# An invitation to time travel: the world-renowned 360 million year old fossil archive at Waterloo Farm, Makhanda

*By Dr Rob Gess*

**Building stones and early clues**

The earliest historical treasures of the district long remained hidden, buried deep beneath the surface of the Zuurveld and the hills to the north. Great rolling wrinkles of quartzitic rock form the Mountain Drive ridge of the Rietberg, to the west of Makhanda, whilst to its east rises a similar quartzitic ridge which includes Governor's Kop. These form part of a continuous layer that is folded deep underground between the two. Above it the ridges are connected by a plane, carved from younger, softer overlying strata more than 60 million years ago. From the south the headwaters of the Kowie River later gnawed the edge of the plain, carving out a basin named eRhini (the Place of Reeds), where the garrison settlement of Graham's Town was built. These distinctive quartzitic rocks (the Witpoort Formation) also underlie much of the Zuurveld, weathering into the pale sandy soils that host heathlands, such as those on the flats near Martindale, and the jagged-edged rocky plateau approaching the Kap River. This sourveld would prove nutrient poor grazing for generations of cattle owners, but is florally rich with proteas, pincushion proteas, white and purple "heather" and other fynbos flowers.

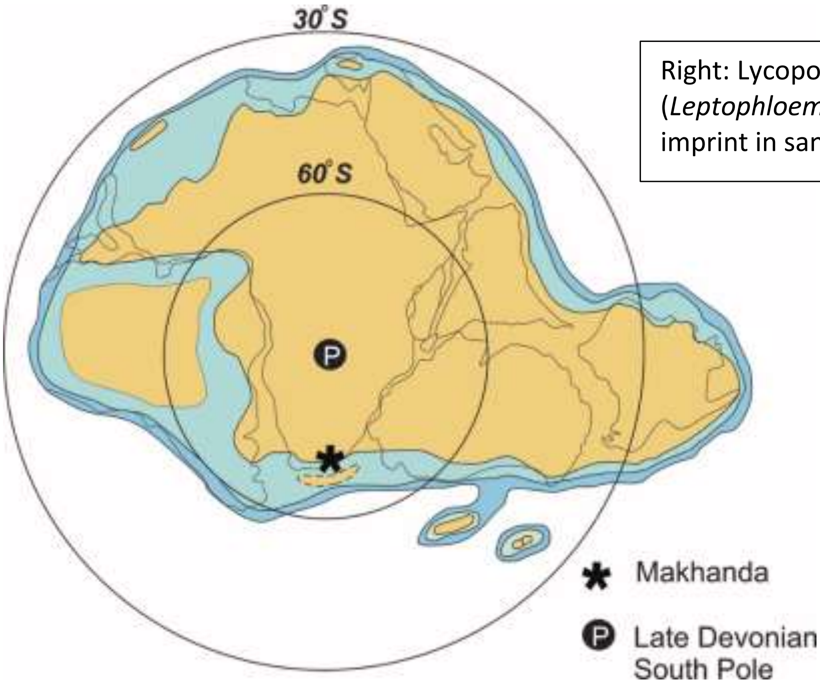
Left: Witpoort formation cliffs overlooking Kap River
(Photo: Rob Gess)

The earliest people to live here found the cleaner quartzites ideal for making stone handaxes, whilst later hunter-gatherers and pastoralists used the resilient stone for making grindstones. Later, when the British arrived, the layers of quartzitic sandstone were quarried and shaped into blocks for building. Amongst the early arrivals was Sergeant William Beadle, a veteran of the battle of Waterloo, who got a job as the quartermaster of Fort England in 1820. Overlooking the fort, at the base of a spur that stretched out from the Rietberg towards it, he built a small farmhouse on a grassy step in the rocky slope, quarrying the stone from the cliff behind. His farm, a little above the spring that watered the Fort's gardens, was named Waterloo Farm to commemorate Napoleon's defeat. The next 100 years would see a proliferation of building with Witpoort Formation quartzite - from the side and back walls of St John's church in Bathurst, to the town hall and towering spire of the Cathedral in Grahamstown, almost all local stonework was done with this indispensable stone.

