THE FISH-TETRAPOD TRANSITION - 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:

Emily Rayfield
Professor of Palaeobiology at the University of Bristol

Michael Coates
Chair and Professor of Organismal Biology and Anatomy at the University of Chicago

And

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

Producer: Simon Tillotson

Transcript:

[Melvyn Bragg] Hello. Around 400 million years ago, some of our ancestors, the fish, started to become a little more like us. And this was one of the greatest revolutions in the history of life. At the swampy margins between land and water, some fish turned fins into limbs, swim bladders into lungs, developed necks and became tetrapods, the group to which we and all animals with backbones and limbs belong. And these descendants of fish, having transitioned into tetrapods, were now ready for the new life of walking on land and, with that, an explosion in diversity of life on earth. With me to discuss the fish tetrapod transition are Emily Rayfield, Professor of Palaeobiology at the University of Bristol, Michael Coates, Chair and Professor of Organismal Biology and Anatomy at the University of Chicago and Steve Brusatte, Professor of Palaeontology and Evolution at the University of Edinburgh.

[Melvyn Bragg] Steve, can you give us some context here? How important was this transition? And I've said 400 million years ago, but what else was going on?

[1:20]
[Steve Brusatte] In today's world, there are tens of thousands of species of animals that have bones and have arms and legs and fingers and toes that mostly live on land. And we are one of them, as are frogs and salamanders and lizards and crocodiles and turtles and birds and all of our mammalian cousins. And all of these animals, those with arms and legs, fingers and toes, are called "tetrapods" and we can all trace our heritage back to a common ancestor which lived somewhere around 400 million years ago in the Devonian period of earth history. And our distant ancestor, basically, as you say, was a fish that changed its fins into limbs and sprouted fingers and toes and moved onto the land and in doing so, it found new ways to breathe air and to move on dry ground. And if this primeval fish didn't make that leap, then we simply wouldn't be here today. And this leap, this move from water to land, is therefore one of the most profound evolutionary transitions in Earth history. It set life on a radically new course and it's one of the textbook examples, really, of a major evolutionary transition - when a group of species changes their bodies so drastically that they can now do dramatically new things and live in new environments and so on. And if you look in a textbook about evolution, you will see this fish tetrapod transition as the exemplar and that's because not only was it such a turning point in earth history, not only was it a transition that ultimately paved the way for us, but because also it's recorded in the fossil record. We have a fossil series of intermediate species that show step-by-step how a fish turned into a tetrapod, almost like still scenes strung together to make a motion picture, let's say.

[Melvyn Bragg] Is it too naive to say, do we know what provoked this?

[Steve Brusatte] I think what we first want to look at is what the world was like when this transition was happening, and this was back in the Devonian time of earth history. ...

[Melvyn Bragg] About 400 million years ago?

[Steve Brusatte] That's correct, about 400 million years ago. And if you looked at a map of the Earth around that time, it would look scarcely like the world today. And unlike today, where most land is in the northern hemisphere, back then, most land was in the south and much of what is in the north today - what's now Asia, North America, Europe - ... [was] closer to the equator (including Scotland!). So imagine that - a tropical Scotland, where surely it was rainy as it is today, but it would have been warm rain and it would have been humid. And in fact, in Scotland, we have some very important Devonian fossils. There's a place up near Aberdeen, in the heart of the speyside whiskey country. It's a little village called Rhiney. And there you can find the fossil remains of one of the first land ecosystems. They're locked into stone. They're preserved in place by a hot spring that was about 410 million years old.

[Melvyn Bragg] But do we know what provoked it?

[Steve Brusatte] Yes. So that world was becoming settled and it was first plants that moved on to the land. And we see those at Rhiney, and these are plants are not like anything we know today. They're these wispy, haunting, almost alien like things, skinny little twigs about a meter or so tall but they were the precursors of forests. And living among them were arthropods, were bugs basically, the ancestors of today's spiders and insects. Now, there was nothing with bones on the land at that time, but the land was now primed for them. There was some food on land, there was some shelter on land, and these new land ecosystems were waiting to be explored.

[Melvyn Bragg] ...Michael Coates, ... let's get it straight from the beginning, what is a tetrapod and how does it differ from a fish?

[5:24]
[Michael Coates] Well, first of all, I want to say that tetrapods [are] best thought of as a special kind of fish. They're a variety of fish. So everything I'm going to talk about, [when I am] saying what [feature] makes a tetrapod, [that feature] is a specialized derived feature of stuff you would otherwise find precursors of in fish anatomy. So, straightforwardly, [when] people think of tetrapods, they're going to think of limbs with digits. But the skeleton inside our limbs, our fingers and toes, is really not that dissimilar from much of the structures you find inside a fish fin. We lack the rays, and the crucial difference between fins and limbs is not so much the digits, it's the wrists and ankles. It's the cross articulation that interpolates between the end of your forearm and where your fingers spread out. And then there's the missing fin rays. Tetrapods have necks. Fish have a kind of rudimentary neck. In fact, if they didn't have one, they wouldn't be able to feed properly, they need to be able to move their skull up and down for suction feeding. But tetrapods can wag their necks and their neck is free of the shoulder girdle. Tetrapods have a sacrum, the pelvic girdle is attached to the spine, the backbone, and that's important for driving tetrapod locomotion. But other stuff ....tetrapods have tongues, they have muscular glandular tongues. Fishes don't, I mean, fishes have the front end of a gill skeleton which is the precursor for a tongue. But [tongues are] what tetrapods have. Tetrapods have a middle ear with sound conducting bones in their stapes. And of course, tetrapods are air breathing and ... have modified blood circulation to allow them to air breathe. And tetrapod backbones are built basically to resist gravitational load. They have special interarticulations between them so they act as a beam, whereas in a fish the backbone acts more of a springy rod for storing and releasing energy.

