like in the age Steve just described? The Triassic. Can you give us a picture?

[6:35]

[Philip Mannion] Sure....So, as Steve mentioned, this was a time when crocs in particular were doing very well.

[Melvyn Bragg] This is 250 million years ago?

[Philip Mannion] Yes. So this is the period from then until, as Steve said, about 200 million years ago. And at this time, the world was very different to the world we see today. So all the continents were connected. So there was the continent, Pangaea, and the conditions were very different to the present day. So this is a much hotter world,

and there was probably sort-of large deserts going through parts of the middle parts of this continent.

[Melvyn Bragg] When you talk about deserts, we don't associate crocs with deserts. Do we associate them with water and swamps and that sort of thing. So how did they get on in deserts?

[Philip Mannion] In the past, crocs had, as Steve, alluded to, lots of different shapes and sizes, but they also inhabited lots of different ecologies, lots of different habitats. So actually, many of the animals that we see throughout the history of crocs are really doing quite different things to their present day representatives. So these are animals that potentially have far less ties to living in fluvial or estuarine environments. These are animals that are actually much more able to live in perhaps semi arid environments.

[Melvyn Bragg] They existed, as I understand it, about the same time as the dinosaurs. Is that right? And if so, what was the relationship between the two?

[Philip Mannion] They both appeared around the same time. There was overlap in some environments, but at the time, most of the dinosaurs were much smaller than what we probably think of when we think of dinosaurs in general. We we lack the really sort of giant dinosaurs that we really sort of think of. When people think of things like Jurassic Park, they think of giant sauropods or things like t-rex or velociraptors. Most of the dinosaurs of a time are much, much smaller, so they were probably living in similar environments. But there's a good chance that some of the food chains were perhaps in the opposite direction that we think of today. Perhaps some of these crops are actually feeding on some of these dinosaurs.

[Melvyn Bragg] What brought the Triassic period to an end? What made the world less hospitable for so many animals?

[Philip Mannion] At the end of the Triassic period - so this is what we call the Triassic-Jurassic boundary....

[Melvyn Bragg] About, when, 200 million? [Years ago]

[Philip Mannion] Yeah, 200 million or 201 [MYa], to be precise.

[Melvyn Bragg] What's, a million years?!...

[Philip Mannion] The Triassic-Jurassic mass extinction is perhaps one of the slightly less well understood of the big five mass extinctions that happened across the last 500 million years. So this one didn't really affect the dinosaurs so much, but it actually affected a large amount of the crocs that Steve has been talking about. So many of those kind of weird and wonderful animals actually disappeared.

[Melvyn Bragg] Why did it affect them and not the dinosaurs? What was going on there?

[Philip Mannion] Well, we're still trying to understand what the differences were between these different groups. So it's possible that actually some aspects relating to

the body size of these animals. So generally in mass extinctions, we see that smaller animals tend to sort-of do quite well. But in a large part, we're not really too sure why some groups, some closely related animals, go extinct and other ones survive. But in general terms, having sort of a broad distribution, having quite a generalist diet seemed to be [the] kind of features that support or make it more likely that a species might survive.

[Melvyn Bragg] Do we know what caused that mass extinction?

[Philip Mannion] This relates primarily to the opening of what we now see today as the Atlantic Ocean. The western and eastern parts of Pangaea are essentially pulling apart from one another and starting to form what we describe as a proto Atlantic Ocean. This releases huge amounts of lava, but importantly, it releases lots of gasses, things like CO<sub>2</sub> and methane as well.

[Melvyn Bragg] Thank you. Anjali Goswami, if you were to look at a fossil, how would you know it was a croc and not a dinosaur or something else?

[10:18]

[Anjali Goswami] Yeah, that's a good question. And so, in a perfect world, I would just list off for you some characteristics that you could easily identify in either of these two groups that you could say, this is definitely a croc, or this is definitely a dinosaur. There's a couple of things that make it a lot more tricky, and the first one is that fossils are not perfect. We'd like to think that when we go out and dig up fossils, we find complete skeletons and we can understand exactly what these animals looked like when they were alive. In fact, what we usually find is just one little piece, a broken skull bone, usually just a tooth, maybe a little bit of the post cranial skeleton, a piece of the foot bone or something like that. With crocs, actually, we very often just find a piece of the dermal armor. Now, that's actually a pretty good diagnostic one, the dermal armor. But so one part of the reason why it's tricky to know is because we very, very rarely find complete skeletons, so we just find little pieces. The other reason it's tricky is because in order to think about what a Triassic crocodile looks like, you basically have to forget everything you know about crocodiles now, because Triassic crocodiles, as Steve and Phil were discussing, don't look anything like crocodiles today. Some of the earliest forms actually appear to be bipedal running around on two feet. They were really narrow bodied. They had long back legs and short front legs. They looked like they were actually built for speed on land, some of them. Their teeth, you know, if you think about croc teeth today, or certainly kind of anytime you'd pick up a crack tooth from the Cretaceous now, it's kind of this standard conical kind of cone-shaped thing with some striations - pretty easy to pick up and identify. But actually, in those early groups, along with that ecological diversity that Steve and Phil were mentioning, there's a huge diversity in things like teeth and the other structures of the skeleton. So if you do happen to find a really perfect skeleton, and there are some around, there are aspects of the ankle skeleton that people point to for identifying which kind of line they're on - whether the croc or the dinosaur line. There's various aspects of the skull. There's aspects of the way the jaw is structured. Those are some of the things. And again, that dermal armor, those scutes, are another key aspect of that. In that early part of the Triassic where both of these lineages or both of these groups are really taking off, there's a huge amount of innovation in their body forms and in their skeletons. And that makes whenever you have these kind of bursts of innovation, it can