Occasionally people noticed long straight scaly looking impressions in the sandstone, which some ventured were fossil snakes. Some were as broad as a bicycle tyre print, with a scaly pattern of diamond shapes. Others, like the one prominently built into the steps at St Mary's, Cuylerville, were more slender with a pattern of small circles. Other than these imprints, which we now know were formed around the stems of giant clubmoss plants, there was little clue as to the secrets in the rocks. These were hidden in layers of black shale, between the thick sandstone beds, though in the natural landscape they were weathered to pale mud for many metres down from the land surface. This obliterated their secrets, and created grassy benches in the hillsides, like the one where William Beadle built his house. The first hint of what awaited came in the 1840s when Andrew Geddes Bain passed through the district upgrading pioneer tracks into colonial roads. Trimming back cliffs and cutting level steps into hillsides for passes he noted (in a short note published in the 1850s) that he encountered fragments of Devonian aged plants in thin black shales at Howison's Poort, Woest Hill and near the mouth of the Kowie[1].

As late as 1985, however, all that was known from these layers were a handful of small fossil plant fragments, mainly kinds of small sticks and lycopod plant stalks too incomplete to properly identify, as well as a couple of small isolated primitive spore capsules (sporangia) and a single type of small, isolated fern-like leaflet. As southern Africa (then part of Gondwana, a supercontinent comprising Africa, South America, India, Australia and Antarctica) was well within the southern polar circle during the Devonian (420-360 million years ago), it was concluded that harsh conditions precluded the abundant life witnessed in similar aged rocks from more tropical regions. Those from Europe, Greenland and America (then parts of the tropically situated continent of Euramerica) conversely provided evidence for many of the most pivotal events in the history of life.

[1] Some plant fragments were later, independently, found in the cliffs behind the PA Railway Station when black shale interbeds were dug out in the hope of finding coal.




Right: Lycopod (*Leptophloem*) stem imprint in sandstone

Left: South polar view of Gondwana in the Late Devonian

**The Devonian world**

During the Devonian Period (from 420 to 360 million years ago) plants evolved from incredibly simple proto- land plants, to the ancestors of all major modern plant groups - with the exception of flowering plants. At the dawn of the period plants consisted of small, repeatedly branching leafless stalks that rarely grew above ankle height and ended in a variety of bobble- and vuvuzela-shaped sporangia. These lacked any woodiness and clung to marshy areas around the water's edge. Yet, towards the end of the period, plants had thoroughly invaded the land: woodlands of leafy progymnosperm trees tens of metres high delved their roots deep into the ground to draw up water so that they could live far from the water's edge; beneath them diverse plants formed layered understories; and the first plant seeds had evolved, allowing plants to reproduce independently of water. Millipedes, scorpions and other terrestrial invertebrates had rapidly followed the plants ashore, though as yet no vertebrates (animals with backbones) are known from on land.

In the water, jawed vertebrates (having made their first appearance just before the Devonian Period) reached their greatest ever diversity of major types, as the ancestors of groups that survive today swam past representatives of others that have long gone extinct. The waters were generally dominated by now-extinct placoderm fish, the earliest form of jawed vertebrates, which had armour plating covering their entire heads and trunks. There were also spiny-finned cartilaginous fish (acanthodians) which included the ancestors of sharks, and had a bony spike supporting each fin. Early sharks lived side by side with these. Ray finned fish that nowadays make up 99 percent of fish species were then an extremely minor group of small sized creatures showing very little diversity. The most prominent group of (non-armoured) bony fish were the lobe-finned fish, then very diverse but now represented by only eight species (two species of coelacanths and six species of lungfish). These fish had flexible fleshy lobes at the base of all their fins - made up of a number of articulating bones covered in muscles – beyond which extended their fin webs. ***Importantly,***

***it is from lobe-finned fish that all four-legged animals (and their descendants, including ourselves) are descended.***

An extremely rare fossil record adequately illustrates how the back and front pairs of fins of lobe finned fish gradually transformed into arms and legs whilst all other fins, except the tail fin, were lost by the latest Devonian. All known examples of these late Devonian four-legged creatures, however, remained living in the water, (though by the Carboniferous we find evidence of them living on land, soon after which they divide into the distant ancestors of amphibians, reptiles and mammals). Most Devonian tetrapod remains, including the only two species known from complete skeletons, came from the tropical northern continent of Euramerica. Apart from these a single jaw fragment was known from China, then a tropical island, and a single jaw was known from Australia, the only part of Gondwana to extend into the tropics. Similarly, abundant Devonian vegetation, including progymnosperm trees and seed plants, were only known from tropically deposited rocks, and terrestrial invertebrates were only known from tropical Euramerica. Textbooks indicated that all the action had occurred in the Devonian tropics, that trees had first spread around the equatorial world, and that ancestral tetrapods had arisen in Euramerica before spreading around the tropics as far as Australia. Polar regions were considered to have been a harsh depauperate (lacking in biodiversity) world.

