Dr. O. P. Singh
Asst. Prof.
Dept. of Zoology
Y.D.PG College Lakhimpur Kheri

Neoteny and Paedogenesis

The two terms neoteny and paedogenesis coined by Kollwann. The term neoteny is derived from Latin neotenia means larval life is extended. Neoteny also called juvenilization, is the retention, by adults in a species, of traits previously seen only in juveniles.

or

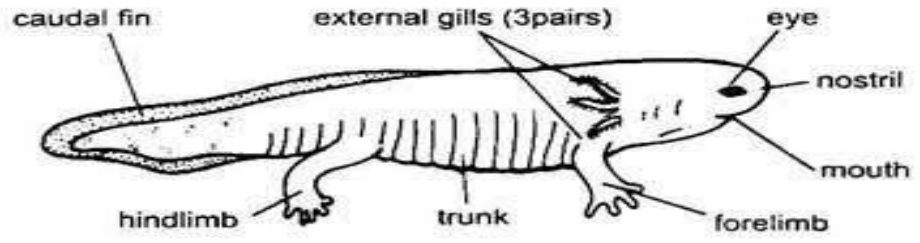
Retention of larval or embryonic features in the adult body. e.g. retention of embryonic cartilaginous skeleton in adult Chondrichthyes and the larval gills in some adult salamanders.

Paedogenesis is the act of reproduction by an organism that has not achieved physical maturity. In other words paedogenesis is the production of offspring by an organism in its larval or juvenile form and elimination of the adult phase of the life cycle. It is associated with progenesis, where sexual maturity is achieved in the juvenile form and further physical maturity is not achieved. Paedogenesis is found in gall fly, liver fluke, salamanders, insects in which the larval stage reproduces without achieving maturity. It occurs in the females of certain beetles, Strepsiptera, bagworms, scale insects and gall midges.

EXAMPLES OF NEOTENY (Amphibian Example)

Classical and most informative examples of neoteny and paedogenesis among Amphibia are furnished by Ambystoma. A. maxicanum lives in Lake Xochimilco in the highlands of Mexico and A. tigrinum in high altitudes of Colorado (North America). Normally they go through typically gilled aquatic larval stages, then metamorphose to become adult air breathing land forms. However under certain circumstances the larvae do not metamorphose, retain their gills and aquatic habitat but become sexually mature. *This sexually mature but morphologically immature larval stage with external gills is called an axolotl*.

Axolotl larva of Ambystoma tigrinum (tiger salamander) possesses three pairs of delicate bushy external gills, four pairs of gill-slits, a flat long tail with prominent tail-fin and a dorsal fin merged with tail-fin. The axolotl larvae possess the power of retention.



Axolotl larva of *Ambystoma tigrinum* (tiger salamander).

The axolotl larvae become sexually mature when they attain the age of 6 months only. The new-born larvae are hatched out within 15 days. The optimum temperature for the development of the eggs is 18-24°C. At the age of 6 months, the axolotls attain a length of 2.0-

2.5 cm and become sexually mature to start breeding. A sexually mature axolotl, at the age of 18–24 months, ranges in length from 15–45 centimetres possess features typical of salamander larvae, including external gills and a caudal fin. Three pairs of external gills are used for respiration, although buccal pumping (gulping air from the surface) may also be used in order to provide oxygen to their lungs.

Types of Neoteny: Kollmann (1882) classified neoteny into two categories, viz., Partial neoteny and Total neoteny. But it can be divided into three categories-

1- **Partial neoteny:** Partial neoteny involves the simple postponement of metamorphosis beyond the normal period due to temporary change in ecological condition or due to sudden physiological abnormality. Wintering of the tadpoles of Pelobates fuscus, Pelodytes punctatus, Alytes obstetricans, Hyla arborea, Bufo vulgaris, Bufo viridis, Rana temporaria, Rana esculenta, Bombinator pachypus and many others furnish the typical examples of partial neoteny. In Alytes the broods usually complete their development within autumn. But the larvae which hatched later in the months of July or August usually hibernate and retain their larval features up to the next autumn.
2- **Intermediate Neoteny:** Intermediate stages between partial and total neoteny are also recorded where the larvae become sexually functional and may metamorphose into adults with the advent of favourable conditions. The sexually mature axolotl larvae come under this category.
3- **Total Neoteny:** In this category the specimens become sexually mature at the larval stage but retain larval characters, like (i) external gills, (ii) tail-fin, (iii) ill-developed eyes, (iv) ill-developed fin on the back and (v) very weak limbs. Total neotenic animals are paedo-genic. Because paedogenesis involves the capability of reproduction at the larval stage. In this case of total neoteny the sexually functional larvae cease to metamorphosis. In extreme cases of total neoteny (e.g., Necturus, Proteus, etc.) the larvae attain sexual maturity and they remain in that stage without undergoing metamorphosis. Total neoteny is seen in many urodele (e.g., Necturus, Amphiuma, Triturus vulgaris, Triton cristatus, Triton waltli, Ambystoma, Triturus alpestris, Siren, Proteus, etc.).

Factors affecting neoteny

In the axolotl, metamorphic failure is caused by a lack of thyroid stimulating hormone(TSH), which is used to induce the thyroid to produce thyroxine in transforming salamanders. Axolotls can be induced to metamorphose by an injection of iodine (used in the production of thyroid hormones) or by shots of thyroxine hormone. Another method for inducing metamorphosis is to keep them in shallow water tanks. They will then, over a period of weeks, slowly metamorphose into adult salamanders. However, most attempts at inducing metamorphosis lead to death. This is likely due to the strong genetic basis for neoteny in pet axolotls. Artificial metamorphosis also dramatically shortens the axolotl's lifespan, if they survive the process. Research indicates that neoteny occurs because the hypothalamus of the brain fails to produce the hormone that causes the pituitary to stimulate the thyroid gland to produce growth hormones that trigger metamorphosis. Some scientists think that neoteny may have evolved as a response to the hazards of life on land.

