j16 Fish with lungs < common in the Devonian >

> That Castel Etzwane should be Anome is strange enough; that he should not be is too much to believe. —Jack Vance *The Brave Free Men*.[1]

Lungs in a fish would be a preadaptation to life on the land. However, one might wonder what use lungs would be to a fish as a fish.

Spore-shedding land plants are riparian (evolved to live in wetlands along water courses) and do not clothe interfleuves. Hillslopes bare of vegetation tend to shed rain, and dry earth inhibits infiltration. Here, "flashy" streams, poorly fed if at all by springs, flow like gutters briefly after rain, Along their courses, pools may either hold water for a while and then dry out, or become stagnant with rotting vegetation. Such an environment existed in the ORS paleocontinent during the Devonian. Not surprisingly, common in freshwater Devonian fish, as well as gills, are lungs. For example, *Cheirolepis*, a ray-finned fish (memorable for Hugh Miller's illustrations of it,[2] although at first take, because of the fossil's missing tail, he thought "his fish" was a turtle) had functioning lungs connected to open nostrils. This condition does not exist in ray-finned fishes (teleosts) today, although any fish will attempt to gulp air when in oxygen deprived water.

The lungs of teleosts have evolved to function as swimbladders. To maintain neutral buoyancy the gas inflated swimbladder is pumped in a physiologically controlled way by oxygen given out or taken in by hemoglobins of circulating blood in surrounding arteries and veins[3] (as, about the ovaries, allowing some to be viviparous—not egg-laying but birthing living young).

One can speculate that teleosts diversified first in freshwater. Some then took to living in the open ocean where water does not become stagnant and the need for lungs is not urgent. Ray-finned fishes without lungs have moved to re-occupy the freshwater niche.

Lungs in fish were a preadaptation for the land but were coopted as a swimbladders when the fish, still living as fish, no longer required a functioning lung.

Crossopterygians The class Choanichthyes includes an order of lobe-finned fishes that had functioning lungs and nostrils in the Devonian. These fossil lobe-finned fishes are the type fish for the order Crossopterygii. Long thought to be extinct, the order has been found to be represented today by the coelacanth (means: "hollow spine," and in life this is oil filled) *Latimeria*, a highly evolved marine genus. This deepwater marine coelacanth does not have functioning lungs and its nostrils are closed. Each female has only one functional ovary. It produces the largest (about 4 inches in diameter) fish egg known. The eggs hatch inside the female. As many as thirty 1.5 foot long pups are carried until they are born alive. The male coelacanth has no obvious intromittent organ, so how sexual mating occurs is unknown. Coelacanths have a slow growth rate. From one, the analysis of an otolith (an ear stone) suggests that a coelacanth may have normal life-span of some sixty years.[4]

Coelacanths have a lethargic lifestyle and slow metabolism. By day, they stay in deep-water caves. At night, they range into deeper waters and, while drifting with the current, prey on other fish that they detect using a rostral organ (in which electrosensitive cells are concentrated) locate in their head. Their sight, in dim light, is aided by a tapetum (a crystal reflective layer behind the retina). The coelacanth sucks in its prey with a gulp facilitated by an intercranial joint, that enables the upper jaw to flex upward about 10 degrees when the lower jaw drops about 30 degrees.

The living Comoros (Indian Ocean), and Sulawesi (Pacific Ocean) coelacanth species [5] are very similar to the most recent of the fossil coelacanths from 75 million years ago. Adaptation to deep marine living, and small populations, can account for their poor fossil record. "Tracing the origins and distributions of these [and extinct coelacanth species] is a very exciting endeavor" enthuses **Meemann Chang**.[6] Coelacanth diversity was greatest, at 16 species, soon after the end-Permian mass extinctions 251 million years ago. The earliest coelacanths lived 305 million years ago (Upper Carboniferous) in the brackish water of a river delta in what is now northeastern Latvia.[7]

Dipnoans Fish today with functioning lungs are the "type fish" for an order, the Dipnoi (lungfish), of the class Choanichthyes (nostril-bearing fishes). Living lungfish are rare and are found in areas where streams are decided flashy and where surface pools dry completely during times of drought. None occur in the open ocean. There are three genera: *Lepidosiren* in South America, *Protopteris* in Africa, and the large (to 10 kg, 1.8 m in length) *Neoceratodus* in Australia. These are not known in the fossil record although *Neoceratodus* has been called a *living fossil* as these closely compare to Triassic (deltaic) lungfish of the genus *Ceratodus* ("horn tooth," Agassiz, 1838).

The name Dipnoi does not refer to lungs (which, during the Devonian, was a common feature of freshwater fishes, regardless of type) but to paired fins in which bones are attached to the body by a single shaft (not radially arranged, as in ray-finned fishes). Comparative anatomy indicates that amphibians diverged from ancient lungfish (*see* Topic *j17*).[8] ❑

Figure j17.1 Changes in the structure of the skull roof (*after* R. L. Carroll)[1] in the transition to an amphibian *Acanthostega* (latest Devonian) via an 'intermediate' form *Panderichthys* (early Upper Devonian) from a typical lobe-finned fish *Eusthenopteron* (late Middle Devonian).

In Devonian amphibians, the frontal bones (black areas) are paired and enlarged in place of the single frontal in the lobe-finned fish. Lost in the Early Carboniferous, but retained in Upper Devonian amphibians, are bones as those identified (dark gray areas) and tagged (pop and anocl). The mosaic pattern of changes in the skull-roof, limbs and braincase are charted against the geologic time scale (millions of years ago). Completed by the end of the Upper Devonian was a progressive consolidation of skull roof bones (in the area delimited by the dark-black line) that in the primitive condition had considerable mobility. The bones in the pale-gray area are not retained.