**<u>Winds of change: dark clouds and a silver lining</u>.**

The 1980s were a time of pivotal change in our country, with an upsurge in civil protest against apartheid. Violence surged on both sides. In Makhanda, then Grahamstown, protesters had a throttle on the flow of traffic between Port Elizabeth (now Gqeberha) and East London – because the N2 passed through town, along Beaufort Street, up Raglan Road, through the townships, and out across the plane towards Governor's Kop. Any group of children armed with rocks and half bricks could bring traffic to a standstill. In 1985 the government responded with a draconian State of Emergency - and an emergency road realignment plan for Grahamstown. They had concluded that the simplest way to remove the protesters' control over the road would be to hastily move the road. Though it would have been cheaper and more practical to take the road across the plain to the north of town, the military, who owned land there, vetoed the possibility. As a result, land was expropriated from smallholders and farmers to the south of town – so that the road could be carved through the uneven drainage basin of the Blaaukrantz branch of the Kowie River. Deep cuttings would go through the spurs, with the debris heaped into great embankments across the valleys.

Waterloo Farm was not spared. The road went right through its farmyard, leaving William Beadle's former house perched near the edge of a huge artificial cliff, and severing from the mountain the sheltering spur that used to run down towards Fort England. But in so doing it carved a deep slice through the unseen black shale that was represented by the step in the slope where the house was built. And so it was that South Africa's greatest Devonian treasure was revealed. Roy Lubke, a botany professor who now owned Waterloo Farm, was having a braai with colleagues one afternoon when one of them wandered off and peered over the cliff, returning to report that there appeared to be plant fossils in the black shale. I heard this via my father, an entomologist and acquaintance of Roy's, and already obsessed as I was with fossils, I got out there on the coming weekend. The beautiful fossils that I found amongst the rubble on my first visit were unlike anything we'd ever seen from the Late Devonian before, twigs with leaves, delicate plant whorls, pieces of seaweeds and a mysterious item I would later find to be a shark's fin spine. I was hooked. I kept going back for more, even as I finished school and studied science at Rhodes. On and off for 40 years, sometimes without funding and sometimes with funding, I have carefully excavated the shale and studied the clues it holds to an ancient lost world. It was the focus of my MSc and PhD and remains the central focus of my research career. Both when the road was cut back in 1999 and again in 2007 the site was at risk of being lost, but the National Roads Agency supported my efforts with a team to manually mine out first 30, and then another 70 tons of shale. This is now stored in sheds where excavations continue. I am not alone in my love of this treasure trove - top experts from around the world regularly visit my lab to collaborate on research into the diverse fauna and flora revealed.

**The Waterloo Farm lagerstätte**

A lagerstätte is an exceptionally rich deposit of fossils, which often includes soft-tissue preservation. Amongst those who study the Devonian the Waterloo Farm lagerstätte is well known. It is the only known window into a high latitude Late Devonian vertebrate fauna, or flora, in the world. Not surprisingly, virtually everything from it is new to science.

During the final stage of the Devonian, the Famennian Age (371-359 million years ago), global climate became unstable. Climatic fluctuations, combined with atmospheric changes and periodic aquatic anoxia [2], eventually resulted in one of the greatest extinction events of all time – the End Devonian Mass Extinction Event. Fluctuations in temperature throughout the Famennian led to periodic ice-cap expansion and contraction – resulting in episodes of global sea level rise.

The Waterloo Farm fossil site in 1990 with the main lagerstätte shale at top left. Circled figures: archaeologists at work

Along the southern margin of Gondwana global sea level rises resulted in periodic flooding of the continental margin - leading to the formation of estuaries, coastal lakes and lagoons (much like some of those along the eastern and southern Cape coasts today). Fine black