make it really hard to tease out what different groups are actually - how they're related to each other.

[Melvyn Bragg] Is that why fossils, skull fossils, are so valuable?

[13:03]

[Anjali Goswami] That's a very good reason why skull fossils are so valuable. Just the different bones in the skull, the different holes in the skull or "foramen" in the skulls can be really, really diagnostic for the different groups. Unfortunately, finding a complete skull is quite rare, extremely rare, but when you do find them, you can not only do a much better job of assigning your animal to one of these groups, but you can also get a ton of information about what that animal actually did when it was alive. And that's because the skull is, in many ways, the center of a function for an organism. It's where they process their food. So their teeth will give you lots of information about what they're eating. For most organisms, it's also how they're actually catching their food. So it tells you a lot about what kind of environment they're moving around in and how they're catching their food. It holds most of the sensory organs, right? So it holds your eyes and your ears and your nose. And so you can look at how it was actually moving around its environment, how it was sensing its prey. Obviously, it contains the brain. And so you can look at the size of the brain case and the different parts of the brain, and that, again, tells you a lot about how it was existing in its environment, how it was processing lots of different sensory information.

[Melvyn Bragg] Thank you...Steve Bersatti, how did the crocs respond to the new world of the Jurassic after so many had disappeared? What were they left without?

[Steve Brusatte] Well, first of all, they survived, and that was the most important thing. They got through that extinction. And as Phil described, the world ripped apart! Pangaea split apart. You had these big volcanoes erupting, all kinds of toxic gases, global warming. I mean, this was a real apocalyptic period of time. It was a few hundred thousand years, most likely, of these eruptions, and that was one of the worst mass die offs ever. And crocs almost went extinct. They almost were a complete fatality of that event. But they did make it through. Not a lot of them, it seems like, but at least a few groups of the crocs made it through. And then once they were on the other side, in the Jurassic period, the next interval of time, they diversified again. They basically were Lazarus. They rose from the dead. But now the world was different. Not only was the supercontinent breaking apart, but the world was now full of dinosaurs. The dinosaurs were the great survivors of that extinction. As Phil said, we don't really know why that was. To me, it's one of the biggest mysteries of [not only] dinosaur paleontology, but paleontology in general. Why did the dinosaurs survive? Especially because, as Anjali was saying, a lot of these early crocs and early dinosaurs were quite similar to each other. But regardless of the answer, and I'm sure some very bright, very keen, young scientists will figure it out, what we do know is we're now in the Jurassic. There's a reason that it's called Jurassic Park, not Triassic Park. If it was Triassic Park, it would be a book and a film about a bunch of crocs. And actually, that would be pretty awesome, I think, because as we're seeing, these crocs were incredibly diverse in the Triassic, but it wouldn't be a book or a film about dinosaurs. But in the Jurassic, it's different. The dinosaurs have survived. They're spreading around the world. They are growing to huge sizes - some of those groups. Some of them are starting to experiment with flying. And there are many new species of

dinosaurs. The dinosaur family tree is blossoming. So the crocs that survived that extinction now had to compete with the dinosaurs. And so they weren't on top anymore. And so some of the crocs did stay on land. There would be land crocs for quite a lot of time. But in the Jurassic, in the early Jurassic, this is when we properly see crocs begin their flirtation with water. At first, the shallow water. Now, there were some Triassic crocs that did kind-of live in those watery, semiaquatic land-shore interface environments. There were some, but in the Jurassic is when the more modern style proper crocs started to do this. The Triassic ones were more distant cousins. But now in the Jurassic, you have these more modern crocs and they're going into the water. Again, at first in the shallows. Some of them became semiaquatic - able to move between the land and the sea. But then some of those crocs in the Jurassic took it even further and ventured deeper into the water, so much so that they never went back to the land. They turned their limbs into flippers. They lost those dermal bones, those plates of armor in their skin that Anjali talked about, a signature feature of crocs. They actually lost those things to streamline their bodies. They started to give live birth in the water. They may have even been warm blooded. And really these crocs, these are crocs that we call Metriorhynchoids. They looked like whales. If you would have seen one of them alive, it would have looked like some strange hybrid between a croc and a whale.

