



THE BIOLOGY OF CHORDATES – Guide

Written and photographed by
David Denning and Bruce Russell
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(THUMBNAIL IMAGES IN THIS GUIDE ARE FROM THE VIDEO PROGRAM)

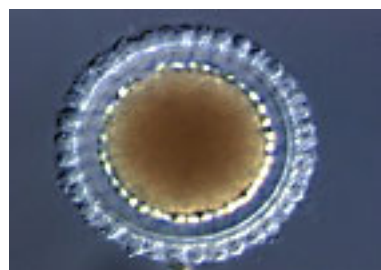
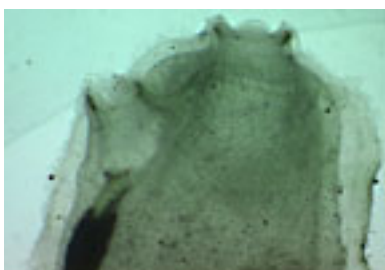


To many students, the phylum Chordata doesn't seem to make much sense. It contains such apparently disparate animals as tunicates (sea squirts), lancelets, fish and humans. This program explores the evolution, structure and classification of chordates with the main goal to clarify the unity of Phylum Chordata.

All chordates possess four characteristics that define the phylum, although in most species, these characteristics can only be seen during a relatively small portion of the life cycle (and this is often an embryonic or larval stage, when the animal is difficult to observe). These defining characteristics are: the notochord (dorsal stiffening rod), a hollow dorsal nerve cord; pharyngeal gills; and a post anal tail that includes the notochord and nerve cord.

Subphylum Urochordata

The most primitive chordates are the tunicates or sea squirts, and closely related groups such as the larvaceans (Appendicularians). In tunicates, the chordate characteristics can be observed only by examining the entire life cycle. The adult feeds using a 'pharyngeal basket', a type of pharyngeal gill formed into a mesh-like basket. Cilia on the gill draw water into the mouth, through the basket mesh and out the excurrent siphon. Tunicates have an unusual heart which pumps by 'wringing out'. It also reverses direction periodically. Tunicates are usually hermaphroditic, often casting eggs and sperm directly into the sea. After fertilization, the zygote develops into a 'tadpole larva'. This swimming larva shows the remaining three chordate characters - notochord, dorsal nerve cord and post-anal tail. Tunicates show three general life styles: solitary, social (where individuals formed by asexual budding remain connected in a communal group); and 'compound' where individuals that develop by budding cluster around a common excurrent siphon.



A related group, the larvaceans (Appendicularians), live throughout the life cycle as part of the oceanic plankton. These animals resemble tunicate tadpole larvae. Several hypotheses have been put forth regarding the origins of the Phylum Chordata. Recent finds in early Cambrian Chinese fossil beds, have discovered fossil tunicates at least 540 million years old.

A popular hypothesis regarding chordate evolution suggests that an ancestral tunicate gave rise to the higher chordate groups through an evolutionary process (paedomorphosis) whereby structural and swimming characteristics of the tunicate tadpole larva were retained into adulthood. Through this process, the tunicate ancestral line was thought to have evolved into the larger swimming chordates. Modern molecular genetics evidence supports a different hypothesis -- that ancestral larvaceans are the ancestors probably to both tunicates and higher chordates.

Subphylum Cephalochordata

By about 520 million years ago, a more advanced group of chordates were swimming the ancient seas, as shown by fossils found in Canada's Burgess Shales. The ancient swimming chordate, *Pikaia*, was a member of Subphylum Cephalochordata, the group containing modern animals known as lancelets. Lancelets, (also known by their former name, 'amphioxus'), such as *Branchiostoma* ('gill - mouth'), live in shallow tropical sandy-bottom environments. They stick their heads out of the sand and feed somewhat like a tunicate. Cilia-driven currents 'suck' water into the mouth and across the pharyngeal gills. The lancelet has a strong supportive notochord, and angled muscles along the body used for brief periods of swimming, such as when the animal is dislodged from the sand.