[Melvyn Bragg] ... How long did [it] take to turn the fish into, dare one say, humans? Or is that [question] too risky...?

[Michael Coates] So the time span between the earliest tetrapods that we have fossil evidence of absolutely. We've got the complete skeleton with digits, et cetera, those clock in at about 360 million years. Humans have been around for a couple of million years, so the difference there is 358 million years to get from there to here. So that's, as was said at the head of the program, this key event of the origin of tetrapods. And of course one of the questions is how does that relate to the water to land transition?

[Melvyn Bragg] I was going to ask you that.

[Michael Coates] Well, that's what we're investigating.

[Melvyn Bragg] How far have you got?

[Michael Coates] Well, one of the big changes that we've made is that the anatomical transition, the move from what we'd think of as a fish like body plan to a tetrapod like body plan, [with] limbs and digits, occurred in primarily, generally aquatic organisms. So it precedes, if you like, the move to land. The earliest terrestrial biota with vertebrates in it that we can look at with confidence is from the Midland valley of Scotland. So we're back to Scotland again, East Kirkton, and that dates at about 335 million years old.

[Melvyn Bragg] So we're not talking about them crawling spectacularly out of the sea like in James Bond and going up a sandy beach, we're talking about them sliding out of swamps.

[Michael Coates] Yeah, that good old image of the kind of optimistic pike sort of heading up the beach with this sort of eternal escalator of life chain-of-being up the beach. No.

[Melvyn Bragg] Doesn't go...

[Michael Coates] It doesn't wash. No. I think we have to think of a variety of different kinds of environments being occupied by these fish-tetrapod, transitional forms, probably doing a variety of different kind of habitats and ecological situations that we don't have precise analogues for today.

[Melvyn Bragg] So I'm going to turn this very, very difficult question over to Emily. Emily Rayfield, we have fish, then we have tetrapods. And the mystery for us, but not for you, is to [learn] more precisely how the one became the other. What tools [do you have at] your disposal to discover this?

[9:41]
[Emily Rayfield] Well, obviously, the bottom line is the fossils. We can't do anything without seeing the fossil evidence. And we've had many new discoveries over the last 20 or 30 years that have helped ...populate our understanding of what's happening across that transition. But I think some of the interesting things that we're able to do beyond there is [that, whereas] previously, people looked at the fossils and ...came up with careful considerations about how those structures may have worked in life, how the animal may have used those limb bones to walk, or how it may have used the jaws to feed, now ... some of the tools that we can use ... that have been particularly useful are things like X rays that allow us to actually take a fossil that's been embedded in rock or even a fossil that's been largely prepared away from the rock...[and] to actually see structures that are preserved internally in the rock. ...[In addition,] from that [X ray and other data], ... we can then recreate digital models of these structures, and that allows us to get a handle on, not only the anatomy, but from that, say, if we've got a fossil that's been completely ....squashed, or it's been broken apart, we can fit those pieces back together in a digital environment. And that gives us a clue as to what the animal may have looked like. And that then can feed forward into things like, well, what actually did its limb look like? And then beyond that, there are other tools available to

us which I think are exciting because they actually allow us to test some of the hypotheses that people had come up before just looking at the skeletons and the fossils. So, for example, with these digital models in a kind of virtual environment, we can fit the bones together and we can test how much they can move against each other.

[Melvyn Bragg] We're not talking about walking at this stage, I think, but can you tell us more about one of the fossils, Ichthyostega?

[11:32]
[Emily Rayfield] So Ichthyostega is a really good example of how some of these digital techniques have been applied to help us better understand how the animal moved and what kind of environments it lived in, but also change our perception of the anatomy and the structure of the fossil itself. So Ichthystega was an early tetrapod. It's been known for many years. But new material was discovered in the 1980s and beyond, which helped us ...

[Melvyn Bragg] Whereabouts?

[Emily Rayfield] This was in Greenland. And this helped us build up a better picture of what the structure looked like. And so this was an animal that was a meter or so - a bit bigger than that. These are quite big animals that we're talking about here. It would have a broad, flat head. It's got what we essentially would look at with limbs and, on the hind limbs at least, has digits. It has a big, chunky hip bone which is attached to the spine. It has well developed ... forelimbs as well, too, but it also has a long tail as well. And so this animal was previously reconstructed as being kind of a classic land walking ... amphibian-style animal. So if you imagine with its hands and feet out to one side and kind-of moving its legs alternately ... backwards and forwards. But then [after] actually being able to look at the fossil in more detail and then ... some more recent careful reconstruction of how those bones actually fit together [the present suggestion is] that, actually, the animal wasn't capable of putting its arms and its legs out to the side like that. And it was still moving its legs mainly backwards and in its forelimbs as well, too. Rather than moving in an alternate pattern like we would imagine, like a salamander moving for example, the range of movement in its limbs - they were quite muscular, as we can tell from kind of the size of the bones and scars or areas where muscles might have attached - but it was probably moving a little bit more like, say, a mud skipper does, which is ... using what's called a "crutching motion" where it kind of moves its limbs, its forelimbs together in one movement and moves either through water or on land in that way.