[2] Lacking in oxygen

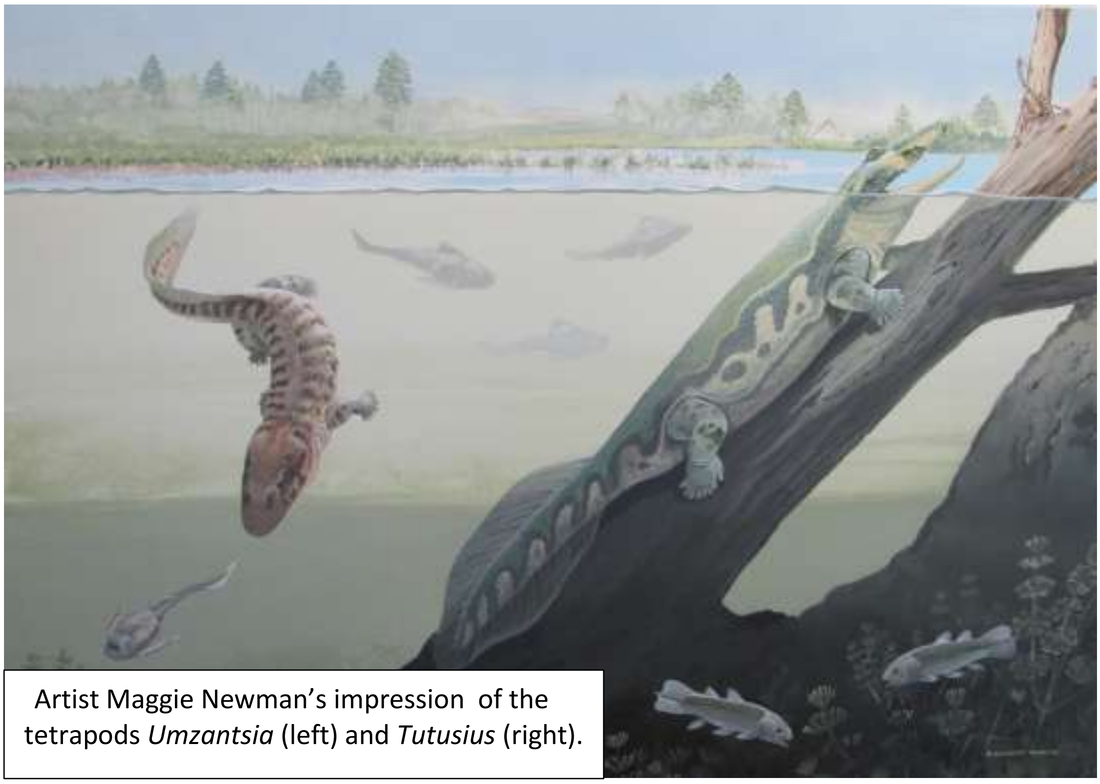
organic rich mud which collected in these estuaries and lakes would become the layers of black mudstone and shale in the Witpoort Formation, packed between thick packages of quartzitic sandstone (our building stone), which was once sand - largely laid down on the coastal plain by rivers, though also probably, at times, deposited along the shore.

Conditions in the ‘Waterloo Farm estuary’ were perfect for preserving fossils: fine mud, brought in by a river, accumulated quite rapidly in a deep estuarine lake, the bottom waters of which were seasonally lacking in oxygen. When such anoxic conditions were prevalent, even the most delicate soft tissued creatures and normally ephemeral plant and seaweed remains were preserved alongside the bones and more robust plant remains that are more usually found as fossils. Deep burial during mountain building 60 million years later transformed the muds into black metashale, and the plants and animals into ghostly silver and white impressions, like photographic negatives, providing snapshots of

the lake floor 365 million years ago. From these we can accurately piece together a detailed picture of an entire ancient ecosystem – by now the most completely reconstructed Famennian estuary from anywhere in the world.

Above: Fossil of the head and trunk armour of the antiarch placoderm *Bothriolepsis Africana,* and artist’s reconstruction, right

preconceptions of Devonian biogeography, have unveiled a world as rich in diversity as overhung by trees and abundant vegetation. Amongst the greatest surprises to science was the discovery of the distinctive bones of tetrapods (four-legged animals), representing not just one species, but in fact two.



Artist Maggie Newman's impression of the tetrapods *Umzantsia* (left) and *Tutusius* (right).

One of these, *Tutusius umlambo* (named in honour of Archbishop Desmond Tutu) was similar to other Devonian tetrapods, but the other *Umzantsia amazana*, has unique primitive characteristics, never before seen in a Devonian tetrapod. Rather than Devonian tetrapods being exclusively tropical and largely Euramerican, discoveries at Waterloo Farm reveal that they had most likely reached a global distribution by the end of the Devonian, extending all the way from the southern margins of Gondwana to the tropics of Euramerica. Had there been just one, average, Famennian tetrapod (like *Tutusius*), it might have been interpretable as an outlier, but the coexistence of *Umzantsia* suggests a deep history of tetrapods in this part of the world. In fact, it now seems equally plausible that tetrapods could have arisen in southern Gondwana rather than tropical Euramerica.

These are also the first tetrapods known from a lagerstatte, and so we also know more about where they lived than we know about any other Devonian tetrapods. The jaws and teeth of early tetrapods (that grew up to about a metre long) tell us that they were adapted to eat smallish fish. At Waterloo Farm we have a whole range of food options, some more likely than others.

