NEWS & VIEWS

PALAEONTOLOGY

A firm step from water to land

Per Erik Ahlberg and Jennifer A. Clack

A project designed to discover fossils that illuminate the transition between fishes and land vertebrates has delivered the goods. At a stroke, our picture of that transition is greatly improved.

The concept of 'missing links' has a powerful grasp on the imagination: the rare transitional fossils that apparently capture the origins of major groups of organisms are uniquely evocative. But the concept has become freighted with unfounded notions of evolutionary 'progress' and with a mistaken emphasis on the single intermediate fossil as the key to understanding evolutionary transitions. Much of the importance of transitional fossils actually lies in how they resemble and differ from their nearest neighbours in the phylogenetic tree, and in the picture of change that emerges from this pattern.

We raise these points because on pages 757 and 764 of this issue[1,2] are reports of just such an intermediate: *Tiktaalik roseae*, a link between fishes and land vertebrates that might in time become as much of an evolutionary icon as the proto-bird *Archaeopteryx*. Several specimens have been found in Late Devonian river sediments on Ellesmere Island in Nunavut, Arctic Canada. They show a flattened, superficially crocodile-like animal, with a skull some 20 centimetres in length. The body is covered in rhombic bony scales, and the pectoral fins are almost-but-not-quite forelimbs; these contain robust internal skeletons, but are fringed with fin rays rather than digits. *Tiktaalik* goes a long way — but not quite the whole way — towards filling a major gap in the picture of the vertebrate transition from water to land.

It has long been clear that limbed vertebrates (tetrapods) evolved from osteolepiform lobe-finned fishes[3], but until recently the morphological gap between the two groups remained frustratingly wide. The gap was bounded at the top by primitive Devonian tetrapods such as *Ichthyostega* and *Acanthostega* from Greenland, and at the bottom by *Panderichthys*, a tetrapod-like predatory fish from the latest Middle Devonian of Latvia (Fig. 1). *Ichthyostega*[4] and *Acanthostega*[5] retain true fish tails with fin rays but are nevertheless unambiguous tetrapods with limbs that bear digits[6]. *Panderichthys*[7] is vaguely crocodile-shaped and, unlike the rather conventional osteolepiform fishes farther down the tree, looks like a fish–tetrapod transitional form. The shape of the pectoral fin skeleton and shoulder girdle are intermediate between those of osteolepiforms and tetrapods, suggesting that *Panderichthys* was beginning to 'walk', but perhaps in shallow water rather than on land[8].

