j17 Did labyrinthodonts evolve from a coelacanth or a lungfish? < back bones, skull bones, limb bones, teeth >

It is always difficult to appreciate a cultural crisis in retrospect. One of the defining characteristics of such a crisis is that it retrospectively vanishes from view. This is the true measure of the "paradigm shift" that has occurred. —William Byers .[2]

Four legged amphibians with forward pointing five-toed feet moved about the swampy Early Carboniferous forest floors. But, except for one such amphibian, *Pederpes* described by **Jennifer A. (Jenny) Clack** (1937-) in 2002,[3] a derth of related fossils for 20-million years before (dubbed by Michael Coates and Clack the "Romer Gap" for Alfred Sherwood Romer's long fruitless search therein)[4] separates the Carboniferous forms from the tetrapod (four legged) fossils that in 1932 Gunnar Säve-Söderberg found in latest Upper Devonian (Famennian) strata, Greenland.[5] He gave these the genus name of *Ichthyostega,* meaning "fish plate."[6] A skull fragment of the first that he examined had that shape. But the bones of the body, which he saw later, had an amphibian arrangement. The Devonian amphibians had sideways pointing feet with more than five toes on each.

The fishy heritage of the *Ichthyostega* is their broad flat, coelacanth-like head and teeth, their fishlike spine, and a small fin on the top of their tail. Not fishlike are their four limbs that terminate in digits (toes, fingers). To support locomotion out-of-water, their forelimbs were attached to sturdy shoulders and they had sturdy rib cages that held up their internal organs.[7] Their hindlimbs were not so well articulated as were their forelimbs. *Ichthyostega* were primarily aquatic and movement over land would have been awkward (seal-like, according to Coates).[8] *Ichthyostega* fossils are 360 million years old. In the same area in Greenland, in rocks of the same age, Erik Jarvik in 1952 found tetrapods more primitive than *Ichthyostega*. These he named *Acanthostega* ("spine plate").[9] These have now been fully described by Clack.[10]

The more primitive tetrapod features of *Acanthostega* are: the radius is about a third longer than the ulna (these two bones are of equal length in *Ichthyostega* to mammals); the radius (thick at the elbow but flat at the wrist) is poorly designed for support; and, attached to an insubstantial (for walking) wrist, are eight (!), multi-jointed, fingers. Most fishlike is the structure of its powerful flexible tail with large fins running along the top *and* bottom of it. In Ireland, a contemporary of *Acanthostega* left 150 footprints. In Pennsylvania, a tetrapod that dates 5 million years older than *Ichthyostega* and *Acanthostega* is represented by a robust shoulder bone.[11]

The transition between fish and amphibians (tetrapods) appear in the fossil record some 365 million years ago in Famennian strata.[12] Intermediate forms between their fish ancestor, as evolutionary theory would have, do exist: Per Ahlberg, Jennifer Clack, and Ervns Lukševi, describe a lobe-finned fish *Panderichthys* close to the ancestry of amphibians.[13] In *Panderichthys*, different from other lobe-finned fishes, and the persisting coelacanth *Latimeria,* both dorsal and anal fins are no more, and its tail is slender. In it, more like the first amphibians, its skull roof has interlocking sutures between the bones of the snout and at the back of the skull table, frontal bones large and paired, and the eye sockets are positioned back and upwards from the jaw line (***Figure j17.1***). In it, not evolved are its paired fins that show no characteristics of land vertebrates and its braincase that shows none of the derived characters of Upper Devonian tetrapods.

Crossopterygians diversified in the Middle Devonian having debuted in the Lower Devonian. A marine branch (from which coelacanths derived in the Upper Carboniferous), the Actinistia, have closed nostrils and so are ruled out as ancestral to land vertebrates. A freshwater branch, of which Devonian *Osteolepis* is typical, has lobes with bones that can be compared easily to the principal bones in the leg of the first amphibian and teeth that have the cone shape and labyrinthine infolding of dentine (hydroxyfluorapatite, $Ca_{10}(PO_4)_6(OH)F$) and enamel (fluorapatite, $Ca_{10}(PO_4)_6F_2$) that are true of the first amphibian (in our teeth, enamel covers over the dentine and acids that release calcium and phosphate ions from it are, in healthy conditions, replaced by these ions that back diffuse though the enamel from saliva,[14] and, for the ever curious, laminin is the adhesion protein that binds a tooth to surrounding epithelial tissue).[15] No other fish groups of the day, or before, had such features.

After the Devonian Period, the choanichthyes (lobe-finned fishes and lungfishes) declined almost to extinction but during the Late Devonian they had given rise to terrestrial vertebrates in a scant 14 million years by changes in the limbs and skull roof in forms transitional via amphibians from choanichthyes (Sarcopterygii is the clade inclusive of tetrapods and choanichthyes). Structure, physiology and behavior needful of change from that of a fish to support locomotion and respiration of a land animal was not all at once in a single species. A mosaic pattern of derived (newly evolved) characters evolved at different rates from some, and leaving alone other, primitive (old) characters in the species leading to amphibians from choanichthyes.[16] Clack in *Gaining Ground*, 2002, persuades that *Acanthostega* evolved their legs as an aquatic adaptation. This agrees with a like speculation put forward by James L. Edwards in the 1970s, that limbs were a preadaptation to living out of water which some fish developed for fish use. He sited living antennariid anglerfish that have evolved pectoral fins that look like and function as legs, even to bearing toelike tips. With their “legs and toes” anglerfish are able to move slowly over coral reefs and grip to rough surfaces while slyly attracting prey with their bioluminescent-bacteria filled lure dangled in front of formidable fangs.[17]

The labyrinthodonts are typed as amphibians. But apart from their legs and toes they look like fish. In that sense they are true missing links. The question is, which line of fish could they have evolved from? Many fish of the day that lived in freshwater had functioning lungs in addition to gills. Comparative anatomists came to reject Huxley’s 1861 conjecture for lungfishes in favor of Cope’s 1892 claim for coelacanths.[18] But genetic data now finds tetrapods and lungfishes to have had a common ancestor different from coelacanths.[19]

Molecular evidence (***Figure j17.2***) indicates that foot digits could be a novel feature of tetrapods not present in lobe-finned fishes. This was first announced by Nils Fritiof Holmgren in 1933 who could find no homologies between the buds of tetrapod limbs and radials of fish fins during their growth.[20] A found, “iconic” missing link between tetrapods and primitive fishes is *Tiktaalik* (“the fish seen in the shallows”) *roseae*.[21] Diagnostic are front lobefins (hind parts not yet found) and the absence of a series of bones to cover its gill openings. The latter is its crucial difference from a fish. “It started to rely on air breathing first, before it left the water.”[22] ❑

Figure j17.2 [23] **Primitive fish**

(a) Bud and the fin with radial fin bones that grow from it.

(b) Conventional interpretation of a tetrapod limb primitive fish derived with the digits (dark gray) evolved from fin bones on one side of the axis (metapterygial axis) and the tibia (pale gray) evolved from fin bones on the other side of the axis. Probable homologous parts are shaded dark gray.

(c) Alternative model for the development of the tetrapod limb proposed by Paolo Sordino in 1995, with neomorphic digits (black) which are not homologous to any primitive fish fin bones. The postulated neomorphic part of the tetrapod bud is shown in black.