Subphylum Vertebrata

One of the next groups of chordates to evolve was the jawless fish (Agnatha). Modern representatives of this group are the hagfishes and lampreys. Hagfishes are generally deep-water marine scavengers. They burrow into the mud, sticking their heads out until they detect waterborne odors of food such as decaying flesh. Then they travel along the odor gradient until they find their food, whereupon they use a rasping tongue to burrow into the flesh. When threatened or attacked, hagfish have the ability to secrete a skin-derived compound that immediately swells into a large ball of slime. This leads to their common name - slime-eels.

Hagfish are clearly an evolutionary intermediate between lancelets and fish. Although better swimmers than lancelets, they lack the jaws, paired fins and gill covers of true fishes, having instead no jaws, a fin-like flap of skin along the body, and only simple pore openings for the gill chamber. The affinities between Cephalochordates and the hagfish/lamprey group are most striking when viewing the larva of the lamprey (ammocoetes larva). These larvae strongly resemble lancelets, with the addition of a pumping gill chamber. Although hagfish and lampreys do not have a segmented vertebral column, their notochord is somewhat calcified, and they are considered the most primitive members of the third major group of chordates - Subphylum Vertebrata.



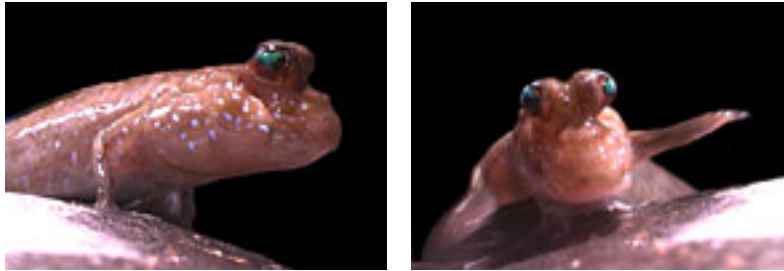
Over 400 million years ago the pace of chordate evolution picked up with the evolution of a variety of groups of fishes. The major ancestral fish line first acquired paired fins. One descendant line acquired a cartilaginous skeleton leading to one of the most successful and ancient group of fishes, the sharks and rays. Another ancestral line developed calcified bones and ray-fins stiffened with spines. Contrary to the old idea that swim bladders gave rise to lungs--new evidence indicates exactly the opposite -- 'primitive' lungs evolved first as a supplement to 'gill-breathing'. Thus, ancestral bony fish that gulped air gave rise to two lines of fishes.

In one line of bony fish, the 'ancestral lung' became the swim bladder. This group, the Class Osteichthys, is the most successful modern group of fishes, with over 22,000 species found in virtually every aquatic habitat.

Another major split in the bony fish line was much more successful in ancient seas than it is today. This 'coelacanth' group (Class Crossopterygia), developed bones at the base of its four stout ventral paired fins. These fish are also called the lobe-finned fishes.



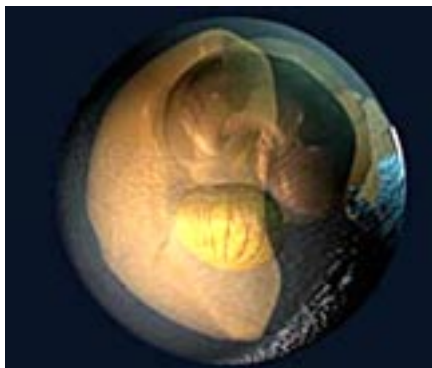
It is interesting to speculate how one line of ancient lobed-finned fishes evolved abilities to walk on land over time. This happened around 400 million years ago, when a combination of conditions allowed previously uninhabitable land to be colonized by plants, insects and other invertebrates. Key among these conditions was the diminishing intensity of ultraviolet light due to the developing ozone layer. Most likely, the invasion of land by chordates was linked, at least in part to the availability of prolific, essentially untapped, food resources (mostly insects).



To speculate on chordate land invasion is one thing, but it is even more fascinating to observe a model for this process. Although not a coelacanth, the mudskipper provides an excellent model for the movement of chordates from water to land over 400 million years ago. Mudskippers live in mangrove swamps where they feed both in water and on the land. They move about by 'walking' with their pectoral and pelvic fins.