[Melvyn Bragg] Steve Brusatte, ... fish didn't need limbs or lungs or rib cages. But why might they?

[13:56]
[Steve Brusatte] What Emily's talking about, Ichthyostega, this was a tetrapod. It had true limbs and digits, even if it wasn't so competent at using those limbs on land yet. But a little bit earlier in the fossil record, when we see these fishes that are, in a sense, becoming tetrapods, we see them and this is the spectacular thing, we see them evolving the features of tetrapods, the things that we have today ourselves that help us live on land. They were evolving these things one by one while they were still living in

the water. And so that's ... [things] ... such as limbs, digits, necks, lungs, all of these things we've been talking about. The ground plan of a tetrapod was inaugurated in the water, which means that these features must have been helping these fishes live in the water because evolution doesn't work with foresight. It doesn't plan ahead, natural selection just works in the moment. So there must have been a reason or multiple reasons why these fishes were developing these features. And, I mean, this is hypothetical, but you can imagine if there was a fish in the water that was evolving stronger and more muscular fins maybe to help propel itself at the bottom of the water. We know, by the way, that some living close relatives of tetrapods like lung fishes, do this. They live in the water, but they use their muscular fins to propel themselves along the bottom. And you can imagine how maybe 400 million years ago, there's a fish that changes its fins that way. Maybe that helps it gather more food or escape from predators better. And in doing so, it might live longer, it might reproduce more. And that new type of fin could cascade through the population [and] be modified further. But still, that fish is still living in the water. We know lungs, which, of course, we use to breathe air. Many fish have lungs, they evolve them either for buoyancy reasons, as a kind of air balloon to help them rise or fall in the water column, or maybe as an extra way to breathe air in addition to the gills they already have. But again, lungs evolved in the water. So the way I like to think about it is if we think of airplanes. When the Wright brothers invented the first airplane, what did they do? They put a lot of parts together that had been invented for other purposes. They put a propeller on that airplane. That's what powered that first airplane in the air at Kitty Hawk. But they didn't invent the propeller. The propeller actually goes all the way back to people like Archimedes, that developed something like that to be used in the water and later was used to power boats through the water. And then the Wright brothers realized that this can also be used to move a plane in the air. So in a sense, evolution kind of worked that way. All of these things limbs, digits, necks, lungs, they were evolved and they originated in the water to help these fishes fit into their environment. And they were later repurposed to allow those fishes to make those first tentative steps onto land. And today we retain those things. They are the very things that enable us to live on dry land.

[Melvyn Bragg] Thank you very much. Michael Coates, in the 19th century, there was a rash of new information, as I understand it. Why did that happen then?

[17:15]
[Michael Coates] Yeah, there was a rash of new information that became available largely as a side effect of the Industrial Revolution. The Industrial Revolution was fueled by coal and oil shale. The coal and oil shale was laid down in the Carboniferous about 300 million years ago in this equatorial band, and sub-equatorial band, of swamps. Out of the coal being hand hewn - this is intense, as we many people know, sort of labor, exploitive and so forth, and yet, nevertheless - people were collecting fossils. They would have common ...

[Melvyn Bragg] The miners themselves?

[Michael Coates] The miners themselves and the foreman and so forth. This is also the rise of the great northern literary and philosophical societies, places like Manchester and Newcastle. And it's in these places where they were first discussing the skulls and teeth of these extinct forms that were coming up at that time. Now, we're talking about 1840s, 1850s, 1860s. Through that period, you've got publication of Origin of Species, 1859, but thinking about evolution precedes that considerably. One of the most popular books to come out in the 1840s was ["Vestiges of the Natural History of Creation" by Robert Chambers of Chambers Dictionary fame] - it was anonymous at the time... So in that work...[even though] it was lampooned at the time... people are looking for transformations. They're looking to the fossil record to look for transitional forms even then. So the earliest amphibians are being discussed, they're coming out of the coal measures, they're being described, they're going into museums, they're going on public displays and so forth. Richard Owen, who found a natural history museum, again, often caricatured as "Darwin's rabid opponent", et cetera. He is obsessed with connecting forms. He was obsessed with lungfish. He describes the first "missing link" at a British Association meeting in 1859 - the same time [as the publication of On the Origin of Species]. And it's not Archaeopteryx, the bird dinosaur fossil link, it's a fossil amphibian with skull bones that look like a fish.

[19:20]
[Melvyn Bragg] Emily, can we continue in this? Can you tell us more about the different types of fin, especially the lobe fin, and why it matters in this story?

[Emily Rayfield] So, most fish around today, cod, tuna, your goldfish, are members of a group called the "ray finned fishes". So they have fins that are made of individual kind of fin rays, which are a type of bone that actually are laid down there, right in the tissue themselves. And they're connected to a series of small bones at the base, which have muscles at the base which help control the fin. The other group [are] the lobe finned fishes. Now, the lobe fin fishes are really not very common at all in our modern day world. They include the lungfish and also the Coelacanth, the animal that was thought to have been extinct since the end of the Cretaceous until it was found by scientists in the 1930s. And these belong to a group called the lobe fins. Now, the lobe fins and the ray fins are all part of the bony vertebrates, so they all make fins made of bone. But the lobe fin fishes make them in a slightly different way. So where they have a kind of a girdle, so this what eventually becomes like the shoulder and the hips attached to that is just a single bone. And then in the tetrapodom of fishes, the fossils that are quite closely related to tetrapods, they also have attached to that one bone, they have two bones. And then beyond that, they have a number of other small bones, and then they have fin rays as well, too, so, like we see in the ray finned fish. But what's important about the lobe fins is that the fin is much more muscular, the muscles extend down into the fin. But that pattern of one and two bones is reflected in all of the tetrapod limbs, including our own. So it sets the scene early on, but in structures that are actually fins rather than limbs.