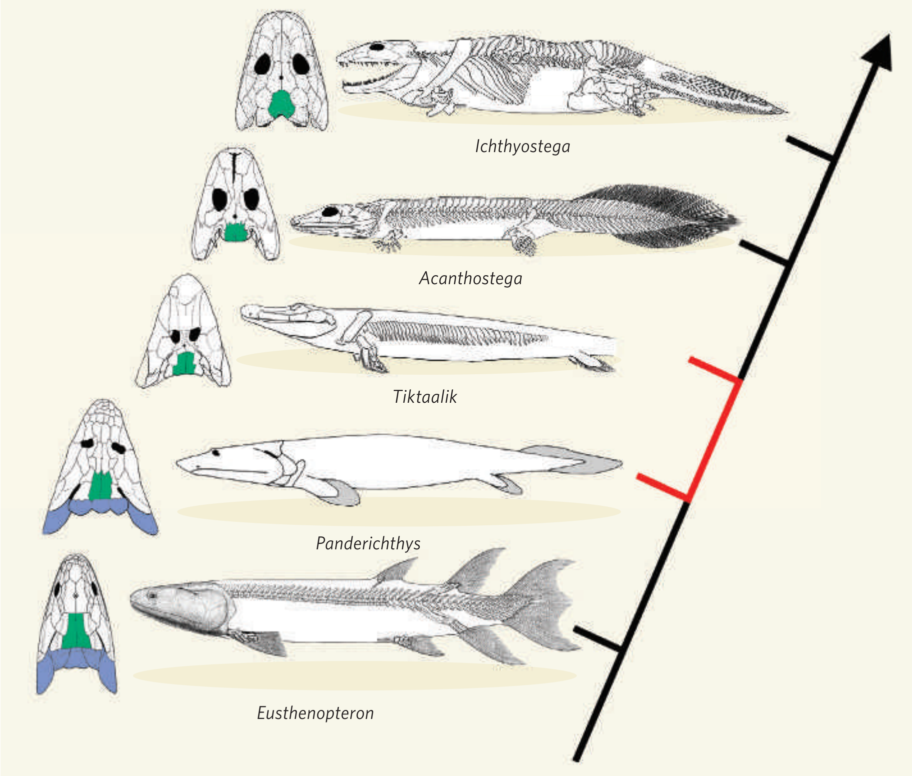

Figure 1 | *Tiktaalik* in context. The lineage leading to modern tetrapods includes several fossil animals that form a morphological bridge between fishes and tetrapods. Five of the most completely known are the osteolepiform *Eusthenopteron*[16]; the transitional forms *Panderichthys*[17] and *Tiktaalik*[1]; and the primitive tetrapods *Acanthostega* and *Ichthyostega*. The vertebral column of *Panderichthys* is poorly known and not shown. The skull roofs (left) show the loss of the gill cover (blue), reduction in size of the postparietal bones (green) and gradual reshaping of the skull. The transitional zone (red) bounded by *Panderichthys* and *Tiktaalik* can now be characterized in detail. These drawings are not to scale, but all animals are between 75 cm and 1.5 m in length. They are all Middle–Late Devonian in age, ranging from 385 million years (*Panderichthys*) to 365 million years (*Acanthostega*, *Ichthyostega*). The Devonian–Carboniferous boundary is dated to 359 million years ago[18].

Panderichthys lived about 385 million years ago at the end of the Middle Devonian; *Ichthyostega* and *Acanthostega* lived about 365 million years ago during the Late Devonian. However, the earliest fragmentary tetrapods from Scotland[9,10] and Latvia[9] date back to perhaps 376 million years ago, so the morphological gap between fish and tetrapod corresponds to a time gap of under 10 million years.

Into this gap drops *Tiktaalik*. The fossils are earliest Late Devonian in age, making them at most 2 million or 3 million years younger than *Panderichthys*. With its crocodile-shaped skull, and paired fins with fin rays but strong internal limb skeletons, *Tiktaalik* also resembles *Panderichthys* quite closely. The closest match,

EVOLUTION

It pays to laze

Hidden beneath small mounds in the Kalahari Desert in southern Africa, Damaraland mole-rats (*Cryptomys damarensis*, pictured) have developed a remarkable caste system. In the life cycle of these animals, which is spent entirely underground, a single 'queen' female mates with one or two unrelated males. The rest of the colony members generally invest their efforts in caring for successive litters of young, hunting for food and maintaining the colony's intricate network of tunnels.

These worker mole-rats are divided into two types: 'frequent' and 'infrequent' workers, the latter being evidently lazy types that may comprise as much as 40% of the community but do less than 5% of the work. Elsewhere in this issue, M. Scantlebury *et al.* describe how they have followed up circumstantial evidence for the reasons behind this division of labour, and show that in certain situations the layabouts spring into action (*Nature* **440,** 795–797; 2006).

Mole-rat workers are thought to postpone their own reproduction (sometimes indefinitely) because of the difficulties of setting up a new colony in the rock-hard soil. Extensive burrowing, and so the chance of meeting a mate from another colony, is restricted to brief periods, maybe once or twice a year, when heavy rains soften the soil.

Is this when infrequent workers pay their dues? To find out, Scantlebury and colleagues examined individuals they trapped at burrow entrances. By measuring the body fat, daily energy expenditure and resting metabolic rate of several individuals during a dry period and after rainfall, the authors show that the infrequent workers are fatter and expend far less energy than the other workers when it is dry. Following rainfall, however, they display bursts of effort not shown by the other colony members. Scantlebury *et al.* propose that, by conserving their energy during dry periods and then digging furiously after it has rained, the fat workers have a good chance of dispersing far enough to find a mate.

As the authors point out, funnelling extra resources into a dispersive caste may well be a sensible strategy for the colony as a whole. These apparent layabouts may spend most of their time reaping the benefits of colony life, such as food and protection, without pulling their weight. But they seem to give good returns when it comes to exploiting environmental conditions to ensure long-term survival of the colony's gene pool.

T. JACKSON/CERU/UNIV. PRETORIA

Lucy Odling-Smee

however, is not to *Panderichthys* but to another animal, *Elpistostege*, from the early Late Devonian of Canada. *Elpistostege* is known only from two partial skulls and a length of backbone, but it has long been recognized as a fish– tetrapod intermediate[11,12], probably closer to tetrapods than is *Panderichthys*. This impression is now confirmed: the authors[1,2] demonstrate convincingly that *Elpistostege* and *Tiktaalik* fall between *Panderichthys* and the earliest tetrapods on the phylogenetic tree.

So, if *Tiktaalik* is in effect a better-preserved version of *Elpistostege*, why is it important? First, it demonstrates the predictive capacity of palaeontology. The Nunavut field project had the express aim of finding an intermediate between *Panderichthys* and tetrapods, by searching in sediments from the most probable environment (rivers) and time (early Late Devonian). Second, *Tiktaalik* adds enormously to our understanding of the fish–tetrapod transition because of its position on the tree and the combination of characters it displays.

