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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.

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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. ■