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Evolution of life on land: how new Scottish fossils are re-writing our understanding of this important transition

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Romer's gap — a hole in our understanding

It has long been understood that at some point in the evolution of vertebrates there was a transition point where they moved from mainly subsiding in water to living on land. However, until recently there had been no fossil evidence that documented how vertebrate life stepped from water to land. This significant hole in scientific knowledge of evolution is referred to as Romer's gap after the American palaeontologist Alfred Romer, and it has been challenging palaeontologists for generations. However, after years of searching, the answers have begun to be unearthed. Recent discoveries from the boarders of Scotland are finally filling in the last piece of this story.

What do we know about the origin of life on land?

For many years our understanding of how and why vertebrates came on land was limited by a lack of fossils. The limbed fish, *Eusthenopteron*, discovered in 1881, has been for much of the 19th and 20th century our only example from the time of the transition. However, new research has shown this is completely aquatic (Laurin *et al.* 2007) — It's about as terrestrial as a salmon!

In the last 30 years our understanding has improved dramatically. Discoveries from Devonian rocks of Greenland and Arctic Canada of limbed tretrapods such as *Acantostega* and *Ichthyostega*, discovered by Jenny Clack and Per Ahlberg, and *Tiktaallik*, discovered Neil Shubin and colleagues, have shed light into this transition. These fossils have proto-limbs, some with up to eight fingers; however, they couldn't support their bodyweight on land and still had functioning gills (Clack 2012).

Meanwhile at a quarry called East Kirkton Quarry near Edinburgh in Scotland vertebrate fossils were discovered that are 10 million years younger than the Greenland fossils. These include *Westlothiana*, which is thought to be the first amniote (egg-layer) or possibly early reptile (Smithson and Rolfe 1990) and *Balanerpeton* an extinct genus of temnospondyl amphibian. These fossils show that 10 million years after *Acantostega* and *Ichthyostega* evolved, vertebrates were completely terrestrial and had started to diverge into the separate groups that make up modern terrestrial vertebrates.

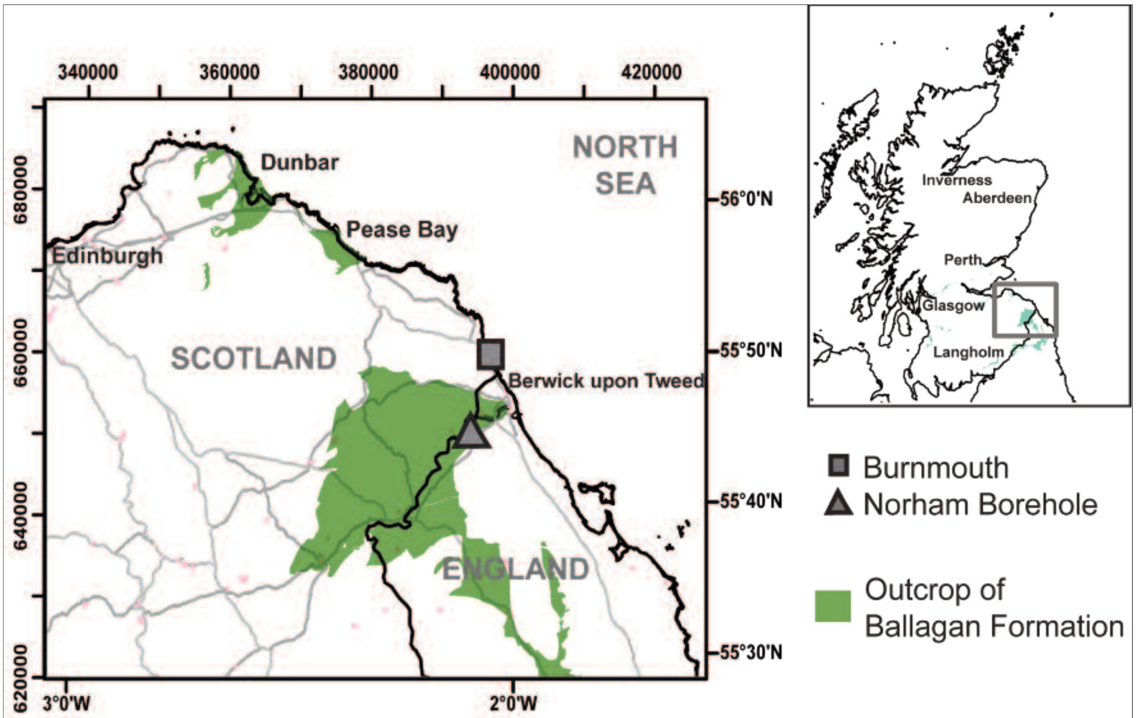
Nevertheless, the actual moment of the transition from dominantly aquatic to dominantly terrestrial life styles still remained elusive, with no fossil evidence to show this transition. So much so that it gained the name Romer's gap. This period of the Tournasian, which is the base of the Carboniferous, does not yield fossils and comes directly after the mass extinction at the end of the Devonian.

