Coelacanths

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What are coelacanths? Coelacanths are a curious group of fish, represented by only two extant species: the African coelacanth (*Latimeria chalumnae*) and the Indonesian coelacanth (*Latimeria menadoensis*). These large, lobe-finned fish live in and around deep-water caves off the coasts of southeastern Africa and Indonesia. Around two meters in length, the coelacanth looks like no other fish alive. In addition to its fleshy limb-like fins with their skeletal supporting structures, it has a unique bicaudal tail and a hinge on the top of its skull which allows it to expand its gape. When hunting they orient themselves vertically, allowing an electrosensitive rostral organ in their snout to assist in the detection of prey. Coelacanths are ovoviviparous, with their eggs developing and hatching in the oviduct before birth.

Only two species? So, why the hype? A number of factors contributed to the fame of what might seem like a rather obscure fish. For one, this fish had been playing an epic 70 million year game of hide-and-seek. Coelacanths were a more abundant and diverse group prior to the extinction event at the end of the cretaceous period (yes, the one that killed the dinosaurs); coelacanth fossils are well represented worldwide, yet conspicuously absent in any rocks after that time. When a living coelacanth specimen was caught off the coast of South Africa and identified in 1938 by Marjorie Courtenay-Latimer and J.L.B. Smith, it was as surprising and unexpected as finding a T-rex, albeit perhaps slightly less intimidating. However, it was more than just the surprise factor that made the discovery of the coelacanth perhaps the most notable zoological find of the last century. The existence of living coelacanths offered the possibility of significant insights into the early origins of the tetrapods (Figure 1), the group comprising amphibians, reptiles, birds and mammals, which is to say, ultimately, insights into our own evolutionary origins.

How so? Coelacanths emerged during a critical stage of vertebrate evolution, and are phylogenetically placed in the sarcopterygian lineage. Sarcopterygians, also known as lobe-finned vertebrates, comprise coelacanths, lungfish and tetrapods. The coelacanth lineage diverged from the tetrapods roughly 400 million years ago, making them a key resource for comparative genomics. Lungfish are located at an equally propitious phylogenetic position as coelacanths but have intractably large genomes, effectively ruling them out as candidates for whole genome sequencing. This particular window of evolutionary time is especially notable because a large number of key tetrapod innovations arose during that period.

I hear the coelacanth genome has now been sequenced... Yes, the coelacanth genome makes it possible to identify, with greatly increased resolution, genomic changes that may underlie the various adaptations that accompanied the transition from life in water to a life on land. For example, we can now distinguish between genomic gains or losses that were specific to the tetrapods and those that were shared with the entire sarcopterygian lineage.

So, was a coelacanth relative the first fish to crawl out of the water? The idea of the first fish to crawl onto the land is one that captures people's imaginations. Identification of the closest living relative of the tetrapod ancestor has long vexed evolutionary biologists. The lobe-finned fishes, of which the coelacanth is a member, with their distinctive fins supported by limb-like bony arrangements were proposed early on, and the discussion moved on to establishing which lineage was the sister group to the tetrapods. The discovery of extant coelacanths made it possible to use molecular phylogenetic analysis in addition to morphological data. A number of studies tended to support the lungfish as our closest living relative, but prior to the publication of the coelacanth genome, no one had been able to rule out the possibility that both lungfish and the coelacanth were equally related to the tetrapods. We now know that the lungfish is definitively the closest living relative of the tetrapods (Figure 1).

How do you make a fish into a land animal? The rise of terrestrial vertebrates is a fascinating success story of evolution. The obstacles for an invasion of the land by fish, exquisitely adapted for life in the water as they are, stretch the imagination. A body previously supported by the water column must now be able to support itself in air, necessitating limbs with strong skeletal elements rather than the delicate fin rays of bony fish; gills that efficiently extracted oxygen dissolved in water must be replaced with lungs for extracting oxygen from the air; and as water becomes a precious commodity that must be conserved, more efficient ways to excrete waste products that don't rely on an unlimited water supply need to be found. Even the senses must be significantly overhauled to match the unique demands of the terrestrial environment.

Don't the coelacanth's fins look almost like limbs already? Yes, sort of. But as with all lobe-finned fishes, they don't have the proper digit field (autopod) and they possess fin rays, or dermal bone, at their distal ends; an arrangement that is good for swimming but not walking on land. Rather, the coelacanth's fins might be thought of as containing the rudiments of the autopod structure. Loss of the fin rays occurred in this evolutionary transition and an inkling of how this could have taken place can still be found by comparing the genomes of the coelacanth and other fishes with those of tetrapods. Genetic antecedents for building the autopod proper have been found in the coelacanth genome in the form of regulatory regions (enhancer elements). In particular, the HOX-D cluster of genes plays a key role in patterning digits in the tetrapod limb. It was possible to find regulatory regions upstream of the HOX-D cluster that were shared between tetrapods and coelacanths, but which could not be found in teleost fish. When such a coelacanth regulatory sequence was placed in a transgenic mouse, it was shown to drive reporter expression in an autopod-specific pattern. This strongly suggests that the developmental program driving limb patterning and formation in modern tetrapods was indeed co-opted from a more ancient sarcopterygian developmental program.