[Melvyn Bragg] Thank you. ...Steve Brusatte, we're still exploring the transition here [with] creatures [that are] not quite fish [and] not quite tetrapods. Can you tell us about one particular fossil called Tiktalic?

[21:20]
[Steve Brusatte] This is a special fossil, and I think it's one of the most remarkable extinct animals that has ever been found. And it was found less than two decades ago. It was discovered in 2004 up in the Arctic part of Canada and then described a couple of years later on the cover of Nature. And very soon after, it became something of a prehistoric celebrity, one of those iconic extinct species, because it looks like it's capturing evolution in action. And I remember, I remember very well when I first saw it,

the actual fossils. I was an undergrad at the University of Chicago at the time. I was taking a class with the esteemed Professor Coates here. And then, by the way, I went to do a master's in Bristol [and] then I learned from Emily, so I've learned from the best. But I was taking a class with Mike, and he taught this class with another professor named Neil Schuben. And I went to see Neil in his lab and just have a chat, and he said, "Hey, I got something amazing here. Do you want to see it?" And that's when I came face to face with something that was about a meter long, which kind-of looked like a Frankenstein monster combination of, let's say, a salamander and a fish. And Neil said, "This is a new species and we're just about to name it. And we're going to call it Tiktaalik". And that's an Inuit word, by the way, And Neil and Ted Daeschler and Farish Jenkins, who discovered it, ... worked with the elders in the Inuit community to come up with this name. It means "large freshwater fish", and it lived about 375 million years ago, still in the Devonian period. And importantly, it is about the closest approximation we have to the ancestor of Tetrapods. The best model from the fossil record of what this ancestor looked like. It was a fish. It was still living in the water, but it clearly looked a lot different than other fish. And it had many features that would later help Tetrapods move onto the land. It had those big muscular fins with the one too many bone pattern that Emily just described. It had a neck. It had a flat head with the eyes on top that kind-of looked like a crocodile's head. It had a really robust rib cage. It surely had lungs for breathing air. But it was still living in the water. And it probably was using its limbs to propel itself along the bottom of shallow streams. And this is where the environment becomes very important. It's not just the fossils of Tiktaalik that are known, the rocks that it has been found in has been very well studied. And we can tell that it lived in an environment of tidal flats, deltas, shallow streams, estuaries - that kind of world. It wasn't living in the middle of the deep ocean, so ...it and its ancestors were probably developing these more muscular lobe fins and necks and rib cages, and so on, to better survive in that shallow water environment.

[Melvyn Bragg] Thank you very much. Mike Coates, what needs to change to move from breathing through the gills to using lungs?

[24:19]
[Michael Coates] A host of things. So if you're breathing in the water using a gilled skeleton, what you're having to do to achieve that is your jaws, your mouth, your throat is working like a two stroke pump. So you've got an open throat with gill flaps there and you're trying to get water into your mouth, close your mouth and get a flow through through the gills and out through the throat. So you've got gas exchange over the gill skeleton. Now, to achieve that, you've got a series of muscles on this retracting and expanding basket of gill arches in the throat that you find in all fishes. To go to air breathing, you've got to close the throat, modify the gill skeleton, et cetera. [The gill skeleton] usually gets reduced or coopted for something else. And the various pouches that [make up the] gills are modified for other structures. But then you've got to find a way of forcing air into the lung, and there are variety of strategies that we can see modern fishes and in fact modern tetrapods use for doing that. There's one way which is called a Bookle [?] pump, where you get, if you like, a mouthful of air and then you compress your mouth and force that bolus of air, that balloon of air, down into your lungs and then hope elastic contraction of your chest will get it out again. Or if you're part of the amniote tetrapods that's ourselves, and reptiles and birds and so forth, you've got big hoopy ribs that form a rib cage and they've got a muscular, if you like, concertina around your chest, which can expand and contract, so you've got negative

pressure in your lungs to fill them full of air. That's part of the story, but the other thing for air breathing is you have to radically alter your circulation system because [with water breathing fishes] you've got the heart pumping blood through the gills to the organs of the body back into the heart, that's a simple circulation. But [with]ourselves [and other air breathing animals] you've got to go to the heart, lungs, heart, body, heart, lungs. So it's a "double circulation". That means you have to ... radically modify the symmetrical arrangement of ... vessels coming off the front of the heart, so that the one at the back gets a whole new sprout that goes back to what was the swim bladder, and that's where it's picking up oxygenated blood. Meanwhile, the rest of it is really bodged something horribly into this hideous asymmetric arrangement that medical students have to understand - to understand [a] circulation [system] that comes off the front of the heart, delivers oxygenated blood to the head and to the rest of the organ system, but also this system to the lungs.

[Melvyn Bragg] What prodded this to happen? I suppose that it's a stupid question, but still...