Evolution of the landscape

At the same time as vertebrates were making the transition from the water onto land, the landscape itself was going through one of the most dramatic changes in the history of the planet. A literature review study conducted in 2012 by Neil Davis and Martin Gibling (Gibling and Davies 2012) has revealed that before the Devonian period fluvial systems were braided and there were no meandering fluvial systems. Anabranching-anastomising rivers were first recognised in sedimentary deposits relating to the Carboniferous age.

The complexity of fluvial systems is linked to the evolution of vegetation and in particular to trees. In order to form floodplains, there needs to be deep-rooted vegetation that can stabilise the banks and flood plains of the fluvial system. Trees evolved on coastal plains, while the interior of the continents was still mostly un-vegetated. Through the Devonian and into the Carboniferous trees advanced farther inland, initially using the rivers as pathways into the uplands. This also had an effect on the rivers themselves, causing them to slow down and enabling wetlands and marshes to form.

Figure 1 Location map showing main tetrapod sites. Green area is from the British Geological Survey DiGMapGB (© NERC 2018). It contains Ordnance Survey data (© Crown copyright and database right 2018.)



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This change may have provided environments that made it possible for vertebrates to come onto land, but without the fossils from Romer's gap it is impossible to prove this link.

Finding Fossils in Romer's gap

The rocks found around the Borders of Scotand and England are of Tournaisian age, the age of Romer's gap. These rocks are in the Ballagan Formation, previously called the Cementstone Formation, which outcrops all the way around the edges of the Midland Valley of Scotland, and on the northern edge of the Northumberland Basin (Fig. 1, *previous page*). A professional fossil collector, the late Stan Wood, and Cambridge University researcher, Tim Smithson, had a hunch; in the Ballagan Formation and elsewhere in the world where fossil fish had been found, tetrapod fossils have also been found. Therefore they surmised that there could potentially be other undiscovered tretrapod fossils in the Ballagan Formation. After ten years of searching all the outcrops of the Ballagan Formation in England and Scotland they finally found tetrapod fossils (Smithson *et al*. 2012).

Based on these tantalising discoveries, a five-year, multi institution research project was started named Tetrapod World: early evolution and diversification (TW:eed). This brought together palaeontologists, sedimentologists, palynotogists and palaeoclimatolgists from the National Museum of Scotland, the universities of Leicester, Cambridge and Southampton, and the British Geological Survey. Our goal was to fully investigate the fossil sites to discover as many tetrapods as we could, as well as to try to understand the ecosystem, climate and landscape that these animals were living on, to understand what was happening during Romer's gap.