Is the coelacanth a 'living fossil'? There has been some push-back concerning the oft-used phrase, living fossil, with regard to the coelacanth.

The term was coined by Charles Darwin, and is operationally used to indicate that a species is a surviving representative of an ancient lineage that still retains some key features shared with archaic fossils. Typically such a lineage will have survived one or more mass extinctions. Examples of living fossils often cited include the sharks, ginkgo trees, metasequoia, lampshell brachiopods, horseshoe crabs, and as defined here surely the coelacanth. However, a common misconception is that the phrase implies that evolution has not acted on the organism over these long timescales, something that is clearly shown not to be true for coelacanths based on gross differences in the skeletal morphology of fossilized specimens, especially of forms prior to the Mesozoic. While it is difficult to measure the rate of morphological evolution of extinct coelacanths, analyses of the coelacanth's protein coding genes have shown, enigmatically, that its relative rate of molecular evolution is slower than that of other fishes and tetrapods. The implications of this relative rate difference remain speculative with respect to the morphological evolution of the coelacanth.

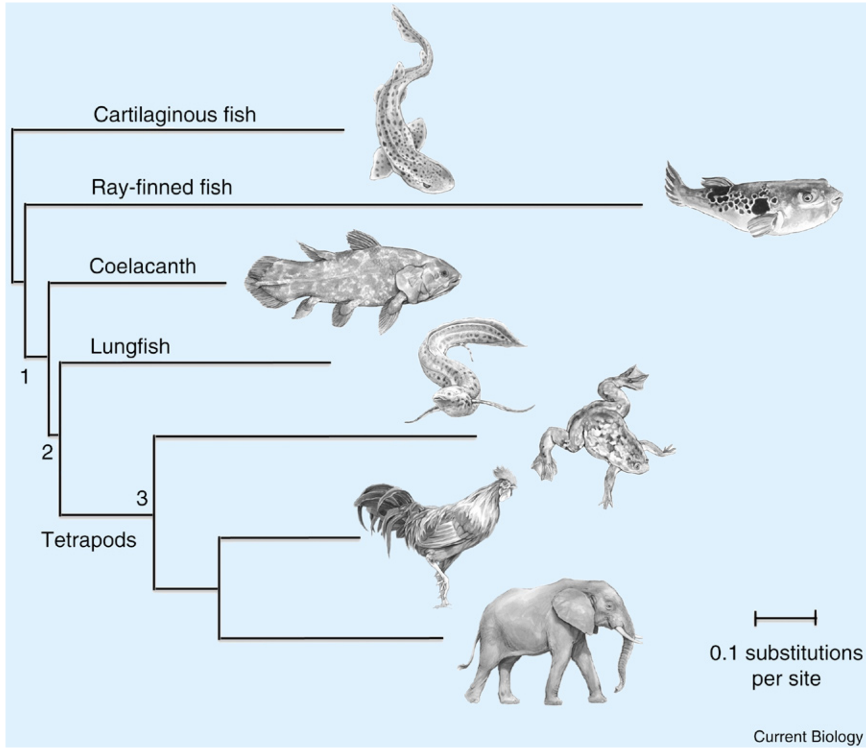

Figure 1. Phylogenetic tree showing major vertebrate lineages.
The tree is based on recent phylogenomic analyses, where branch lengths indicate evolutionary distances. (1) The Sarcopterygii (*sensu stricto*) includes the coelacanth, lungfish and Tetrapoda. The coelacanth and lungfish occupy key positions, bridging the gap between the ray-finned fish and the tetrapods. Their more substantial internal skeleton, especially with respect to elements of the fins, was an important preadaptation utilized by early tetrapods. (2) Lungfish + Tetrapoda. The development of a specialized lung and associated respiratory physiologies allowed lungfish, and presumably early tetrapods, to extract oxygen from the air in habitats that periodically dried up. (3) Tetrapoda. Tetrapods completed the transition to a terrestrial mode of life by developing well supported limbs and stronger skeletons, modifying their sensory systems and becoming more efficient at conserving water. Drawings by Catherine Hamilton.

What does the future hold for the coelacanth? Many companion genome papers that report surveys of various aspects of coelacanth biology have been published or are soon to be published. The coelacanth genome will continue to play a key role in evolutionary developmental biology studies with respect to the origin of the tetrapods and their unique adaptations. Furthermore, sequence data from additional coelacanth specimens are starting to provide important insights into the genetic diversity in modern populations, insights that will be needed for future conservation efforts given its endangered status. Accurate estimates of coelacanth population sizes are still lacking, but evidence suggests they have extremely restricted ranges. Accidental captures by oilfish fishermen seem to be placing these endangered fish under increasing pressure. The Coelacanth Conservation Council and the South African Coelacanth Conservation and Genome Resource Programme were specifically launched to help research and tackle these urgent issues. Many intact specimens of coelacanths have been captured and preserved within the past few years from the eastern coast of Africa, enabling more in-depth anatomical investigations. And fossil coelacanths are continually being discovered, including a recent form from the Triassic that differs greatly from the modern day *Latimeria* by virtue of its fork-tailed morphology. We have lots to learn about this iconic species.

Where can I find out more?

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