Tiktaalik Roseae – A Missing Link?

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Tiktaalik roseae is a fossil that in some respects seems to close the gap between the fish *Panderichthys* and the tetrapod *Acanthostega*. The scientific report appeared in the journal *Nature* (6 April 2006) and news of it was immediately promulgated in press and radio across the world. *The Guardian* went so far as to say it was one of the most important fossil finds in history: a missing link between fish and land animals showing how creatures first walked out of water and onto dry land. *Nature* itself was only a little more phlegmatic. In the covering news and views item Jennifer Clack and Per Ahlberg said they expected it to acquire the same iconic status as *Archaeopteryx*. Was the hype justified?

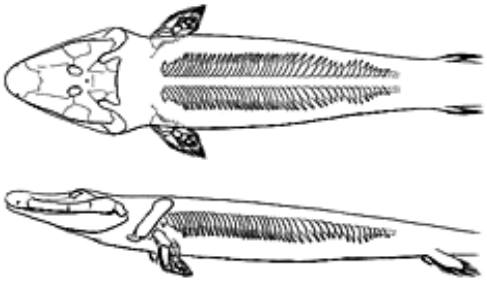
Overview

The following review concentrates on what is said in the scientific papers. The authors, Edward Daeschler, Neil Shubin and Farish Jenkins, introduced their find as follows:

> The relationship of limbed vertebrates (tetrapods) to lobe-finned fish (sarcopterygians) is well established, but the origin of major tetrapod features has remained obscure for lack of fossils that document the sequence of evolutionary changes. Here we report the discovery of a well-preserved species of fossil sarcopterygian fish from the Late Devonian of Arctic Canada that represents an intermediate between fish with fins and tetrapods with limbs, and provides unique insights into how and in what order important tetrapod characters arose. Although the body scales, fin rays, lower jaw and palate are comparable to those in more primitive sarcopterygians, the new species also has a shortened skull roof, a modified ear region, a mobile neck, a functional wrist joint, and other features that presage tetrapod conditions. The morphological features and geological setting of this new animal are suggestive of life in shallow-water, marginal and subaerial habitats.

Tiktaalik is a lobe-finned fish, in the same broad group as coelacanths and lungfish. In the Devonian period lobe-finned fish were more diverse than they are today and *Tiktaalik* now adds to that diversity.

In more detail


Tiktaalik roseae

Although it was a fish, *Tiktaalik* had some features that were tetrapod-like, and one could (depending on one's point of view) interpret the whole animal as transitional to tetrapods. These features include: a lengthened snout (measured from the eyes to the tip of the skull), a mobile neck, overlapping ('imbricate') ribs and a pectoral girdle

that may have given it an ability to lift the front part of its body by its fins. On these grounds the animal is analysed as being intermediate between the lobe-finned *Panderichthys* and the four-limbed *Acanthostega* and *Ichthyostega*. That is, *Tiktaalik* went on to evolve in two separate directions, *Acanthostega* on one branch and *Ichthyostega* on the other.

Still, some caution is appropriate, even with these tetrapod-like features. Among sarcoptery- gians the mobile neck is not unique to *Tiktaalik*, being also found in *Mandageria*, a fish closely related to *Eusthenopeteron* and not thought to have been an ancestor of any tetrapod. In evolutionist terms the feature must therefore be interpreted as 'convergent', i.e. it evolved in *Mandageria*, disappeared in *Panderichthys*, then re-appeared on another branch in *Tiktaalik*.