The team focused on several sites in the Borders of Scotland, principle among them is the coastal section at Burnmouth where the entirety of the Ballagan Formation is exposed. Inland the project looked at all the known exposures of the Ballagan Formation, and on the River Whiteadder the river channel was restricted to expose the river bed where Stan Wood had found some of the most complete tetrapod fossils (Fig. 2). Also, a 500m borehole was drilled near Berwick-upon-Tweed to core the entire succession to create a high-resolution chronology and palaeoclimate record next to which the fossils could be plotted.

Tetrapod discoveries

Five new tetrapods were found *Perittodus apsconditus*, *Koilops herma*, *Ossirarus kierani*, *Diploradus austiumensis* and *Aytonerpeton microps* (Clack *et al.* 2017). All of the fossils came from relatively small creatures — the largest skull was only *c.* 80mm long (Fig. 3, *opposite*). The smallest was *Aytonerpeton microps*, knicknamed 'tiny', which had a skull of 10mm and was found by 'accident' by a Masters student at Cambridge University, Ben Otto, who had been given the task of CT-scanning a small piece of rock that was thought to contain some fish bones in it, but he was surprised to find most of the skeleton of a tetrapod in it! (Fig. 4, *opposite*)

Phylogenetic analysis of the new tetrapods suggested that three of the taxa were stem tetrapods: meaning they are not part of either amniotes or amphibians. These all showed features associated with Devonian and Carboniferous tetrapods, suggesting that they were diversifying. The other two tetrapods had features associated with stem amphibians, suggesting that the amphibians had already started to become a separate group at the beginning of the Carboniferous (Clack *et al.* 2017).

Other fossils and the ecosystem

The tetrapods were not the only fossils that were found (Fig. 5, *page 38*). There were many fossils of lungfish, similar to lungfish living today. There were also examples of Actinopterygian fishes and other types of bony fish, as well as *Gyracanthus*, a extinct type of bottom feeding shark. There are examples of stranger animals, too. We have fossils of Eurypterids, often informally called sea scorpions; and on land we have evidence of Myriapods (centipedes). Some of them are thought to be more than one

Figure 2 TW:eed Project fieldwork in the Borders of Scotland.

meter long, and probably bigger than the tetrapods. However, these are not likely to be the top predators in this ecosystem; that is likely to be a Rhizodont. These are large eel-like fish with sharp fang-like teeth. The biggest Rhizodonts we found associated with the tetrapods was 1m long, but elsewhere, at this time some have been found that are as big as 7m in length.

Figure 3 The Fossil remains of 'Ribbo' the biggest tetrapod found in the Ballagan Formation (British Geological Survey image).

Landscape and climate

To put the fossils in their context and understand what might have been driving their evolution, the sediments and palaeoclimate were also studied. In the Tournasian the UK was at tropical latitudes, and the Borders of Scotland were a low-lying wetland that stretched through the Midland Valley of Scotland and out into the North Sea. To the south of the Southern Uplands was a shallow sea, which went as far west as Belfast harbour and was connected to a range of shallow, tropical seaways that continued to Nova Scotia in Canada. The Atlantic had not opened yet.