[Melvyn Bragg] Can I ask Phil? Can you take that on?

[18:02]

[Philip Mannion] These were really thriving in the marine environments. There were other marine reptiles at the same time, but obviously dinosaurs were not one of those groups. So potentially this was a niche that they were able to invade and really do quite successfully. So they had quite a lot of features, as some of them still looked quite a little bit like crocs, as we might imagine today. But some of them started to look quite radically different. One thing about crocs is actually they ... several different groups throughout their history invaded the marine realm. So this is actually just the very first of these invasions, but this happened at least two more times over the next sort-of few tens of millions of years.

[Melvyn Bragg] How patchy is the evidence that we're talking about on this program?

[Philip Mannion] This is a bit of an odd one because the croc record is actually pretty good both before and after that extinction event. But the terrestrial realm is not so good in the immediate aftermath. So I think that is partly the problem there. But in general terms, actually, the fossil record is very good. We have good record pretty much from all continents throughout much of their evolutionary history. It obviously is a part of the problem, but I don't think it's sort of a major confounding factor as it might be perhaps for some other groups where we have sort of very bad fossil records.

[Melvyn Bragg] Anjali, you were talking about the skull. Can we come back to it? Because you were telling us in detail about what the skulls revealed.

[Anjali Goswami] Picking up on what I was saying in terms of how the skull relates to things like diet and the environment that the animal is living in and how it's kind-of processing information about that environment, it can really help filling in some of these transitions. Now, one of the things that has really, I think, transformed the study

of crocs in the last few years really is the new technologies that we can bring to bear on these questions. And so from bones like or from structures like the skull, we can use things like CT scanning and laser scanning, which we just really couldn't really do 10 or 20 years ago. And we cannot just look at the outside of the skull, where we can kind of just look at the shape, but we can actually get inside the skull and start looking at how these different structures inside the skull are actually informing how the animal was moving around and what it was doing. So in thinking about this transition from the terrestrial to the marine realm, you could look at structures like the inner ear, which is something that Steve's been involved with recently. And you can look at the inner ear, which is very different between a terrestrial organism or a terrestrial animal that's moving around in an environment that is basically an air-based environment and moving into water.

[Melvyn Bragg] What would that show you?

[Anjali Goswami] The inner ear, because it kind of navigates, it kind-of sets your balance, right, and how you move around in an environment. And so if you're moving around in a denser medium like water, you're going to have ... and also you have to do things like change the way you're hearing in that medium. So changing the medium that you're moving around with, whether air or water, will be reflected in structures like the inner ear.

[Melvyn Bragg] Thank you. Steve, I know this is a difficult one because you've said as much earlier in the program, but could you speculate? I think the audience will be fascinated to know, why did dinosaurs do so much better than crocs in the Jurassic, in your view?

[Steve Brusatte] In the Jurassic and then in the Cretaceous, the next interval of time, this was the age of dinosaur dominance, there's no doubt about it. And there were a few things that dinosaurs were doing better than crocs, if we can use a value judgment like that. But one of those things is the dinosaurs simply got bigger. Some of these long-neck dinosaurs in the brontosaurus or diplodocus family, what we call the sauropod dinosaurs. (And by the way, these are the dinosaurs that Phil is one of the world experts on. So really, Phil might have more to say.) But what I'll say is they were big. They got really, really big. And in the Cretaceous, you had some that weighed as much as a Boeing 737 airplane. No crocs got to be that size. Some of the meat-eating dinosaurs also got really big. Not as big as an airplane, but things like t-rex got to be the size of a proper double-decker bus. And the other thing that dinosaurs did in the Jurassic was some of them got small. Not all of them got big. Some of them got smaller. These were the raptor dinosaurs, like the velociraptor group. And they developed wings, and they started to flap those wings, and they started to fly. And those were the dinosaurs that became birds, as we talked about a few years ago on the feathered dinosaur chat, when Mike Benton and Maria McNamara and I were chatting with you about that whole story. So crocs never started to fly. So there were things that dinosaurs were able to do in the Jurassic, maybe in part because of their intrinsic biology. They got to be big, probably in part (again, Phil would have a more informed opinion than me) but they've very advanced lungs; they could take in more oxygen, these dinosaurs; they had air sacs that could lighten their body and cool their body and so on. So that helped them become bigger. And so that's undeniable that dinosaurs became this great majesty in the Jurassic and in the Cretaceous. But I think