In some respects, *Tiktaalik* and *Panderichthys* are straightforward fishes: they have small pelvic fins[13], retain fin rays in their paired appendages and have well-developed gill arches, suggesting that both animals remained mostly aquatic. In other regards, *Tiktaalik* is more tetrapod-like than *Panderichthys*. The bony gill cover has disappeared, and the skull has a longer snout (Fig. 1). These changes probably relate to breathing and feeding, which are linked in fishes because the movements used for gill ventilation can also be used to suck food into the mouth. A longer snout suggests a shift from sucking towards snapping up prey, whereas the loss of the gill cover bones (which turned the gill cover into a soft flap) probably correlates with reduced water flow through the gill chamber. The ribs also seem to be larger in *Tiktaalik*, which may mean it was better able to support its body out of water[1]. The only real peculiarity of *Tiktaalik* is its poorly ossified vertebral column that seems to contain an unusually large number of vertebrae.

These character distributions paint an intriguing picture. *Tiktaalik* is clearly a transitional form, more tetrapod-like than *Panderichthys* in its breathing and feeding apparatus, but with similar locomotory adaptations. Crucially, because *Tiktaalik* occupies a position closer to tetrapods on the tree than does *Panderichthys*, their shared characters can be inferred to be attributes of the segment of the tree between the branches that carry the two animals (Fig. 1, red). *Panderichthys* showed us a morphology that could be interpreted as directly intermediate between osteolepiform and tetrapod. But only the similar yet 'upgraded' morphology in *Tiktaalik* demonstrates that this interpretation is correct: this really is what our ancestors looked like when they began to leave the water.

Two aspects of *Tiktaalik*'s anatomy relate to the origin of new structures in tetrapods: the ears and limbs. The tetrapod middle ear has arisen as a modification of the fish spiracle (a small gill slit) and hyomandibula (a bone supporting the gill cover). *Panderichthys* possesses a widened spiracle, interpreted as the intake for air or water, and a shortened hyomandibula[14]. *Tiktaalik* shows an almost identical condition, but with an even wider spiracle, indicating that this morphology too is genuinely transitional.

The pectoral fin skeleton of *Tiktaalik* is notable not only because of its transitional nature, but also because its excellent preservation has allowed the individual bones to be freed of the rock and manipulated to estimate ranges of movement[2]. It turns out that the distal part of the skeleton is adapted for flexing gently upwards — just as it would if the fin were being used to prop the animal up. Although these small distal bones bear some resemblance to tetrapod digits in terms of their function and range of movement, they are still very much components of a fin. There remains a large morphological gap between them and digits as seen in, for example, *Acanthostega*: if the digits evolved from these distal bones, the process must have involved considerable developmental repatterning. The implication is that function changed in advance of morphology.

The body form represented by *Tiktaalik* and *Panderichthys* was evidently an actual step on the way from water to land. Just over 380 million years ago, it seems, our remote ancestors were large, flattish, predatory fishes, with crocodile-like heads and strong limb-like pectoral fins that enabled them to haul themselves out of the water. Further information will emerge from the full description of the fossils, and from detailed comparisons with Devonian tetrapods such as the very primitive *Ventastega*[15].

Of course, there are still major gaps in the fossil record. In particular we have almost no information about the step between *Tiktaalik* and the earliest tetrapods, when the anatomy underwent the most drastic changes, or about what happened in the following Early Carboniferous period, after the end of the Devonian, when tetrapods became fully terrestrial. But there are still large areas of unexplored Late Devonian and Early Carboniferous deposits in the world — the discovery of *Tiktaalik* gives hope of equally ground-breaking finds to come. ■

Per Erik Ahlberg is in the Department of
Physiology and Developmental Biology,
Uppsala University, Norbyvägen 18A,
752 36 Uppsala, Sweden.
e-mail: per.ahlberg@ebc.uu.se
Jennifer A. Clack is in the Department of Zoology,
University of Cambridge, Downing Street,
Cambridge CB2 3EJ, UK.
e-mail: jac18@hermes.cam.ac.uk

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SEMICONDUCTORS

Spray-on silicon

Lisa Rosenberg

Reports of the death of silicon electronics may well have been exaggerated. A technique that allows the deposition of silicon films from solution could harbinger the era of the inkjet-printed circuit.