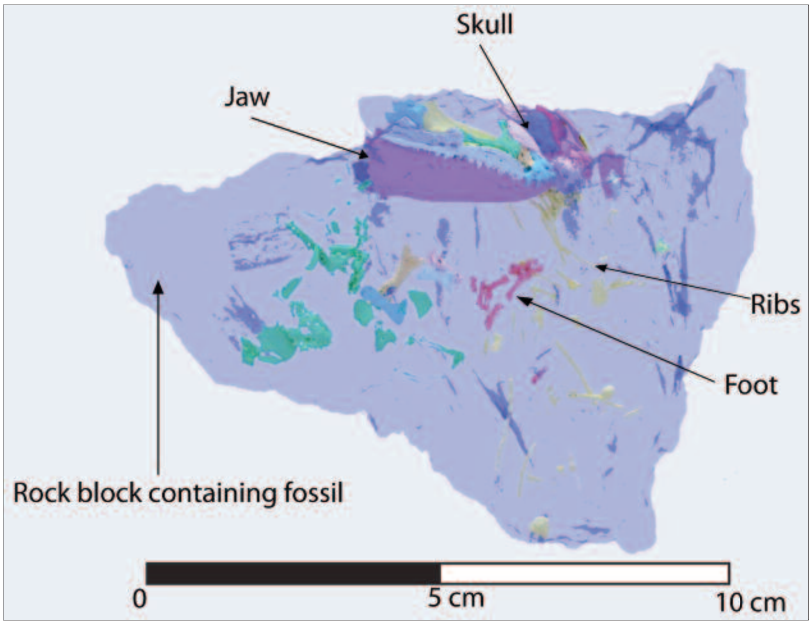
The sediments of the Ballagan Formation are dominated by siltstones that were deposited in shallow lakes and by floods. Many of these siltstones were then altered by root action and soil processes to form palaeosols. There are also beds of sandstone that show trough cross-bedding fading up into trough cross-ripples, with laminated tops on top of which sit abandoned facies with palaeosols (Bennett *et al.* 2016). These represent sinuous fluvial channels forming on a low-lying floodplain. There are also thin beds of dolomicrite and evaporates, which formed in saline alkaline lakes — open lakes with a marine connection (Bennett *et al.* 2016).

The section has a large diversity of root traces, from small plug roots to the occasional root of Lycopod trees. Many of these root traces are preserved as carbon films, suggesting that they were growing in permanently waterlogged conditions. Some of the palaeosols are reddened and contain desiccation cracks, suggesting that some areas were not waterlogged. All this evidence points towards a landscape that was similar to the modern everglades (Fig. 6, *overleaf*).

Using the geochemistry of the palaeosols it is possible to estimate the mean annual rainfall that fell on the floodplain. These give an estimate of 1,000mm to 1,500mm of rain per year, which, given the tropical latitude of Scotland in the Carboniferous, suggests there was a monsoonal climate. This conclusion is also supported by the occurrence of evaporites and desiccation cracks (Kearsey *et al*. 2016).

The tetrapods fossils themselves were found associated with flood deposits overlying the palaeosol. The degree of articulation of the bones suggests they had not moved far, indicating that they lived on the land surface rather than in the rivers and lakes.

Figure 4 Fossil remains of Aytonerpeton microps *discovered through CT scanning.*



Why did vertebrates come on to land?

The new discoveries from Scotland and Northumberland have shown that 'Romer's gap' is a collection bias, and we now have fossils that appear both to show Devonian and Carboniferous characteristics. If this was the moment that our ancestors spent more time on land than in the water, then we need to ask, 'What is the reason this happened?' Almost certainly there was not just a single factor at work. The increase in diversification of fluvial systems from braided to meandering from the Devonian Period and after created new environments that could be exploited by tetrapods. The highly seasonal climate seen in the Ballagan Formation would have favoured creatures that could survive both in water and on land, especially as lakes and pools became evaporate and more saline. Finally, the presence of large predators in rivers and potential prey on land also added to the evolutionary pressures.