we also have to remember that not only were crocs eclipsing the dinosaurs for the first 50 million years back in the Triassic, but then in the Jurassic, when dinosaurs survived and proliferated and became these marvelous animals that we all know, the crocs had to fit into those ecosystems. And they were very adaptable. They were very, in an evolutionary sense, very innovative. And these whale crocs are a prime example of that. They went fully into the water. They left land completely behind. That's something that \*no dinosaur ever did\*. It's one of the few things that dinosaurs never did. There were never any, whale, dinosaurs. There's some birds, of course, that spend most of their time in the water, but other than that, there's nothing. And so we have to give crocs credit in that sense. It wasn't just merely the age of dinosaurs and the Jurassic and the Cretaceous, but the crocs were doing some spectacular things too.

[Melvyn Bragg] Do you want to add to that, Phil? Steve's giving you the green flag on that. Do you want to add to what's been said?

[Philip Mannion] Steve's very right that actually, the Jurassic was sort of an early peak in croc evolution, but I think the Jurassic and Cretaceous was really a second wave. They were in the shadows of the dinosaurs for certain. But actually, as well as going in the marine realm, crocs were going into lots of different environments and clearly sort-of managing to carve out a niche or multiple niches for themselves. So we again have crocs that were probably able to run in quite upright sort of stances; crocs that were living in environments very different to today - so these are crocs that were living in quite semi arid environments and again, able to sort of run around quite quickly, probably; we have crocs everywhere across the globe, getting into the Arctic as well; and we even have crocs that were almost certainly herbivorous as well; so going into all sorts of different kinds of dietary niches as well. So although they very much were not the poster boys of the Jurassic and Cretaceous, I think they were also having a pretty great time out there as well.

[Melvyn Bragg] Anjali, do you want to add to that?

[25:02]

[Anjali Goswami] Certainly the Cretaceous is a really great time for crocs in many ways. There are lots of (really, my favorite group of crocs) the notosuchians, which are these really small well, they vary in size, but some of them are quite small terrestrials. They're entirely living on land. These are the ones that were probably plant eaters or specialist plant eaters, some of them. And you find them pretty widely distributed, certainly across the southern hemisphere at this point especially. And so you have these guys doing really, really well in the Cretaceous, first appearing in the Jurassic. Also in the Cretaceous is actually when the crocodiles that we would recognize today show up. And so in many ways, what we think about as crocodiles is really a Cretaceous story, which makes it actually even more interesting to think about what happens. We've talked about a couple of mass extinctions and how they shaped croc evolution, right, with the Permo-Triassic and then the Triassic-Jurassic. But of course, there's another big one coming up, which is the end of the Cretaceous. And when you think about the end-Cretaceous mass extinction and what's happening with crocs in that event, it's important to recognize that actually, when we think about crocs, they're very much the new kids on the block kind-of, at that point in Earth history.

[Melvyn Bragg] Why... Have they always been cold blooded? And why does that matter?

[Anjali Goswami] That's a good question, and I think there are very few people that would claim to know the answer to that definitively. They are now certainly - the ones that are around today. But I think there's an open question as to whether that's something that evolved later and actually whether ancestrally or certainly in the earlier crocs, warm-bloodedness may have evolved. As I said, as we've been discussing kind of throughout, the crocs of the Mesozoic are nothing like the crocs of today until our modern crocs kind-of show up in the late Cretaceous. And so they were living very different lifestyles. They were certainly living quite active lifestyles. Right? Some of these things are looking like they were fast running organisms. Well, it's rather hard to be a real fast runner, and also something that for extended periods of time without some higher metabolism.

[Melvyn Bragg] Steve, what was left of crocs after the Cretaceous-Paleogene extinction, how did they rebound?

[27:34]

[Steve Brusatte] They did rebound as they've always done. The extinction.... I think a lot of us know the story. The asteroid falls out of the sky... huge asteroid 6 miles wide or so smashes into the Earth... releases over a billion nuclear bombs worth of energy and unleashes tsunamis and wildfires and earthquakes and...

[Melvyn Bragg] This is about 60 million years ago. Is that it?

