

# Changing patterns of ontogeny from osteolepiform fish through Permian tetrapods as a guide to the early evolution of land vertebrates

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## Abstract

Larval stages of both recent and fossil amphibians provide an added dimension – ontogenetic change – that can be used for phylogenetic analysis. This is especially important in regard to the origin and early radiation of tetrapods. A continuous growth series in *Eusthenopteron* shows that a close sister taxon of tetrapods had direct development, without a recognizable larval stage. Gilled larvae of labyrinthodonts are known no earlier than the Upper Carboniferous, although they may have evolved by the Viséan. There is little evidence as to whether the larval stages of temnospondyls and seymouriamorphs evolved from a common ancestry, or by convergence. All lepospondyls show direct development, with even the smallest fossils resembling the adults in body proportions and in possessing highly ossified vertebral centra but lacking external gills. The ancestry of the three “lissamphibian” orders can all be traced to separate Paleozoic lineages, based on both adult anatomy and the pattern of larval development. Frogs and primitive salamanders share similarities with temnospondyls in having gilled larvae, and in the rate and sequence of vertebral development. The sequence of ossification of the skull bones of conservative extant salamanders is identical with that of the early larval stages of the branchiosaur *Apateon*. The adult cranial morphology of extant salamanders could have been achieved by truncation of ossification prior to the appearance of additional skull bones that developed at a later stage in Paleozoic temnospondyls. The ancestors of salamanders may have been facultatively neotenic, with long periods of larval development, but the antecedents of frogs may have gone through a period of direct development before evolving the highly specialized tadpole larvae. Caecilians resemble lepospondyls in the rapidity of vertebral ossification. Most caecilians lose the external gills soon after hatching, which might have been the case in lepospondyls.

## Devonian fish and amphibians

Amphibians have long been recognized as transitional forms – broadly intermediate between fish and fully terrestrial tetrapods, the amniotes. Many living amphibians, including the bulk of the more primitive species, depend on standing water for reproduction and go through an aquatic larval stage before metamorphosing into terrestrial adults. Many Paleozoic tetrapods that retain lateral line canals and/or aquatic larvae as well as primitive osteological characters shared with osteolepiform fish, are also referred to as amphibians although their affinities with modern amphibian orders remain contentious.

The biphasic life history of many amphibians reflects their origin from obligatorily aquatic forms, but also makes it possible for them to adapt to divergent habitats and ways of life. Fossils of larvae enable paleontologists to study an essentially embryonic stage in their life history, not available in other vertebrate taxa, that provides additional characters to aid in their classification.

Detailed studies of primitive, Upper Devonian tetrapods by CLACK (2000) and COATES (1996) provide extensive evidence that their closest known sister taxon among fish is the genus *Panderichthys*, but the best known of closely related fish is the tristicopterid *Eusthenopteron* (ANDREWS & WESTOLL 1970, JARVIK 1980). We not only have very detailed knowledge of the osteology of adults of *Eusthenopteron*, but

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