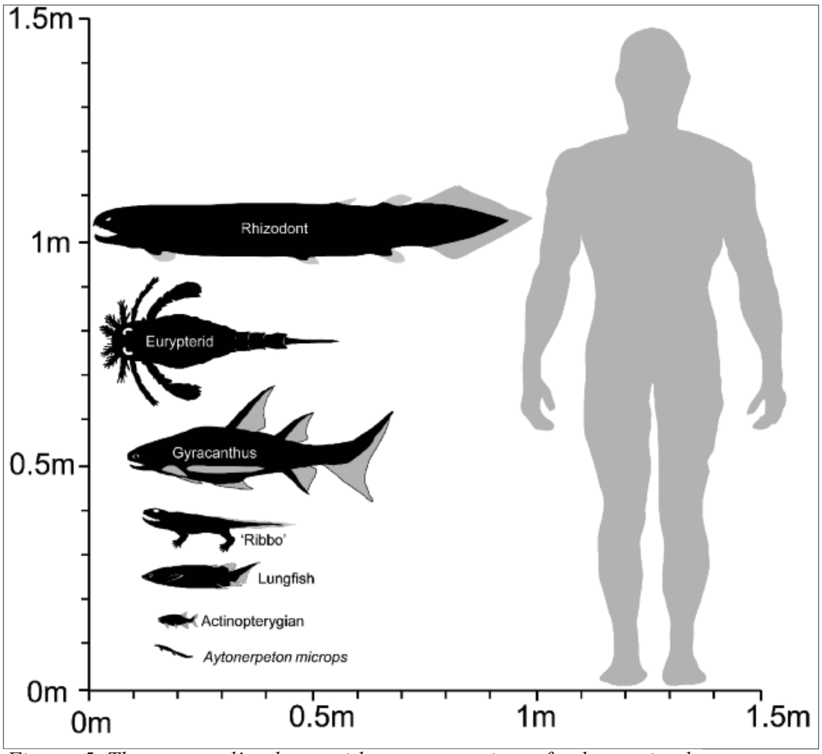
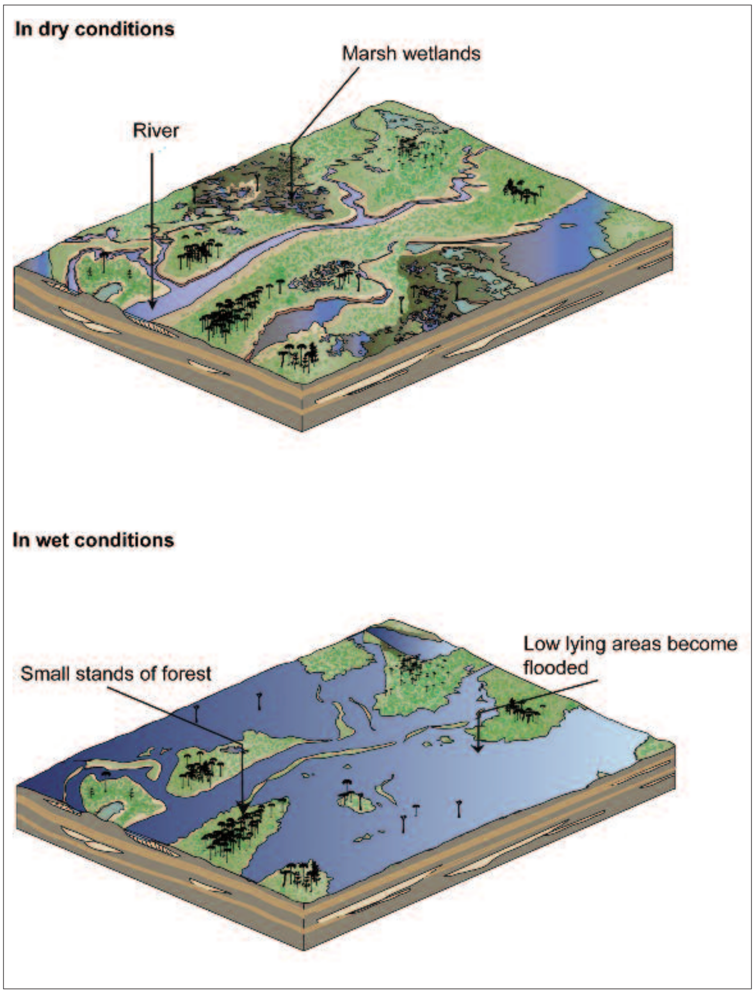


Figure 5 The tetrapod's along with reconstruction of other animals found in the Ballagan Formation with a human for scale.

Overall, the TW:eed project has started to fill a significant gap in scientific knowledge and put the Borders of Scotland at the heart of our understanding of the evolution of life on land.

Figure 6 Reconstruction of the environment the tetrapods were living in the dry and wet season.



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