[26:57]
[Michael Coates] Reasons to breathe air... We can see analogues today. They're not perfect analogues. It's difficult for us to judge exactly what the conditions were back in the Devonian for fishes to breathe air. But if you're in stagnant waters, if you're able to get a burst of air into the system, so oxygenate your blood because the gills aren't doing it effectively enough, that gives you a competitive advantage. [As for identifying] the prompt to do it, and why this really takes off at the end of the Devonian, we've got some clue about changing environment, we've got [some] clue about changing climate, we've got glaciers near the equator, [the] sea level is dropping. Coincident with that, we find black shales, and the black shales are deposited in anoxic conditions off the coast. So the kind of conditions that today you associate with massive algal blooms, which again... one could imagine that could be a driver [to be] an air-breathing fish. If you've got a swim bladder, you can co-opt for air breathing, so it's not only there for buoyancy but to give you just that edge, when oxygen levels go down and you're at the continent margins, you can stay there, hunker down and survive [by] gulping [air] from the surface. [On the other hand, if you were not able to breath air] ...you [might need to] move upstream [where the waters are shallower], and there you're going to have more temperature fluctuation; it's a much more stressful environment. Can you cope with that? Again, air breathing is going to be an advantage.

[Melvyn Bragg] Emily, when creatures move from having their heads in water to having their heads in the air, how does that affect what they do? How does that affect eating, for instance?

[28:37]
[Emily Rayfield] Well, eating is in water, and on land is quite a different prospect, basically. So water is 800 times more dense than air, so animals that feed in water can take advantage of suction feeding. So if they can expand their mouth or their throat and their throat cavity, perhaps the back of their gill skeleton as well too, then they can increase the volume of their mouth and that will lower the pressure and it will draw in water. And hopefully [for] the animal it will also draw in whatever prey is in the water as well. ..Now, because of the different fluid environments on land, of course, suction feeding doesn't work. So animals on land need to take active measures to actually

capture their prey and retain it within their mouth as well. .. And so there are very different ways in which you need to feed on land compared to feeding in water. Now, actually, we can look for evidence of whether some of these fossils were actually feeding in water by suction or feeding on land by looking at the bones, by looking at whether there's flexibility in parts of the head and the gill skeleton and by looking at whether some of the bones are really tightly joined together, which might indicate that they're biting quite hard, or whether the bones are moving past each other. And actually, in some of the fishes that are closely related to tetrapods, we see good evidence that they were probably still suction feeding, but they may also have been biting as well. They were starting to get a much more, what we call "consolidated" skull. So these earliest tetrapods with the limbs and digits were probably also still feeding in the water as well...and taking advantage of suction, but also using some kind of biting or prey retention as well...

[Melvyn Bragg] Thank you. Steve Brusatte, what advantages do these, let's call them, "transitioning" creatures have?

[30:19]
[Steve Brusatte] These creatures that were transitioning, that were undergoing these shifts, they were still living in the water. So the fundamental thing is that all of these features we've been talking about, they were developed while these fishes were still in the water. So they must have been helping these fishes fine tune themselves to those environments. And again, the important thing is not to just look at the fossils themselves, but ... to put them into the context of the environments they lived in and what the broader world was like at the time. And as Mike was saying, this Devonian world, you have glaciers developing on the poles, you have big changes in sea level. You have a mass extinction later in the Devonian, probably because climates were changing so dramatically, because all of these new forests on land were sucking CO_2 (carbon dioxide) out of the atmosphere.. and [it was] like the "reverse greenhouse" effect was happening. The world was getting colder. So there were big changes afoot. And these fishes were not living in the open ocean. These things were living closer to land in shallower waters, in streams, in estuaries, in deltas and in the tidal flat zones. So the limbs and the digits and the lungs and the necks and so on were helping those fishes adapt to that particular world. And it just so happened that those different features which evolved probably for a variety of reasons to help fishes live in the water, those features came together almost like a Lego set being assembled, being assembled accidentally. And lo and behold, those things allowed some of these fishes to make the first tentative forays onto the land, to move themselves onto the land. Why they did that, who knows? Maybe they were trying to escape predators. Maybe they were chasing a tasty bug. Maybe they were trying to breathe more air. But those things, they were evolving in the water allowed them to move at least a little bit onto the land. And at that point an evolutionary threshold was crossed and natural selection could then fine tune these fishes even more to living on that new land environment. And just imagine that you were one of these fishes at the time and you were able to get yourself out of the water a little bit onto land. That would have been a whole new world, a world that you could explore and make your own.

[Melvyn Bragg] Mike, what do you learn from seeing living animals in their environment? What do you learn about the tetrapod situation?