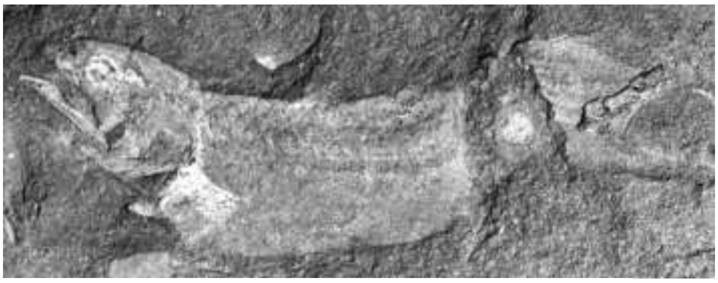
The most diverse group of fish at Waterloo Farm are placoderm fish. These fish (all of which would go extinct at the end of the Devonian) were descendants of the earliest kind of jawed vertebrates. Whereas modern bony fish generally have, in addition to a skull, a bony cover to the outside of the head, placoderm fishes had a bony cover over the whole head AND trunk, with a hinge between the two to allow the head to move.

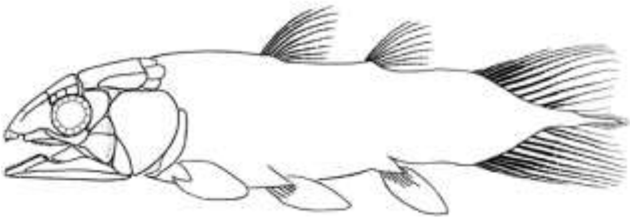
The arthrodire placocderm, *Groenlandaspis riniensis*: whole preserved 2.5cm long baby (left), and artist's impression (above)

At Waterloo Farm we have discovered remains of at least seven kinds. We're fairly sure that most of these were permanent residents of the estuary as we find remains ranging from whole baby fish a few centimetres long, to the bony plates of members of the same species, some of which evidently grew up to a metre long. Amongst the latter was *Bothriolepis africana*, a strange kind of antiarch placoderm that, rather than have a pair of front (pectoral) fins,  had a pair of flattish armour-plated jointed arms. It was clearly a bottom dweller as its eyes were close set on top of its head, set in a kind of bean shaped opening. They may have eaten seaweeds, many types of which are preserved at Waterloo Farm.

All the other Placoderm species at Waterloo Farm were 'phlyctaniied arthrodire' placoderms which had somewhat shark-like front fins. These stuck out on either side through a pair of holes in the trunk armour. On the outside of these were a pair of sled runner-like spinal plates. Some of these like *Groenlandaspis riniensis* grew to a metre in length. Their simple tooth plates suggest that they may also have eaten seaweeds, though some younger examples have small bivalve shells inside them, suggesting that they may also have eaten the latter. Two  species of arthrodire placoderms, *Africanaspis doryssa* and *Africanaspis edmountainus,* only got about 40 cm long, but were characterised by a huge spike-like extension of the top of their trunk armour - which probably discouraged predators. The bigger placoderms were as large as the tetrapods so they were probably too big for them to eat. More likely, their abundant young, sheltering in waterweed-filled shallow waters around the edge of the lagoon, would have been a major food source – even if the tetrapods just ate their tails!

We have evidence for diverse charophyte waterweeds in which fish will have sheltered, and many baby fish of different kinds. Evidence for extensive use of the estuary as a nursery area by both resident species and visiting marine fish suggests the possibility that exploitation of young fish in these shallow environments may have driven the evolution of primitive tetrapods. Certainly, their flattened bodies, loss of unpaired fins, alligator-like eyes, breathing holes on the back of their heads, and stubby sidewardly directed legs would provide good adaptations to hunt in the shallows where other predatory fish could not go. Though these adaptations could not originally have been for going on land - as evolution cannot plan ahead - once acquired, they would have made those future first steps onto dry land possible.





The coelacanth *Serenichthys kowiensis*, 5.5 cm juvenile specimen (left), and artist Anton Brink's reconstruction (below).