On page 783 of this issue, Shimoda *et al.*[1] set forth a radical way of incorporating silicon into that most basic of electronic components, the transistor. Their technique uses a novel liquid precursor of solid silicon to allow the 'printing' of semiconductor films via familiar inkjet technology. It could thus permit unprecedented control over the size and placement of semiconducting silicon in future generations of high-performance electronic equipment.

When its structure is delicately disrupted, ultra-pure silicon is the quintessential semiconductor. As such, it controls the electrical impulses that in turn control the computers and other electronic devices that many of us take for granted. Semiconducting silicon is obtained from highly purified natural silicon — which occurs in the form of silica (silicon dioxide) in quartzite rock and sands — by adding tiny amounts of appropriate impurities (the process known as doping), or through specialized crystallization methods. Whichever way is chosen, enormous effort goes into extracting, refining, shaping and processing silicon to make it technologically useful.

Recently, the need for semiconducting transistors to help transform electricity into coloured light for displays and screens has begun to present a challenge for existing silicon manufacturing technologies. In particular, the demand for screens with ever-increasing pixel resolution that are thinner, brighter, wider and lighter — or even flexible — has stretched the solid-state patterning techniques used to produce silicon circuitry to the limit. It has also fuelled intense research into alternative, more processable semiconducting materials, including organic molecules and polymers[2–4].

Electronic devices based on solid layers of silicon still provide the benchmark for semiconductor performance, however. Conventional techniques for their manufacture involve, for instance, heating ultra-pure silicon in a vacuum to create a mist of free silicon atoms that condenses onto a supporting surface, preferably an inexpensive plastic. But multiple refining and deposition steps are still just the start of the delicate and convoluted manufacturing process that leads to a finished transistor (see Fig. 4d on page 785). Once deposited, the solid film must be sliced or etched to produce circuit elements, and then attached to the rest of the electronic components. All this must be done without compromising silicon's semiconducting properties. That places severe limits on semiconductor thickness, patterning and connectivity, and therefore on advances in electronics design.

Controlling a liquid is generally easier than sculpting a solid. Sophisticated, high-resolution printing technologies already exist that could be used to introduce very thin layers of liquid semiconductor in complex patterns over a variety of surfaces. The advantage would be particularly great for the mass production both of very small devices and of displays that cover huge areas, as their transistor components must typically be no more than about a thousandth of a millimetre thick. In both such applications, it is difficult to consistently reproduce transistor size, thickness and pattern using solid-state techniques.

But how can silicon be produced in liquid form? Molten silicon is out of the question here: with its melting temperature of 1,414 °C, it would destroy the other components of the device, as well as the printing equipment. Shimoda and colleagues' solution[1] is to delve into the realm of decades-old synthetic chemistry. They focus on a binary compound of silicon and hydrogen, Si_5H_{10} or cyclopentasilane, that is liquid at room temperature. When baked at a temperature of 300 °C or higher, this compound loses hydrogen gas, leaving a residue of pure, elemental silicon. It is thus, apparently, an ideal liquid precursor for silicon thin films.

But there is a problem. Cyclopentasilane tends to boil off during baking, making it difficult to control the amount of silicon that is actually left behind. The authors circumvent this obstacle using a technique called 'ring-opening' polymerization chemistry. They shine light of ultraviolet wavelength on to the five-membered silicon rings in the cyclopentasilane liquid, causing them to open and join end-to-end. The result is long, non-volatile chains, known as polysilanes, that have the characteristics of viscous oils or even solids. If this polymerization is halted part-way through, the polysilanes already produced dissolve in the remaining unconverted cyclopentasilane, resulting in a solution from which an elemental silicon residue can form. The amorphous network of silicon atoms, a-Si, obtained does not have the optimum three-dimensional structure for semiconducting behaviour, and so, as a final step, high-intensity ultraviolet light is applied to rearrange it into a more ordered, polycrystalline form (poly-Si).

Shimoda and colleagues are thus the first to produce relatively high-performance silicon films by processing from solution. They first prepared films by simple spin coating — essentially, spraying a thin layer of solution onto a quartz surface before baking — and found that the properties of the films were comparable to those of high-quality poly-Si produced by conventional techniques. Although this performance was lower for films deposited using inkjet-printing technology, it was still much higher than is typically achieved for solution-processed films based on alternative, organic materials[4].

This method dispenses with some high-temperature refining of metallurgical silicon extracted from silica and replaces it with chemical synthesis and milder distillations. Admittedly, this liquid polysilane precursor is highly sensitive to contamination by oxygen both during and after its preparation. Such contamination can drastically diminish the electronic performance of the eventual film, and dictates that air and water must be rigorously excluded at all stages of the process. These precautions are, however, no different from those taken for traditional routes to silicon thin films.

But it is the potential for taking advantage of highly controlled printing techniques in the