The invasion of land by chordates has been detailed significantly by recent fossil finds. One line of lobe-finned fishes eventually developed good abilities to walk over land, and although these ancient land chordates began with 8 digits on their feet, their line eventually led to the 5-toed, 4-legged tetrapod ancestor to all modern land vertebrates. This ancestral line split into several groups. One group, the Amphibians retained more ancestral features including the dependence on water to complete their reproductive cycles.



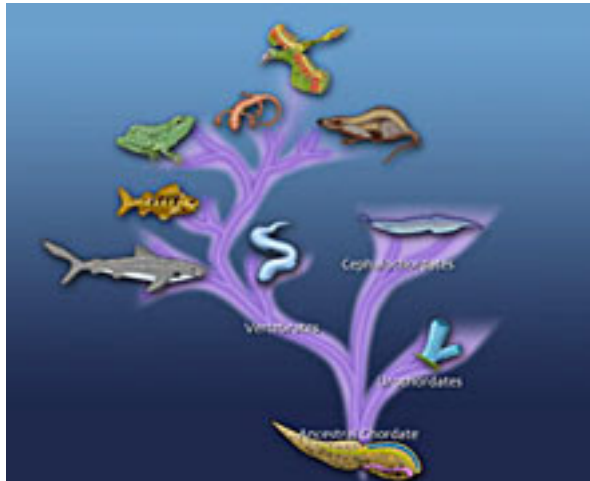
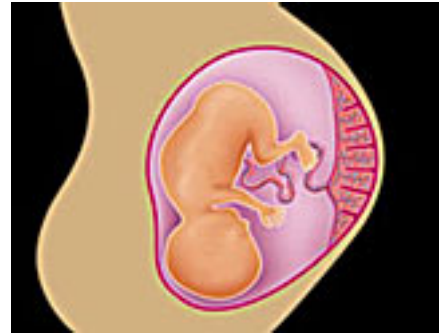
Other groups were liberated from the water through the development of a fluid-filled package to hold the developing embryo - the egg. Of these ancestral groups, one that developed scales led to modern reptiles and to the dinosaurs. Although the dinosaurs are thought to have finally died out with the Cretaceous extinction of 65 million years ago, evidence now clearly indicates that a group of dinosaurs developed feathers and give rise to survivors of the Cretaceous extinction -- the birds.

The earliest mammal-like reptiles also laid eggs. This ancestral group developed hair rather than scales, and eventually led to the mammals. The earliest mammals probably laid eggs in a pouch. This is the reproductive approach of the most primitive extant mammals, the Monotremes. The duck-billed platypus and the echidna are both restricted to the Australia region. The echidna egg is leathery. After it hatches, the developing larva remains in the pouch, feeding off a patch that secretes milk - a primitive mammary gland.



In another group, the Marsupials, young are born as worm-like larvae, after a short period of embryonic development in an egg inside the mother's reproductive system. The larva squirms into the mother's pouch and attaches itself to a mammary. Their use of the marsupial pouch (marsupium) continues even after they have grown to active juveniles.

A third group of mammals has been the most successful. In this group, the ancestral condition of development in the egg has been replaced by development in a womb. The mother nourishes the developing embryo, and removes its wastes, through an exchange organ, the placenta. Placental mammals are born at a relatively advanced degree of maturity, and they are by far the most diverse and successful group of mammals. Over evolutionary time, members of the group have also returned to the sea.



As diverse as they may first seem, the chordates represent a unified monophyletic line of evolution on the animal portion of the tree of life. Living chordates, such as sea squirts, larvaceans, lancelets, hagfish, sharks, bony fish, salamanders, turtles, snakes, birds, and mammals all reflect descent from a common ancestor with the four chordate characteristics: notochord, dorsal nerve cord, post anal tail and pharyngeal gill. As but one tiny branch on this section of the tree of life, we humans can appreciate the remarkable sequence of evolutionary changes that produced the current diversity of chordates from our simple ancestor of over 540 million years ago.

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