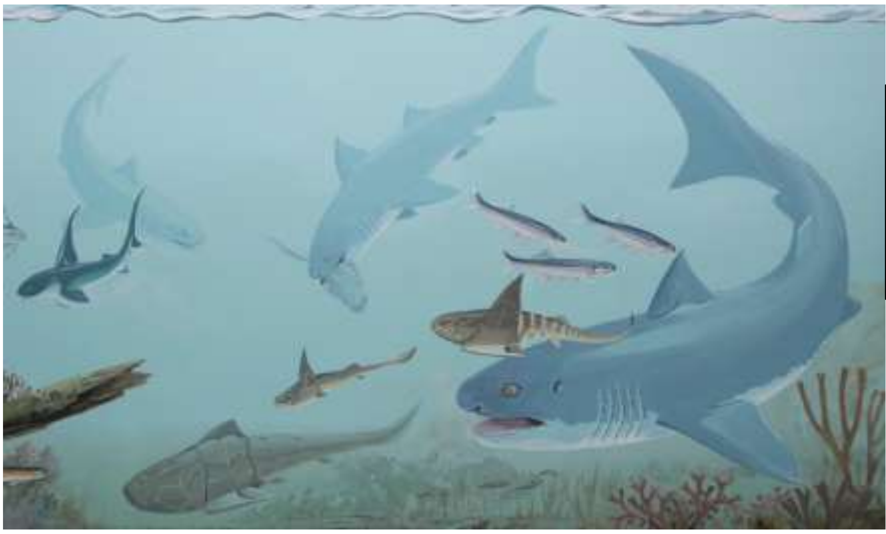
Amongst the marine fish that used the estuary as a nursery were coelacanths (*Serenichthys kowiensis*). I have found dozens of babies, almost all 3.5 to 5.5 centimetres long. We have fragmentary remains of a few teenagers, but no remains of adults (that probably reached about 30 cm long). This suggests that the adults gave birth in the estuary, and that once the young were beyond infancy the adults returned to the sea, much as many marine fish do today. This is the earliest, though not the only, evidence of ancient coelacanths using estuaries as nurseries. *Serenichthys* is also the earliest coelacanth ever described from Africa. (What a strange coincidence that the type material comes from a mere 100km from where Africa's youngest coelacanth, *Latimeria chalumnae* was caught!)

Coelacanths are of course lobe-finned fish, which were abundant and diverse during the Devonian, but today are only represented by coelacanth and lungfish – the latter more closely related to us than coelacanths. Apart from coelacanths at Waterloo Farm, lobe-finned fish included small, snack-sized onychodonts (similar to coelacanths but with smaller lobes), lungfish, and giant lie-in-wait predators called rhizodonts and tristichopterids. The latter belong to the fish-like fish group most closely related to tetrapods. *Hyneria udlezinye*, the tristichopterid from Waterloo Farm, would probably have been one of the greatest sources of terror to our ancestral tetrapods. These huge predators were the largest hunters in the less marine portions of the estuary, reaching up to 3 metres long with robust jaws, lined with teeth and fangs. For them tetrapods would have represented a pleasant meal, if they could find one straying out of the extreme shallows.

Ray-finned fish (the ancestors of most modern fish) were represented by one species that reached up to about 20cm in length, and judging by the presence of juveniles and adults it was a fairly uncommon species that spent its life around the margins of the estuary. Without spines or armour plating it would probably have made quite a nice snack for our ancestors.

Cartilaginous fish were represented by both acanthodians and sharks. Most acanthodians were probably awkward to eat as they generally had sharp bony spikes in front of all their fins. Two types of diplacanthid acanthodians were particularly spiny. One of these, *Diplacanthus acus*, is described from an absolutely exquisitely whole preserved specimen about 10 cm long. It is unique amongst acanthodians with body proportions very like a modern angelfish, so we can easily picture it manoeuvring through the dense jungle of waterweeds. Acanthodidids, also found at Waterloo Farm, were likewise small but more eel-shaped, with far smaller spines - so they may have provided a better food option. The largest acanthodian present was *Gyracanthithes riniensis*, which was up to 60 cm long with robust pelvic (front paired fin) spines a third of its body length. Adults would probably have been too much of a mouthful for the tetrapods, though curiously the associated spines of one specimen are sheared clean in two, suggesting perhaps the action of the powerful jaws of *Hyneria*.

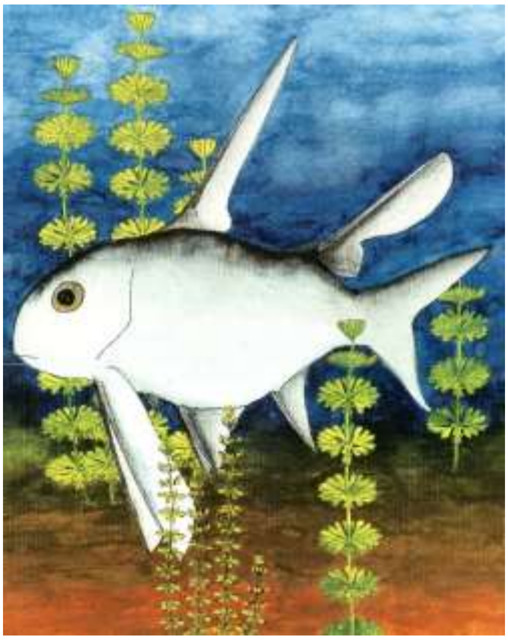
The other terrors of the deep came into the river mouth from the sea, in the form of two kinds of sharks, the larger of which (*Antarctilamna ultima*) may have reached 5 metres in length. They likely came in to hunt everything else in the estuary, though discovery of a 2.8 cm long baby of *Antarctilamna* suggests that, in addition, they used the estuary as a nursery area.