[Steve Brusatte] About 66 million years ago, right at the end of the Cretaceous. And it's the most famous mass extinction. It's the most recent mass extinction also, but it's the most famous because that's when the dinosaurs died, except for birds. But t-rex! T-Rex was there face down! The asteroid... Triceratops was there... and they didn't make it through! But crocs, believe it or not, this time were the survivors. One of the most famous groups of survivors. So we've kind-of seen dinosaurs and crocs have had this waltz over their history where one rises, the other falls, then there's an extinction, and then things are kind of reset. But this time, the crocs, many of them, made it through. ... As Anjali said, this is when we're seeing the more modern, crocodilian type crocs. The ones that are living in those semi-aquatic environments that are starting to look like the alligators and crocodiles that we know today, and the ones that are probably warm [cold??] blooded and lived a similar lifestyle. They were living in rivers and in lakes, largely. And those ecosystems seem like they were buffered against the extinction. In other words, they were like a refugia. The horrible effects of the asteroid didn't hit those ecosystems as badly. And the reason why is probably because the asteroid kicks all this dust and grime into the atmosphere. It causes a global nuclear winter. The sun is basically blocked out probably for several years. Plants can't photosynthesize. There's no or very little sunlight. So plants die, forests collapse. Plant eaters don't have anything to eat. The meat eaters don't have anything to then eat. And the ecosystems collapse like houses of cards. But the crocs and also turtles and a lot of different types of river fishes and lake fishes were not part of ecosystems that were based around forests or plants. They were in the water and they were in detritus based ecosystems. So basically, the base of the food chain is not plants, but it's dead stuff falling into the water. Well, you can imagine if that's the kind of stuff you ate. And if

you were part of those food webs, a mass die-off of plants was actually a pretty good time to be alive. So it seems like crocs, at least the more modern types of crocs, the crocs and alligators that we're familiar with, they had that winning lottery ticket, really, by dumb luck, really. And those environments helped them survive. And so they did survive. And then, as usual, after the extinction, they rediversified yet again.

[Philip Mannion] So everything Steve said is entirely correct in terms of what we currently think. But there were also other crocs that also survived that mass extinction as well. And this actually sort of bears out a lot of what we sort of think about why some groups do survive and some go extinct. So, for instance, Anjali mentioned a group of crocs called notosuchians before which were much more terrestrial than most of the other crocs. And actually many of those did go extinct to the mass extinction. But then there was also marine crocs that did pass through. This is a different group of marine crocs and we think that they maybe survive because they were actually living in quite a wide range of environments. So they were also living in sort of estuarine and coastal environments as well as fully marine. So it does seem to be some sort of signal that essentially groups that were either living in sort of riverine environments or that were sort of living in quite a range of environments also did very well.

[Melvyn Bragg] How does the diversity of crocs today compared with what went before today?

[Philip Mannion] Today, there is something like 25 species of crocs. So most of these belong to the genus *Crocodylus*, which includes the Nile crocodile and the saltwater crocodile and then a large amount of them belong to alligator and its close relative the cayman. And then there are a couple of gharials. So I said there's probably 25 because we're still trying to work out whether some of these species actually represent multiple species. Some of them look identical to one another, but their DNA shows that they are actually quite distinctive. So the numbers have been sort of gradually going up over the last ten years. Very gradually we've gone from something like 22 or 23 to around 25 or maybe up to 27, but that might change a little bit more in the future.

[Melvyn Bragg] And how many were there before?

[Philip Mannion] Over their entire history we can recognize something like over 500 species of croc, but that is over a 250 million year period. So in the past there's probably been times where diversity has been greater than today. But I think the key, rather than sort of whether there are more or less in 25 species is the breadth of diversity. So at those times in the past there were lots and lots of different types of crocs around.

[Melvyn Bragg] Thank you. Anjali, crocodiles and alligators are sometimes described even today's living fossils. Do you go along with that?

[32:45]

[Anjali Goswami] Not at all, no. I think it's a terrible term to assign to this group for lots of reasons. I think kind-of picking up on Phil's point about the breadth of crocs in the past. They have this immense diversity. And if we just think about we recently measured this. If we look at just the diversity of their skull shapes, today's, crocs

probably represent a quarter to a third of the variety of forms that they were in the past. And the term living fossil would suggest that they've always been kind of the same as they are today. But of course the crocs that are around today are kind of the newest kind of croc that's around. And if we look at the Mesozoic there was this immense diversity of different kinds of crocs. And so if anything, if crocs were today were even remotely representative of their fossil record, they would be hugely diverse. So I think calling them a living fossil doesn't do justice to them in the past, but it also doesn't do justice to how they are evolving today. And so actually, even though crocs, largely, with some exceptions, with the marine crocs that do make it through the K-PG mass extinction, even though most of them today are largely semiaquatic kind of carnivorous fish-eating forms, they actually still are evolving quite rapidly. And we can actually do this using new methods. We can measure how fast evolution has been happening in the crocs over the last couple of hundred million years. And actually, if you look at the modern radiation of living crocs, especially ones in areas like the IndoPacific, those are actually evolving at a really fast rate of evolution, actually kind of similar to the rates we might have seen in terms of generating new shapes and things that we might have seen in the Triassic and in the Jurassic. The difference today is that they're kind of reinventing the same things over and over, so they're kind of re-evolving the same sort of semi-aquatic skull shapes and niches. So I don't think the term living fossil applies for lots of reasons. I do think it generally suggests that they have had a boring evolutionary history. And of course, if we were going to call every group of organisms that today is only represented by a small number of species compared to, say, a past, more diverse group of species, and we would also say horses and hyenas or even humans are living fossils, right? Because we certainly had more diversity in the past than we do today.