[32:51]
[Michael Coates] As I think I mentioned earlier, there are no terribly good analogues of these early transitional forms, but there are a number of different fishes we can look at and see glimpses or aspects of their behavior, their structure and what they do, which give us some degree of insight. So, for example, fishes that walk. Why have limbs in the water? There are actually a wide variety of fishes today that use all the gaits we see in tetrapods underwater. Some of them are doing it in the shallows, some of them are doing quite deep. And examples, if people want to search for themselves and look them up, classic ones would be frogfish. Frogfish go through all the gaits. They're the world's slowest underwater gallop. They're charming. They're worth a look. And what's more, their fins have evolved. There's a thing called a handfish - you get fins that have independently converged on hand-like anatomy, but they've taken the fin rays, round the internal skeleton, and they have hands that more or less can grip and they can slowly maneuver their way through coral and various other ... structurally complex environments, often not to move, but to hold still, station holding. So that's one aspect, another one we can look at are fishes that will actually actively strand themselves out of water. So why do that? Because you can then occupy rock pools and you can move through another shoreline or a sort of muddy bank environment to obtain food. So you're not coming out of land with a view of, "oh, I'm going to colonize" - you're coming out to forage and then going back in again. So already we've heard mudskippers mentioned by Emily. They're one classic example with their weird crutching locomotion. They take a mouthful of water and hold it there and survive for some time on the oxygen in the water in their mouth. They're not air breathing. ... Perhaps the most surprising one that's been talked about recently in the scientific press...is a small shark called an epilette shark. They've been known to take excursions out of the seawater and on the shore and walk. They'll walk underwater, but they'll also walk between rock pools. It's now been noted that they can manage that for a couple of hours. That means they've got the physiology to cope with oxygen stress and the heat stress for that amount of time. And it's a shark of all things that's doing this, and it's part of their normal behavioural repertoire.

[Melvyn Bragg] Emily, how would the transition have affected the senses?

[35:19]
[Emily Rayfield] So this is another case where actually there are a lot of advantages to going onto land, as we've seen, and there are living animals that are able to take advantage of that for certain periods of time. But if you're actually going to fully move onto land, actually, things like vision and hearing are actually really difficult if you're going to move on to if you're going to move from an aquatic environment onto land. So, for example, light doesn't travel as far in water as it does on land. And so actually being able to see well on land, and presumably taking advantage of being able of the potential opportunities to capture new prey, needs a kind of reorganization of how the eyes work. Another thing as well is to do with sound, for example, sound travels further and it travels faster in water than it does on land. So they're moving on to land means that actually, if you want to be able to hear better, you need to make modifications to your auditory or hearing system as well...to be able to pick things up. It needs to be almost kind of fine tuned in some ways to be able to detect sound.

[Melvyn Bragg] Steve, what do we know about the more permanent change from tetrapods basing themselves in water to living on land?

[36:36]
[Steve Brusatte] The first experiences on land for these fishes, as they evolved these features that allowed them to start experimenting on the land, ... would have been awkward. And these early tetrapods, the first ones with proper limbs and digits, still would have spent a lot of time in the water, maybe even most of the time in the water, and they probably went back to the water to lay their eggs and so on. It took quite a long time, really tens of millions of years, as Mike mentioned earlier, for diverse land ecosystems full of really well adapted tetrapods to appear in the fossil record. So the first tetrapods moving on to the land, they wouldn't have just galloped across the land right away. It took some time to make them ever more adapted to the land. But in the Carboniferous interval of time... that's the time that came after the Devonian, the Devonian ends with some big changes, [a] big mass extinction, then the Carboniferous dawns. Until quite recently, we didn't know very much about what tetrapods were doing over the first 10 million years or so of the Carboniferous, because there were not many fossils, just by the dumb luck of geology, of what gets preserved where. But over the last decade or so, a lot of new ones have been found, particularly in Scotland. And they show that throughout the Carboniferous period, tetrapods became better and better at living on the land. They basically divorced themselves from the water. They probably would only go back to the water to lay eggs like frogs and salamanders do today. But they evolved bigger arms and legs with stronger muscles and stronger shoulder and pelvic girdles to anchor those limbs. And they simplified their digits, so most of them would have five fingers or toes like us. And they evolved bigger ribcages and more muscular necks. And they refined their sensory systems, as Emily was talking about, to really be able to hear and to see and to smell in the air. And you see them adapting to the land because their fossils then become very common later in the carboniferous. And then later on, some of them even evolve a new type of egg, an egg that has membranes that keep it waterproof. And that is what allowed that final break from the water. And it was these tetrapods that split into two great lines, the reptile line and then what we call the synapsid line. And that's what eventually would lead to mammals many, many tens of millions of years later.

[Melvyn Bragg] Mike, it's towards the end of the program now, but what do we humans retain from these fish ancestors?

[39:16]
[Michael Coates] Well, practically everything in a way. All of our anatomy is derived from fish. We are "run through" like the proverbial stick of rock or something like that....it's there in our anatomy, and there are some really good examples. I mentioned the circulation system coming off the heart. Another example actually thinking about gill skeleton is for example, where our thyroid is. Why have a thyroid gland in the throat? Thyroid is going to important for hormone production, et cetera. It sequesters important iodine and so forth from the environment. It regulates calcium in the blood. That's because in fishes, thyroid gland is, if you like, in the gutter at the base of the gill skeleton. And the gill skeleton is where you're going to get ion exchange, gas exchange, and if you like, mineral salts and so forth like that. So your thyroid and your parathyroid and a whole system of calcitonin and so forth is located in the throat because that makes total sense if you've got gills, because that's where you're going to absorb the minerals and the necessary signals and send ... mucus down the throat to

the rest of the body. Another example of the legacy of fish is we've got two arms and two legs, okay? Just four appendages - tetrapods. That is part of the most fundamental aspect of the body plan of a jawed vertebrate. So you have to think of fishes as a much larger, more inclusive group within which tetrapods are a subset.

[Melvyn Bragg] Thank you very much. Emily, finally, what would you especially like to learn now? Is there a next stage? If so, what is it?