Artist Maggie Newman's reconstruction of 5 metre long adult sharks *Altarctilamna ultima* hunting in the estuary. Far left: a 2.8 cm long juvenile facing right

Another marine fish that used the estuary as a nursery was *Priscomyzon riniensis*, the oldest known lamprey in the world. Lampreys still exist today and, along with hagfish, they are the only surviving fish lineages descended from jawless fish (that predated the evolution of jaws). Although many early jawless fish had a bony external armour (inherited by early jawed fish), lampreys were a specialised group that lost all their external bony covering and had an internal skeleton made purely of cartilage. As a result, they are hardly ever found as fossils. Modern lampreys occur around every continent except Africa as they favour cold waters. They are eel-shaped creatures that have a large sucker disc, covered in teeth, around their jawless mouth. With this they suck onto other fish before rasping a hole in their victim using specialised teeth on their tongue. Their saliva prevents their prey's blood from clotting and they use pumping actions to drink the blood until they are satisfied. Though *Priscomyzon* is smaller (the only adult being 4.2 cm long) and more tadpole-shaped, it has proportionately the largest sucker disc of any lamprey living or dead, suggesting that it also enjoyed a bloodthirsty lifestyle. As such it may have been both prey for and a threat to our tetrapods. Modern lampreys have a life cycle that begins with them hatching out of eggs as simple invertebrate-like larvae that burrow into the sand of freshwater streams where they live by filter feeding – before metamorphosing into adult lampreys. This has long been thought to give insights into the evolution from invertebrates into vertebrates. Incredibly, we have managed to assemble a growth series of *Priscomyzon* from recent hatchlings (14 mm long) to adults, and although their body proportions changed as they matured, they clearly lacked an invertebrate-like larval stage, challenging the long held theory based on modern lampreys.

Below: *Priscomyzon,* the world's oldest fossil lamprey, 4.2 cm long fossil adult, and right, reconstruction of Acanthodian, *Diplacanthus acus*, among waterweeds.



Below: artist (Maggie Newman)'s reconstruction of fish nursery area amongst charophyte waterweeds at Waterloo Farm: note coelacanth (*Serenichthys*) giving birth (middle left), arthrodire placoderm, *Africanaspis edmountainus* (mid right). The charophyte, *Octochara crassa* (front left), bivalves (front middle), baby *Groenlandaspis* (second from front right) and baby *Antarctilamna* sharks (bottom right).

Artist Maggie Newman's reconstruction of terrestrial scene at Waterloo Farm: note *Archaeopteris* trees (top left), *Leptophloem* (resembling giant paintbrushes) and scorpions (*Gondwanascorpio*) on fallen *Archaeopteris* branch (centre front).

Notably, in addition to our window into life in the estuary we also have an almost unparallelled record of the plants that grew around the estuary, as their remains were washed or blown in and preserved beside the aquatic remains in the fine black mud. These include a complete record from herbaceous plants up to trees. Delicate whorls are reconstructed as one of the oldest known ancestors of horsetails (*Rinistachya*); strange shrubs are related to the ancestors of ferns (*Flabellopteris*); other branching shrubs bore primitive seeds (the oldest known from Africa); and leafless creeping plants that forked at intervals and unravelled from crozier-like tips represent the youngest known Zosterophylls. The latter are the ancestors of lycopods or clubmosses. Clubmosses are still represented by a few creeping herbaceous forms today – actually far more closely related to ferns than mosses! In the mid to late Devonian floras were often dominated by lycopods and a number of different types occur at Waterloo Farm. These include ‘herbaceous’ lycopods that branched up from runners to form clumps of cat-tail like leafy stalks reaching up to knee height (such as *Colpodexylon mergae*). Others (*Leptophloem*) were the forerunners of the ‘giant clubmosses’ that dominated the later coal swamps of the European Carboniferous. *Leptophloem* was more modest than those to come, rising unbranched from a rooty corm to a height of about two metres, with a leafy tip resembling a giant paintbrush. It was stems of these, with their diamond-shaped pattern of leaf scars, that were long known from the Witpoort sandstones, and sometimes mistaken for fossil snakes. Within this undergrowth rustled the earliest known land animals from the continent of Gondwana, scorpions (*Gondwanascorpio*) and millipedes -previously only known from the latest Silurian[2] and Devonian of Euramerica.

