

8.7 Neoteny

The term 'neoteny' or 'paedogenesis' is defined as the phenomenon of the retention of larval characters in the sexually mature state. In this process the metamorphosis of larva is retarded and the larval characters are retained beyond the normal period. This phenomenon has been observed in amphibians, both in Urodela and Anura. In urodela this phenomenon is of common occurrence and very conspicuous.

It has long been observed that the larvae of spotted salamander sometimes attain the size of 80 mm, while the majority metamorphose when they measure

40 mm. Larvae of *Triton* have been observed with fully developed sexual organs while still possessing functional gills. De Fillipi (1861) also reported occurrence of specimens which were sexually mature but still retained their gills. The discovery by Dumeril (1876) that the Mexican gill-breathing axolotl would metamorphose into lung-breathing terrestrial *Ambystoma* led to a series of observations and experiments by Marie Von Chauvin, Koelliker, Camerano (1896) and many others.

It was Kollmann (1882) who coined the term **neotenie** (neoteny) for the phenomenon of retention of larval characters beyond the normal period and attainment of sexual maturity. He classified neoteny into two types:

(1) Partial neoteny and

(2) Total neoteny

(1) Partial neoteny In this type there is simple retardation of metamorphosis beyond the normal period due to temporary changes in surrounding habitat or some sudden physiological disorder. Examples of partial neoteny are mostly found in anurans like the tadpoles of *Rana esculanta*, *Rana temporaria*, *Bufo vulgaris*, *Alytes obstetricans*, *Hyla arborea*, *Bombinator pachypus*, etc. In *Rana esculanta* most of the tadpoles remain in the larval stage for one or two years after which they metamorphose. It may be noted that in partial neoteny there is simple retardation of metamorphosis and the larvae do not attain sexual maturity.

(2) Total neoteny In this category the animals retain larval characters but become sexually mature. The larval characters retained are external gills, tail fin, ill-developed eyes, ill-developed dorsal fin and weak limbs. Animals exhibiting total neoteny normally do not metamorphose and remain as sexually mature larvae. In some cases, however, such larvae may undergo metamorphosis under favourable conditions as the axolotl larva. Total neoteny is observed in urodèles only. Examples of total neoteny, and intermediate stages between these two types are not uncommon.

Causes of Neoteny

In order to provide a satisfactory explanation of the causes of neoteny extensive studies have been carried out by many workers (Chavin, Koelliker, Camerano and others). While some workers attribute it to some external factors, others have suggested that some internal factors are responsible.

A. External factors According to some authorities the phenomenon of neoteny is the result of adaptation to the surroundings which make it advantageous for the animal to retain its larval features. Presence of abundant food and other favourable conditions in aquatic habitat may be the cause of this phenomenon (Gadow, 1903). Weismann tried to explain neoteny as cases of reversion. His assumption that all the amphibia were originally gill-breathing, aquatic and limbless animals and that the larva reflects the ancestral phylogenetic stages is not tenable. Others believe that the environmental

physical factors somehow or other retard metamorphosis. Lack of adequate food supply, rise in temperature and drying up of water bodies may be responsible for retardation of metamorphosis. In some experiments larvae were reared in water holes with steep walls, so that they could not change from aquatic to terrestrial life. This abnormally forced and prolonged use of the gills and tail stimulated further growth of these organs, while growth of limbs and related structures for land life remained retarded. Further, axolotls could be forced to metamorphose when they are slowly accustomed to terrestrial life. Experiments on the effect of temperature on metamorphosis (Huxley, 1978) showed that larvae exposed to temperature range above 5°C could metamorphose quickly, while those exposed to temperature range below 5°C failed to metamorphose. In both cases the level of thyroxine concentration was the same.

Researches on the role of external physical factors on metamorphosis do not provide any basis to conclude that they are the sole factors. It has been observed that typical neotenic and overgrown specimens frequently occur side by side with metamorphosed adult specimens. So, it is reasonable to say that some internal and physiological factors also come into play to control metamorphosis.

B. Internal factors It has been shown experimentally that a gilled axolotl may change into a form without gills. It has also been experimentally shown that injection of thyroid hormone (thyroxine) or implantation of iodine crystals beneath the skin induces metamorphosis. On the basis of recent researches it has been revealed that metamorphosis is mainly influenced by the level of thyroxine and also the degree of responsiveness of the larval tissues to the hormones. In this connection it has been established that prolactin plays an effective role in metamorphosis as its level is high in early stages prior to metamorphosis.

The genetic explanation advanced by Etkin and his co-workers (1968) is that formation of prolactin is increased by concerned genes, while the genes responsible for the synthesis of thyroxine are switched off by concerned operator genes in the early phase of larval life. Now the hypothalamus becomes sensitive to the low concentration of thyroxine and secretes thyrotropin-releasing factor (TRF) which stimulates the anterior lobe of pituitary to produce thyroid-stimulating hormone (TSH) which in turn increases the rate of thyroid secretion. The increase in the level of thyroxine brings about the initiation of metamorphosis. It should be noted that while the level of TSH increases, the level of prolactin drops off. Studies have shown that the thyroxine secreting alveoli of the thyroid gland in neotenic larvae remain in underdeveloped condition. It has been observed that if the rudiment of hypophysis in the late embryos is removed or destroyed they fail to metamorphose, but the metamorphosis can be again initiated if pieces of hypophysis from adult frogs are implanted. Even fully-developed thyroid

Animals sometimes fail to secrete adequate amount of thyroxine and under such circumstances transplantation of a few more thyroid glands induces metamorphosis.

Significance of Neoteny

Weissmann (1875) regarded neoteny as a case of atavism which is a phenomenon of reversal to ancestral characters. This implies that all amphibians were originally gill-breathing aquatic creatures which is not true. Internal gills of urodèles are now regarded to be secondary specialization serving as additional respiratory organs. Also, other larval features of neoténous larvae do not represent atavism, but are characters secondarily acquired for aquatic life.

Noble (1954) pointed out that retention of larval characters is in no way connected with the phylogeny of the amphibians. The great heterogeneity of pinnibranchiate forms which are all neoténous, proves this point. So, it may be concluded that the larval features are retained due to some intrinsic factors combined with environmental factors, and are advantageous for the neoténous individuals.