[Melvyn Bragg] Thank you. Steve, when you look across this amazing timescale you've been throwing around between you, how do you see the future for crocs in evolutionary terms? Is it possible to map it out, as it were?

[Steve Brusatte] Crocs are down. You know, maybe it's their lowest ebb ever. As Phil says, it's hard to tell for sure. And the fossil record over time is 25 species, the lowest they've ever been. And there have been times that are more or less I mean, the fossil record is so biased, it's hard to tell. But as Anjali and Philip been explaining, there has been such a breadth of diversity in the past in terms of size and diet and behavior. We don't have that now. Most of the crocs that are with us are pretty much the same. They look very similar. They live in similar tropical, subtropical, near-shore environments, and they are vulnerable. Those environments are very susceptible to climate change, especially sea level rises, temperature changes. So these things could be very problematic. Some croc species today are heavily endangered. So I don't want to look into the future and predict anything. It's a hard thing to ... Paleontologists [are] always looking back, and we want to inform on the present and the future. But the one thing I would say is that if we've learned anything from the fossil record, it's not to count the crocs out, because as we've seen for over 250 million years, they have been survivors. They've faced two terrible mass extinctions each time they were knocked down to the mat. But they've gotten back up, and they've not just survived, but they've re-diversified; they've invaded new niches; they learned new evolutionary tricks. So I would not bet against the crocs.

[Melvyn Bragg] Phil, are there new techniques for looking at croc evolution?

[Philip Mannion] Both Anjali and Steve have mentioned these, and both of them are doing this kind of work, looking at crocs and other groups. They are using CT scans to kind-of look inside the croc skull in particular and try to understand aspects relating to hearing, how their brains have evolved, all these kind of things that we can start to understand a lot more about these animals. But there's lots of other aspects, too. We're gradually starting to build a much more complete understanding of their family tree, so how they were evolved to one another. And that kind of information is really important for actually addressing lots of the kind of questions that we've been talking about today. And one thing that I think is particularly exciting is there was a relatively recent publication which managed to produce ancient DNA for a relatively-recently extinct croc species. This was a species of croc that was living on Madagascar until probably just about 1000 years ago, probably driven to extinction by ourselves. And so those authors are actually able to extract DNA from this extinct species. And it's quite possible there are other crocs that only went extinct in sort-of modern human times. So it'd be really exciting to actually be able to produce ancient DNA from those species and really build this amazing picture of some of these extinct species that probably just ten years ago, we would never have dreamed of being able to actually reconstruct.

[Anjali Goswami] One thing... I think Phil is also being humble here, because one of the other really interesting things that people are doing with crocs and their fossil record that they really haven't been able to do until relatively recently is actually look at climate and how climate has actually impacted croc evolution across hundreds of millions of years. And that's because of better understanding about how climate has changed in the past, and also just better methods to model how species respond. And that's something that I think will really transform our understanding of what's been driving their evolution.

[Melvyn Bragg] Thank you. Could you give us some idea of the great unanswered questions about croc evolution and how they might be answered?

[38:53]

[Anjali Goswami] One of the things that I think bothers me a lot about the end Cretaceous mass extinction and crocodile diversification, or croc diversification afterwards is why ... when we see through these multiple kind of extinction events and changes in the Mesozoic, they always reinvade these marine niches, they reinvade these terrestrial niches. And yet, even though terrestrial crocs were doing well until the very end of the Cretaceous, we certainly find them in our field sites right before the Cretaceous mass extinction, and yet they never reinvade those niches, and it's been 66 million years now. They've had time. So why do we never see that same diversification that we saw over and over again in the Mesozoic reappearing in the Cenozoic? Is it just competition with mammals? Is it competition with other things in the ocean, well, mammals largely in the ocean also? Or is it that there's some sort of intrinsic kind of developmental constraints or something like that that has arisen in the living lineages that just can't kind of recapture that sort of variation? I don't know. But that is certainly, I think, one of the big questions with crocs, and I hope Steve is right, that there's more surprises in store from the crocs, because I personally would love a terrestrial kind of cat-sized croc.