Towering over the undergrowth were *Archaeopteris* trees up to 25 metres tall, with fern-frond-like branches of leaves. When we described *Archaeopteris* trees from Waterloo Farm during the mid 1990s we provided the first evidence of this genus from outside the tropics, indicating that it had reached global distribution by the Late Devonian.

30cm long frond-like leafy twigs of *Archaeopteris notosaria*.

These ‘Progymnosperms’ were the first kind of tree with properly woody stems and roots. This allowed them to live far from the water’s edge, where plant life had previously been concentrated, delving their roots deep into the ground to reach the water table and pumping it up to their leafy branches.

The resultant sudden forestation of the world permanently changed the planet. Notably their spread, towards the end of the Devonian, coincided with growing climatic instability, which culminated in the End Devonian Mass Extinction Event – the second of five great extinction events that have pruned the tree of life during its history. It is debated whether the extinction event resulted solely from the spread of forests, or whether they brought the biosphere to the brink of catastrophe and some other event tipped it over. Certainly though, their effect was profound. Firstly, the sudden forestation of the planet resulted in

[2] 444-420 million years ago

massive drawdown of $CO_2$ from the atmosphere. This occurred in two ways, the most obvious being the massive increase in biomass – trees, like all plants, are primarily made up of molecules in the form of one or multiple rings of carbon atoms, with lesser amounts of hydrogen, oxygen, nitrogen and other elements. The carbon involved is absorbed from the atmosphere in the form of $CO_2$ and fixed into solid forms by plants using photosynthesis. Less obviously the spread of trees changed the nature of the weathering of rocks, which had previously been largely mechanical in nature. Humic acid from the trees' roots and the decay of plants reacted with minerals called feldspars to reduce them to clay. This reaction, however, also involves a large input of $CO_2$, which is co-opted from the atmosphere. Together these processes greatly reduced the concentration of $CO_2$ in the atmosphere, causing massive global cooling (the inverse of the greenhouse effect), which culminated in an ice-age at the end of the Devonian. In addition, massive unaccustomed influx of nutrients, washing off the land into water bodies, led to episodes of eutrophication as excessive micro-algal activity exhausted oxygen dissolved in the water. Whilst today we live in a finely balanced tree-mediated environment, this first arrival of forests brought a close to a previous chapter of life. We, and the plants and animals around us, are descended from the survivors.

Something that is emerging from the study of Waterloo Farm is that amongst the creatures that first appear in the fossil record of tropical Euramerica after the Extinction Event, are some most closely related to creatures found in polar Waterloo Farm before the extinction. It seems likely that whilst, with plummeting global temperatures, tropical creatures went extinct, some cold adapted ones survived by moving to relatively warmer equatorial climes – thereby helping to seed the emerging new faunas. Could these have included the earliest land-living tetrapods? We don't know, but due to the fossils of Waterloo Farm we know that this is a possibility. Terrestrialisation of tetrapods ultimately requires the presence of 1) aquatic tetrapods, 2) shady environments on land, and 3) creepy crawly food sources on land. Before we studied Waterloo Farm these three conditions were only known from Devonian equatorial regions, with all three only known from Euramerica. Thus, it was assumed that this pivotal evolutionary transition occurred in what is now Europe or America, and that from there land-living tetrapods spread out and colonised the world.

Now we know that all the necessary conditions were also present in polar southern Gondwana, ***making it equally possible that what is now southern Africa could have been the original setting for the movement of tetrapods onto land.***

Left: the scorpion, *Gondwanascorpio emzantsiensis*, Gondwana's oldest described terrestrial animal, 2.5 cm long pincer at left, and sting below.

**Rob Gess**

**With deep roots in the Eastern Cape, Rob Gess was born in (then) Grahamstown, the son of two ecologists. Fascinated by fossils since childhood he majored in Zoology and Geology at Rhodes. He has a PhD in palaeontology from Wits and is South Africa's primary researcher on Devonian vertebrates and plants - based at the Albany Museum. A lover of travel and camping, he shares a sizeable ecologically-designed garden in Bathurst with his wife Serena, two cats and an ancient crow**.

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