

Chapter 45

Evolutionary Aside 45.1--Evolution of Metamorphosis: Loss of Metamorphosis

Evolution occurs by loss as well as by gain. In chordates, the process of metamorphosis is common. Metamorphosis produces a complete remodeling of the body that often also includes changes in lifestyle. Within groups that show metamorphosis some lineages have lost this feature from their life cycle.

This has been studied in detail in the two main amphibian groups—anurans (frogs and toads) and salamanders—which have undergone some interesting variations in loss of metamorphosis. Metamorphosis in amphibians is driven by the hypothalamic-pituitary axis, with the final signaling molecule being thyroid hormone. In some anuran species “direct developers” have arisen that do not undergo metamorphosis. In at least some cases, metamorphosis actually occurs, but during embryogenesis. So what appears to be a loss is really a change in timing, or heterochrony.

In salamanders, the loss of metamorphosis is also accompanied by paedomorphism, defined as an adult species' ability to retain characteristics of the larvae of ancestral species. Paedomorphism has been studied in detail in the genus *Ambystoma*, which has given rise to multiple independent species that are paedomorphic. These are often called axolotls (*Ambystoma mexicanum*). You may have seen them in an aquarium: they are quite striking as they retain the external gills found in larvae (see figure 48.3). It is now clear that this feature is not due to a loss of the ability to undergo metamorphosis because several paedomorphic species of *Ambystoma* can be forced to undergo metamorphosis by treatment with thyroid hormone. So, the entire signaling pathway functions properly, as well as the morphogenetic machinery necessary for this transformation. Genetic analysis has shown that a single major-effect quantitative locus is involved, and it is not thyroid hormone receptor. A recent genomic analysis indicated that thyroid hormone treatment leads to up-regulation of a large number of brain transcripts.

In contrast to the *Ambystoma* species in which paedomorphism appears to be facultative, a few obligate paedomorphic salamanders species also occur. One of these, *Proteus anguinus* is a cave-dwelling species that also no longer has eyes. The other is *Necturus maculosus*, also called a “mudpuppy”. Neither of these species can respond to thyroid hormone treatment, although their thyroid gland appears normal.