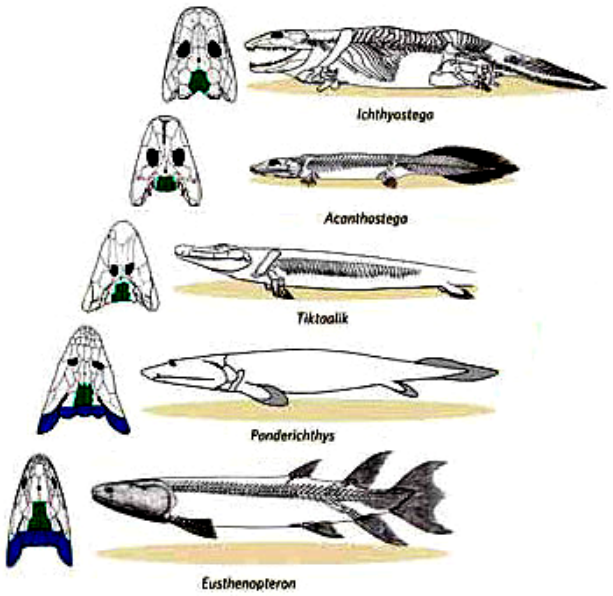
Imbricate ribs do not occur in any other fish, nor in *Acanthostega*, but do occur in *Icthyostega*. Shubin *et al*. state that 'expansion and imbrication of the ribs is a feature … seen in some early tetrapods such as *Icthyostega*'. Apart from *Tiktaalik*, however, they seem to be unique to *Icthyostega*, and since even *Icthyostega* was primarily aquatic, it seems unjustified to suggest that they played a role in supporting the weight of the animal. The stiffening of the spine produced by this arrangement would have inhibited horizontal flexion (the wiggling motion characteristic of most fishes) just as it would have done in *Icthyostega* (Clack 2005), and this fact alone is sufficient to explain the mobile neck and fin joints: without some compensating mobility the animal might not have been viable as a predator.

In overall morphology, the ribcages of *Tiktaalik* and *Icthyostega* are totally unlike each other.

It is also debateable whether the pectoral fins can be regarded as transitional. They more closely resemble the large fins of the sarcopterygian fish *Sauripterus* than they do the forelimbs of *Acanthostega* (the forelimbs of *Icthyostega* are incomplete). With its digit-like radial bones, *Sauripterus* is regarded as having an anomalously 'advanced' fin. Shubin *et al* comment:

> A Devonian rhizodontid, *Sauripterus*, is known to possess digit-like radials, but phylogenetic analyses indicate that this group is not the closest relative of tetrapods.

The gap between the pectoral fin of *Tiktaalik* and the front foot of *Acanthostega* is large, as Ahlberg and Clack note. The gap between the pelvic fin of *Tiktaalik* and the hindlimbs of both *Acanthostega* and *Icthyostega* is so large that the authors omit to comment on it, except to say that *Acanthostega* does not have *Tiktaalik*'s numerous lepidotrichia (fin rays). Figure 2 of the main paper, showing a photograph of the specimen, shows only the anterior, better preserved half of the animal. In the drawing the pelvic fins are illustrated as fleshy lobes.



Overall, this is not an animal that falls plumb in the middle between *Pander- ichthys* and *Acanthostega*. It is a fish, albeit an unusual one, and while there is only a relatively small gap between *Panderichthys* and *Tiktaalik*, there remains a big gap between *Tiktaalik* and *Acanthostega*. In a significant number of features – body scales, fin rays, lower jaw, palate – the fossil resembles sarcopterygians that are considered to be evolutionarily less advanced. As Ahlberg and Clack say, 'we have almost no information about the step between *Tiktaalik* and the earliest tetrapods, when the anatomy underwent the most drastic changes.' It may be reasonable enough to link the first pair into a group that had a common ancestor (the 'elpistostegalian fish'), but it requires a lot more extrapolation to link the second pair together.

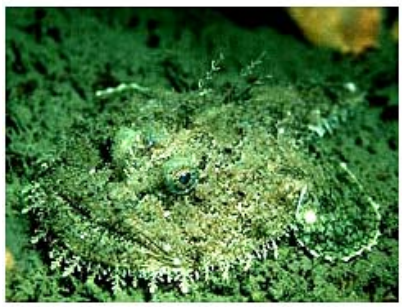
There is, moreover, a large gap after *Icthyostega* as well as before it. It often fails to be noticed that, so far as the fossil record is concerned, both *Acanthostega* and *Icthyostega* are dead-ends. They shed no light on the origin of modern tetrapods.

Did *Tiktaalik* walk on its fins?

According to *Nature*'s announcement of the fossil, *Tiktaalik* was a fish that crawled out of the water, but if so, the lineage must have crawled back again, for *Acanthostega* 'rarely, if ever, made forays onto dry land and its legs would have almost certainly been incapable of supporting its body had it done so' (Clack 2002, p 128f). That's less than is being claimed for this animal. We are told in one breath that *Tiktaalik* had a long snout that would have been suited to catching prey on land, in the next that it hauled itself onto land only to escape predators. It has, one feels, been impressed into the 'how life conquered the land' story a little too enthusiastically.