[Philip Mannion] The other thing we can think about with that mass extinction is that crocs do fairly well across that boundary. Dinosaurs are almost entirely wiped out with just some birds. Even most birds went extinct [in] that mass extinction. But today we have 25 species of crocs and something like 11,000 species of birds. So really trying to understand why those are the two closest living representatives of that long sort-of radiation of crocs and dinosaurs, why is one group hyperdiverse and why is one group potentially on the brink of extinction?

[Melvyn Bragg] Finally, Steve?

[Steve Brusatte] For me, there's three things I'll just quickly highlight that get me really excited. And I think these are the questions that, you know, young paleontology enthusiasts might want to think about, because if you can answer these, that would be fantastic. The first is at the end of the Triassic when Pangaea split and the crocs are decimated, but the dinosaurs survive largely at extinction. Why was that? And secondly, we touched on it, Anjali touched on it here, were crocs warm blooded in the past? And if so, how did they compare to birds and mammals? And then why did they lose that warm bloodedness today? And the third thing, maybe this seems like something completely random, but did some of these fossil crocs have feathers? We know dinosaurs had feathers. We know that pterosaurs - pterodactyls, the closest living .. not living, but the closest ... relatives to dinosaurs, had feathery type structures. The next branch on the family tree is the croc. So did some of these fossil crocs have feathery structures in their skin?

[Melvyn Bragg] Well, thank you all very much. That was terrific. Thank you, Steve Brusatte, Phil Mannion and Anjali Goswami and to our studio engineer Duncan Hannon.

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And the in our Time podcast gets some extra time now with a few minutes of bonus material from Melvyn and his guests.  
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[Melvyn Bragg] What didn't you have time to say that you would like to have said? Who wants to start off?

[42:10]

[Anjali Goswami] I have one thing, actually that occurred to me after I finished the last question ... which is kind of along the lines of why crocs never regain their diversity. I wonder if it's something about being semi-aquatic. And this leads into Phil's question about why do they never get the kind of hyperdiversity of birds. I often wonder, and also this comes up with other groups, whether being semi-aquatic and kind of having to live between two worlds stops you specializing for either of them and also makes you kind of less competitive in either of them. And so that just kind of limits your evolutionary capacity by ... living this kind of double life of a croc as opposed to just being a terrestrial mammal or an oceanic whale or something.

[Steve Brusatte] Well, I think Anjali raised a good point towards the end about mammals. Anjali is one of the great world experts on mammals. And, you know, Phil and I are starting to study mammals a little bit more in our work, ... but, you know,

when the dinosaurs go extinct, other than birds, you know, mammals are the group that took over. That's the story we always tell. And of course, mammals did - they diversified; they started to grow to really big sizes - much bigger than they ever got when they were living alongside the dinosaurs and the more primitive crocs earlier on. But, you know, the crocs did diversify a bit as well afterwards. And there ... even after the dinosaur extinction, there were some crocs that did still live on the land, at least for another 15 million years or so, maybe even more. I'd have to check the numbers. But there was a group called the Pristichampsids, and these were crocs that had hooves. I mean, they were really fast runners. Why did those things go extinct? Was it because there were mammals with hooves that really became specialized for running that kind-of forced them out? Or were they kind of cold blooded or not quite fully warm blooded? And they were living in a world that was much warmer. And as the world started to cool and ice sheets started to form, eventually culminating in the ice ages, could they not survive in that kind of world as much? Phil probably has, again, a much more informed opinion than me there, but I just find it interesting that even after the dinosaur extinction, you get this new wave of diversification. It's not like all the crocs are just still in the water or in the semi-aquatic environments, but you still had some on land, but they kind of just wasted away over time, leaving this pittance today.

[Philip Mannion] Yeah, I guess in the climate aspects ... We've touched upon us a few times. We know very much that crocs today have this very kind of latitude and restricted range - so living in the subtropics roughly sort of 25 degrees either side of the equator. But throughout much of the early parts of their evolutionary history, they were pretty much everywhere. And so right up to about 50 million years ago. We know they were living up in the Arctic, almost certainly, probably getting into Antarctica at times. And pretty much the entire story of their evolution seems to track the change in climate to the globe. So during much of the interval we've been talking about - the Triassic, the Jurassic, the Cretaceous, the world was just much warmer than it is today, and that included going up to the poles. So at times in the Cretaceous and in the early parts after the Cretaceous, for instance, there was no ice at the poles. And so these were probably sort of conditions much closer to almost what we think of the modern tropics getting into these high latitudes. So crocs were really thriving at those times. But as the Earth started to cool, particularly around about sort of 30 million years ago onwards, the range of crocs really shrank. And so this might also be sort of a key aspect of their kind of reduction in numbers of species, because essentially they had much smaller amount of the Earth to inhabit. And so we do really seem to see that their diversity does seem to tie in with how climate has changed across the globe, and probably periods of warmth has allowed crocs to really thrive. But it's got into this colder world. It's really kind of stopped crocs really doing as well as they could do. And definitely, I think Anjali is probably right, they probably were just limited somehow to not being able to sort of take advantage of the niches. We don't find any crocs living in trees, we definitely don't find any of them flying. So they really seem to have missed out on a lot of habitats and niches that lots of other species just took advantage of.