Extrinsic factors: ● Gadow (1901) advanced the idea that the cause of retention of larval features in axolotl is the abundance of food and other favourable requisites in aquatic life. ● Shufeldt holds that deep water and coldness inhibit thyroxine secretion which retards metamorphosis. ● Drying up of swamps, lack of adequate food supply and rise in temperature in surrounding water induce metamorphosis. ● Weissmann again claimed that the retardation of metamorphosis of the axolotls is possibly due to the saline nature of the water of the lakes where they live. ● In an investigation to establish the role of physical factors in neoteny, tadpoles were kept in water-holes with high vertical walls, so that they were not allowed to reach the land above the water-holes. It has been observed that this forced and prolonged use of larval gills and tails cause their further development, whereas the growth of limbs and other structures necessary for terrestrial life remained suspended. ● It has further been observed that the axolotls which were not likely to metamorphose in normal habitat could be forced to metamorphose by

Intrinsic factors influencing neoteny:

● Zondeck and Leiter (1923) established that calcium delays metamorphosis in axolotls. Gressner (1928) also advanced that insulin hormone inhibits metamorphosis. ● But recent researches incline to reveal that the metamorphosis is primarily influenced (i) by varying threshold levels of thyroxine and its analogs and (ii) by the degree of responsiveness of the larval tissue to hormones. ● During early pre-metamorphic stage in amphibian development, the level of thyroxine (T4) is kept very low in the body by genetic mechanism. Etkin (1968) and his collaborators have also established the role of prolactin on metamorphosis. ● They have shown that the level of prolactin which acts as an inhibitor in the overall control of metamorphosis remains high at this time. In the light of modern genetics it may be suggested that the structural genes guiding the synthesis of thyroxine are 'switched off' by some operator genes whereas the genes guiding the formation of prolactin are 'switched on'. ● In such condition the hypothalamus becomes sensitive to the available level of thyroid hormone in the blood stream. The neurosecretory apparatus of the hypothalamus produces a substance, called thyrotropin-releasing factor (TRF). TRF stimulates the anterior lobe of the pituitary to produce thyroid-stimulating hormone (TSH) which in turn enhances the rate of thyroid secretion. ● As the level of TSH rises during pro-metamorphosis, the level of prolactin suddenly falls. So the metamorphosis starts. The time of shift in hormone balance is possibly determined by the initiation of positive thyroid feed-back to the hypothalamus. Poor secretion of thyroid glands and the irresponsiveness of the larval tissues to the hormone are responsible for neoteny. ● Kuhn (1925) studied the thyroid glands of neotenous larvae of the warty newt and observed that the alveoli which secrete thyroxine remain undeveloped and even axolotls possessing normally developed thyroid glands failed to pour their secretion in the blood stream. ● Transplantation of at least two more thyroid glands in addition to the normal glands causes the metamorphosis of axolotls. This result indicated that the thyroid gland of axolotls is able to produce one-third of the required quantity of thyroxine and that the larval tissues are only one-third responsive in contrast to normal specimens. ● Bytenski and Saez have experimentally exchanged the pituitary gland between a salamander larva and an axolotl larva and found that axolotl's pituitary gland is as efficient as that of salamander larva. But the tissues of axolotl failed to respond to the pituitary gland of the salamander. This indicates the irresponsive nature of axolotl's tissues to hormones.

Genetics of Neoteny: The role of thyroxine in urodele metamorphosis has been revealed by studies in genetics. The thyroid hormone binds to nuclear receptors that are in immediate contact with DNA. The hormone helps to change the transcription of genes that also influence to develop the larval characteristics to one, these gradually change into juvenile and adult characteristics. But the exact role of genetics in paedomorphosis or neoteny has not clearly understood. However, a single gene hypothesis is thought to control the axolotl's life cycle. If this theory is correct, then there are two alternate alleles at a major locus primarily responsible for determining the expression of metamorphosis or paedomorphosis.

Significance of Neoteny:

● Neoteny is looked upon as a consequence of adaptation to neighbouring environments where retention of larval gills and other larval features may be advantageous. ● Weissmann (1875) regarded neoteny as a case of reversion to atavistic ancestral conditions by assuming that all amphibia were originally gill-breathing aquatic creatures and that every feature seen in a larva represented a phylogenetic stage and the axolotl as such is a case of reversion to an ancestral stage. ● External gills of urodeles have been evolved as an adaptation to aquatic life. The external gills actually developed first in the embryos as additional respiratory organs. The external gills were first initially restricted to embryonic life, which may be prolonged in aquatic larval life. ● Possession of long external gills in the viviparous embryos of Salamandra altra supports the contention that the external gills are embryonic but not larval features. So existence of such gills in neotenous larvae is a secondary but not an atavistic feature. Besides external gills, the tail with tail-fin and epidermal sense organs of the neotenous larvae are secondary acquisitions rather than ancestral reminiscences. ● G. K. Noble (1931) regarded that the retention of larval features during sexual maturity has nothing to do in the phylogeny of the amphibians. This is quite evident from the heterogeneous characters of the Perennibranchiata where all the neotenous species are included. Neoteny as such may have some importance in the individual groups.