Walking is not an unknown behaviour with certain kinds of fish. In her monograph Clack mentions several examples, including the frogfish, which uses its jointed, grasping fin-rays to cling to the weeds amongst which it lurks for prey. Epaulette sharks sometimes propel themselves along the sea-floor using their paired fins and have even been observed crawling out of the water and walking over 15 metres of exposed coral rock. Here is a recent report of a monkfish 380 metres below sea-level (Laurenson 2005):

> One of the monkfish was observed to move along the seabed for several metres at a time by walking. Several "walks" were observed. The gait involved both the pelvic and pectoral fins and the body and tail were lifted clear of the seabed. The pelvic fins appeared to be the main weight bearing fins lifting the body up from the seabed. They also seemed to be responsible for a considerable proportion of the forwards propulsion.



There is no reason to 'think evolution' when observing such behaviour. It's just an example of how wonderfully unconventional life can be under water, as if whoever designed it was a non-conformist, a person who deliberately subverts stereotypes.

Thinking that was less ideologically driven might not go amiss in the present case. It is not even clear that locomotion was the

function of *Tiktaalik*'s front fins (imagine a body up to 3 metres long being dragged any distance in this manner). Monkfish, which like *Tiktaalik* have a wide mouth, flattened skull and eyes on top of the skull rather than on the sides, again alert us to other possibilities, for in addition they use their fins to scoop out sediment from under their bodies and make a hollow in which, having camouflaged themselves to match their surroundings, they lie in wait. At the right moment, they strike the prey by suddenly pushing with their fins upwards and forwards. The feeding strategy of *Tiktaalik* won't have been the same as the monkfish's, but it may have been similar.

A triumph of Darwinian prediction?

Much has been made of the fossil's being just what palaeontologists would have expected to find – even just what they did expect to find. The scientists who discovered *Tiktaalik* went to Ellesmere Island purposely looking for intermediates between *Panderichthys* and the first tetrapods, and they were not disappointed. However, we have seen that in many respects the fossil was surprising.

As it happens, a very explicit prediction was made in the pages of *Nature* four months earlier (22 December 2005), when Catherine Boisvert was discussing the pelvic fin and girdle of *Panderichthys*:

> The pelvic girdle is even less tetrapod-like than that of … *Eusthenopteron*, but the pelvic fin … shares derived characteristics with basal tetrapods despite being more primitive than the pectoral fin of *Panderichthys*. The evolution of tetrapod locomotion appears to have passed through a stage of body-flexion propulsion, in which the pelvic fins played a relatively minor anchoring part, before the emergence of hindlimb-powered propulsion in the interval between *Panderichthys* and *Acanthostega*.

What Boisvert is saying here is that *Panderichthys* had 'front-wheel drive': its front fins were bigger and more powerful than its rear fins. However, the early tetrapods were 'rear-wheel drive'. Consequently, evolution theory predicted that the emergence of hindlimb-powered propulsion would be seen in the interval between *Panderichthys* and *Acanthostega*. *Tiktaalik* fails that prediction. Indeed, it was more of a 'front-wheel drive' animal than *Panderichthys* was.

Actually it's a red herring!

As discussed elsewhere on this site, the question of how one fills the gap between *Panderichthys* and *Acanthostega* is ultimately a side issue for the thesis that lobe-finned fish evolved into land-dwelling tetrapods. Apart from the problem of identifying *Ichthyostega*'s descendants, the crucial questions include:

- How does one account for tetrapod trackways in tidal/supratidal sediments that predate even *Tiktaalik* by 10 million years?
- How does one fill the gap between *Tiktaalik*, which was a fish with no legs, and an aïstopod such as *Lethiscus*, which within 20 million years had supposedly acquired legs and limb girdles and then lost them again, and changed from a fish to something more like a snake than any tetrapod?

That is the burden of proof that needs to be discharged. As Clack remarked in an academic paper earlier in the year, *Lethiscus* suggests that 'a great deal happened in the course of tetrapod evolution that we know very little about'. This is one of the trade secrets of palaeontology to which Darwinians do not like to draw public attention. Until the problem is solved, however, it seems reasonable to conclude that we know very little about tetrapod evolution at all and to regard *Tiktaalik* in much the same light as one now regards the lung-fishes, which, for all their superficial attractiveness as intermediates, are no longer seen as ancestral to tetrapods. The fossil record continues to surprise us because, in certain respects, animal life was once more disparate and more diverse than it is today. It will go on surprising us, whatever our point of view.

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