[Emily Rayfield] One of the things that's fascinating, and this has been touched on by some of the discussions that we've had, is how did animals actually really adapt to those terrestrial environments. We've established that actually a lot of the features that make tetrapods, that make us "us", have been established in an aquatic environment and then we know that there's this kind of slightly more patchy fossil record and then the animals become actually properly adapted to the terrestrial environment. We know the kind of things that they need to do to be terrestrial adapted - to be able to walk efficiently on land, to be able to feed on land without using suction, to be able to deal with all of these sensory and physiological things like not losing water, like being able to hear properly and then eventually also being able to break away from water for reproduction as well, to be able to lay your eggs somewhere that doesn't need to be in water or in other moist environment. And ... I would love to know more about those earlier stages there as well.

[Melvyn Bragg] Well, thank you very much. Thank you Emily Rayfield, Michael Coates and Steve Brusatte and our studio engineer Gail Gordon.

And the In Our Time podcast gets some extra time now with a few minutes of bonus material from Melvyn and his guests.

[Melvyn Bragg] What would you like to have said that you didn't have time to say?

[42:20]
[Emily Rayfield] I think we can maybe talk a bit more about hearing. We didn't talk so much about that. We talked about breathing, we talked about feeding. But kind of intimately linked to those functions is also how hearing evolved as well too, and so while I was talking about how the jaw moves during feeding and creating suction, that's also linked to how some of these early animals were breathing as well too, some of the fish and some of the tetrapods, so creating this kind of depression and then forcing air into the lungs as well too, and one of the structures that's actually sitting just behind the jaws and kind-of supporting the jaws and connecting it to the brain case is a structure called a highoid arch. And the top bit of that is a structure called the hyomandibula. And that plays a role in supporting kind of the back of the jaws and attaching them to the brain case in some of these early sort-of tetrapodomorph fishes. But over time that structure we know, evolves into what we would call now the "stape", ao one of the bones in our ear, one of the bones of the middle ear in everything that's not a mammal, the bone in the middle ear that actually detects sound. And one of these... there's a pouch that sits in between the back of the jaws, and this highoid arch that in fishes was probably bringing in water and passing it through the gills in some of these tetrapodamorph fish. And it was maybe bringing air in and passing that through

to the lungs as well.... And later on, it appears that this pouch then becomes ... the air-filled cavity of the middle ear. And then sitting over that, eventually, we get a membrane to the tympanic membrane, which is the eardrum. And that structure that was once providing structural support at the back of the jaws has now become important in detecting airborne sound. And indeed, I think in Acanthostega [it was] maybe suggested that it was also detecting some waterborne, some kind of aquatic sound as well...

[Michael Coates] Well, for fishes, you're bathed in sound. What's remarkable is the number of times hearing has evolved and specialized. So there's suggestion, looking at amphibians and amniotes, this impedance matching system, as it's called, with a sound conducting bone in the middle, has evolved independently - that [both classes of animals have] converged on airborne sound hearing [by] coopting the same redundant bits of skeleton in the skull. So nature takes advantage of all the bits and pieces that are knocking around in the system.

[Melvyn Bragg] Steve, do you want to come in here?

[Steve Brusatte] One thing that I just like to pay some respect to are some of the people that have made a lot of these discoveries. And chief among them is somebody who Mike and Emily know very well, Jenny Clack, who passed away very sadly a few years ago. Jenny did the seminal studies on Ichthyostiga and Acanthastiga in these early tetrapods. She was an absolute legend in the field, even for people like me that came, know, studying dinosaurs and things that were very far away from fish. Everybody knew Jenny and knew her discoveries. We all have her book on our shelves, this book, Gaining Ground, that she wrote in a couple of editions that's really the best technical, but also digestible, summary of the fish tetrapod transition. She was an absolute giant. Another person who also passed away not too long ago, Stan Wood, who was not an academic. Jenny was a professor at Cambridge. Stan Wood was a guy who was ... an insurance salesman. He kind-of worked on the docks. He did a lot of things over his life. And when he was a bit older, actually, I think when he was about my age, he started to collect fossils just as a hobby up here in Scotland and he was very good at it. He just had the most incredible eye, and he went to places nobody else bothered to look, places that were said to be barren of fossils. He didn't care. That didn't stop him. And he went out and he discovered a lot of these Carboniferous Age tetrapods in Scotland, the ones that were living right after the Devonian, the ones that were becoming better and better adapted to land. And although Stan has passed away, that work continues. There are many researchers, including researchers up here at the National Museum of Scotland, that still work on these sites.

[Michael Coates] Well, ... thanks for mentioning Stan Wood and Jenny. I worked closely with Jenny and Stan and in fact, we all came out of effectively a lab together in Newcastle - Alec Panchen aho ran that. There's two things I'd like to mention - further developments where next with this stuff. One is the point that there's so much more to discover in the Devonian. The impact of the end of End-Devonian extinction is still being explored. And what we don't know is whether the radiation of modern tetrapods, the last common ancestor between you, me and a frog and a salamander, evolved after that extinction event. So you can imagine extinction, it's kind of like everything's cleared the decks. Is that an opportunity for a new radiation? If you like [the] pressure is off [and evolution] can experiment more. Or alternatively, was the radiation earlier?