[Anjali Goswami] So, Phil, can I ask.. Given what you were just saying, do you think then, given how crocs do seem to track climate, that the next 100 years is going to be the rise of crocs? Again?

[Philip Mannion] I think if we weren't here, in which case, obviously, we wouldn't have a warming world, but if we weren't here, I think crocs would actually do probably quite

well. We generally see the diversity of most groups seems to do better during warmer intervals, but it's all the other associated aspects that come with changing climate. It's all the loss of habitat, that degradation that really is problematic for crocs. And also, ultimately, these species in a normal warming world without humans around, would probably move pole-wards - they would disperse into other areas. But obviously those areas are going to be towns and cities. There's no way that crocs are going to be allowed to sort-of disperse into those areas. So I think global warming and all the other aspects that come with climate change are going to be pretty devastating for most crocs. There's a few species of crocs that are doing very well and probably flourish, but we ... definitely do face sort of the extinction of several species. Steve mentioned before that several of them are a high extinction risk and several species are down to the last fewer-than 1000 individuals in the wild and their habitats are greatly shrunk. These include in lots of different parts of the world in China, but also in parts of Central America too. So [for] several species of that 25 group that is really a danger and some of those species are really the last remnants of the croc radiation. So for instance, a very good chance we will lose the gharials over the next 100 years because of things like climate change.

[Anjali Goswami] I think you raise a really good point, because sometimes when we think about previous periods of warm intervals, like the Miocene, right, is is a classic one that's between 5 to 20 million years ago. And it was this period that the Earth is unlike the Triassic world, where you have Pangaea and the supercontinent ... After the Cretaceous, the world starts to look a lot more like it does today in terms of where the continents are. And certainly in the Miocene, you're basically looking at the modern world in terms of how the continents are organized, but it is a few degrees hotter than it is today and so in some ways it's a really good model for what might be happening. And of course, when we think about the Miocene and croc diversity, there's actually a huge diversity of crocs in the Miocene - really huge things actually, especially in South America in the kind of tropics. You get these - I think some of them are 10 meters long, right? *Purussaurus* is about 10 meters long. So you have these massive crocs that I personally don't really want to see re-evolve. But of course, the problem with only basing our predictions on the climate of the past is that there's always the human factor and that's going to kind of throw everything out of whack, as it usually does.

[Melvyn Bragg] Phil, can I ask you the throwing around of these 250 million years ago, 200 million years ago, and so on and so forth, are you any nearer getting more precise in these datings?

[Philip Mannion] I think it's a balance, obviously. To some extent when we're trying to explain these patterns, we often want to round up to a number that sounds a bit more easy to digest almost. But for some of them we have sort-of very precise dates. We know that essentially pretty much within about 10,000 years, exactly when that asteroid struck the Earth, for instance. The date is really sort of well calibrated. We have fossils that go right up to that boundary, so we know that they are around about 66.001 million years old or something like that. So often we can be quite precise. Other times though, we really are sort of only able to assign a particular fossil to say like-a 5 million year period because we lack that information. It's mainly because we're not actually able to date the fossils themselves. We're dating the rocks that they're in. And for that to be possible, we need certain things to be preserved in those rocks. Either something like volcanic beds, maybe above and below which we can date properly, or



sometimes things like zircon crystals are in the rocks. But without this, often we are unable to date these things to anything more than, say, within a million or a few million year period.

[Anjali Goswami] I think the other part of that also is that it's not just a problem with dating the rocks that the fossils are in, but remembering that when we find fossils and can identify them, that is really the minimum age that they evolved. We don't know how much of the record of their lifespan or the lifespan of that lineage beforehand we're missing. And so when we're trying to date fossil occurrences to precise environmental effects, we have to build in a little bit of uncertainty in terms of when that thing actually showed up. So if we have a fossil that is showing up at 50 million years ago, are we sure, how precise can we be that it wasn't around, but we don't have fossils for it 55 million years ago or 52 million years ago? So there's lots of really complex models to try and account for that uncertainty, but really, throughout the process, we have lots of different kinds of uncertainty and ideally, what will happen is that we run lots and lots of different models that try to estimate all this uncertainty and we find out that our results are really kind of robust, regardless of what we don't know.

[Melvyn Bragg] Thank you all very much. That really was fascinating.

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In our time. With Melvyn Bragg is produced by Simon Tillotson.