So you've got a lot of apparently sophisticated-looking tetrapods that we're barely picking up yet, ready to move in [after the extinction]. So the fuses of those later evolutionary radiations are survivors of that extinction event at the end. Added to that, there's trackway evidence. Trackway evidence is that - you mentioned 400 million years at the beginning - trackway evidence at the moment putative trackways, contentious ones, I'll get flogged for saying so, go back 385 million years. Now, some of those are more credible than others, but the implication, and from more fragmentary evidence, is that we've got perhaps 25 million years of swamp beasts that we haven't sampled yet, which is a phenomenal record. Now, there may be low abundance, but there's plenty more work to do. And the other aspect on that is we'd better start collecting all the other fossils from those localities, because at the moment it's rather like old-style archaeology - treasure hunting. People go and they bring back fossil tetrapods. They're not bringing back so much in the way of the invertebrates - the bugs, the critters, certainly all the kinds of fish, the plant material and so forth. So we're not getting quite the insight into the biodiversity of the environments that these things are living in. So we [have got an idea of the changing world through the Devonian that would set things off for the post Devonian. (I got something else I'd like to rant about, too.)

[Emily Rayfield] I would say what's interesting about those tracks as well, too, is that there's a suggestion that these animals are moving in a kind of amphibian style way, like one limb forward, one limb back. But actually we don't have any evidence for that even much later than some of the animals that we have evidence for limbs and digits with. So in terms of how those limbs are moving and how the animal is actually moving over the ground as well, there's even bigger kind of discord there. timing.

[Michael Coates] Yeah. I mean, what sort of track would Acanthostega leave behind? Or Ichthyostega with this weird flipper hind fins?

[Emily Rayfield] It would be nothing like the tracks, the tracks that we see.

[Michael Coates] Yeah. It makes you wonder if you've got trackways that we're not recognising as tetrapod but in fact just doing something weird down there so they're being discounted as something else.

[Melvyn Bragg] What was your second rant?

[50:03]
[Michael Coates] My second rant is about "evo devo". So one of the big discoveries that happened... So Jenny Clack comes back with a lot of material about Acanthostega. Jenny and I set to work on it. She divided the animal at the neck. Jenny gets the skull. I get everything behind - the rubble. I was lucky. I got this fantastic post-cranial material in that we find still the most primitive digited limbs. We get the Ichthyostega material too. And what we find is that those limbs have more than five digits. At that point, the idea of the "pentadactyl" limb, the five-digit limb, is kind of paramount - it's "Holy Writ" in comparative anatomy and biology. It's been used at that time heavily by developmental biologists who are using vertebrate limb development - looking at chick embryos and so forth - to understand the processes that are involved in the development from egg through embryo to fetus to adult. Now, at the time that we come out with polydactylline ...variable digit numbers that is exactly the time when the

Developmental Genetic Regulatory Toolkit ["Evo-Devo"] is becoming available. People are discovering that genes are conserved between fishes and flies and our cells and so forth, genes are evolving in families just like organisms do. And at the same time they're working out how these are beginning to regulate important parts of patterning of embryos. So they're thinking about "how do you pattern a five digit limb"? And we're saying, you know what? That's not primitive. We can put the arrow of direction of character change on it. We can point out minimum dates. So we're getting down to rate and date because any fossil you find is a readout of developmental processes. So we've got a patchy incomplete history of the evolution of vertebrate development. So the evo-devo synthesis, evolutionary developmental biology, has a place in it for fossil data and comparative methods. And that's been a sea change and it's brought together experimental and comparative biology in a new synthesis.

[Melvyn Bragg] Steve, you want to come in here?

[Steve Brusatte] To me, this isn't something I primarily study. I teach about it and I do a little bit of work here on the Scottish sites. We lead a lot of field trips there. And I'm becoming more and more interested in ways that we can re-examine some of these historic collections here in Scotland. But I've watched a lot of this from a bit of a distance and I've just been awed at how it's a combination, really, of fossils, amazing fossils, very important fossils like the ones from Greenland studied by Jenny, and Tiktaalik, you know, and some of the others we've talked about. Plus these new emerging records of these footprints - the traces that some of these early tetrapods and their close fish relatives left behind. Are they or are they not the tracks of tetrapods? You have to do that "reverse Cinderella" thing, and kind of see if the feet of any of these things fit these footprints. These footprints often look like they have fingers and toes, but are they actually records of animals moving on land? This is becoming a huge focus of study, and, as Mike says, there's a lot we can study about the development of animals today. You can study fishes and you can study salamanders and frogs and so on, and see what genes control limbs and digits. And putting all of this together, it's a great synthesis. It's really helping us learn a lot about evolution. And for me, what's fundamentally so interesting about it is - this is the major transition, this is the textbook on a certain type of animal changing into something very different, colonizing, a new environment. And I think, although we know the broad outlines of this story, there is still a whole lot to learn.

[Melvyn Bragg] Can I just ask one question? ... I last ask one last question. I started ... saying, "first of all, there was dust, then there were fish, then there were us". What next? [laughter]

[Emily Rayfield] ...Rats and cockcroaches...[laughter]

[Michael Coates]...Actually, one thing is "detritivores" things that survive on rubbish, because when you look [at the fossil record] after these extinction events, survivors are often those things that seem to be when people are looking at what they call disaster faunas - things that are often aquatic and often living capable of living on rotten remains. And this sort of abundance of "crap" that's coming in the water.

[Melvyn Bragg] That's a pleasant prospect. ... Thank you very much for that...

In our time with Melvin Bragg is produced by Simon Tillotson.