

DEVELOPMENTAL BIOLOGY

Metamorphosis

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Metamorphosis is defined as the change in the form of the organism due to the dramatic developmental reprogramming. This developmental reprogramming is generally seen in those animals where the post embryonic stages of an animal are different from that of the adult. These post embryonic stages are called **larvae**. Metamorphosis is thus a change from completely different form that is larva to the adult.

Direct and indirect development: As we have studied earlier, that egg laying animals are called **oviparous** but those animals which give birth to young ones are called **viviparous**. In oviparous animals, the egg stores reserve food material in the form of yolk. In vertebrates eggs have been categorized on the basis of amount and distribution of yolk. The polylecithal eggs with large amount of yolk can cater to the nutritional requirements of the growing embryo totally, therefore, there is no larval stage in their developmental history as exemplified by the eggs of reptiles and birds. Amphibian egg is a mesolecithal egg with the moderate amount of yolk which is not sufficient for the complete development of embryo so that it has self feeding, independent life form at a very early stage which later metamorphosis into the adult. (Fig7.1). In Protochordates like Herdmania, there is a non feeding larval stage. The larval development is for easy dispersal as the adult is sedentary. In many endoparasites, free larval condition is to facilitate infestation of new host. Thus, there are two types of developments in the development history of animals, **direct** and **indirect**. Direct development is without the larval stage whereas indirect development is with the larval stage.

Larva is the juvenile stage of the animal different from the adult in its habit and habitat. Accordingly, the larva possesses various morphological, anatomical and physiological adaptations for feeding, locomotion, respiration etc. to successfully exploit new habitats thereby avoiding competition with the adults for the limited food resources available. The duration of larval life varies in different animals. The change from larva to the adult can be both **progressive or regressive**. It is called progressive when the simple larval structures transform to complex organization of adult (Example; Frog, insects). Regressive metamorphosis or retrograde metamorphosis means the transformation from complex larva to simple degenerate adult as in Herdmania.

Amphibians are the transitional vertebrate group which have not abandoned the aquatic life completely when they ventured on land, the reason being, the mesolecithal, noncleidoic egg. Most of the amphibians lay their eggs in water bodies or in moist damp places and the larva is formed in the aquatic medium whereas the adult is terrestrial.

This chapter includes the study of amphibian and insect metamorphosis as an example from chordates and non chordates respectively.

Amphibian larva is a fish like transparent and aquatic larva called **tadpole (Fig. 7.2)**. It is almost black or brownish black in color. It has broad head followed by narrow region behind the gills and then an elongated body terminating in a diphyrcercal tail fin. The tail fin ends at the anal opening on the ventral side. The larva has horse shoe shaped paired oral suckers which help in attachment to the aquatic vegetation. Just after hatching, it undergoes intermittent movements and then again attaches with its sucker. It does not feed during this brief initial period. It has three pairs of external gills which are later on covered by the operculum or gill cover. Nasal pits appear as two small apertures on the anterior side of head. The outline of eye and auditory region can be identified behind the nasal aperture. The important feature of larva is the series of V-shaped muscles called myotomal muscles extending from trunk to tail which help the larva to undergo free swimming movement. The presence of heart is apparent on the ventral side behind the oral sucker by the rhythmic movements of body wall. The mouth aperture is bounded by the horny lips with rows of

horny teeth. All along the lateral side is present the lateral line system which is the important receptor system of the body. Skin is thin and transparent with large pigment cells. Intestine is long and coiled like a watch spring. The eyes are lateral in position compared to frontal position in the adult for its insectivorous predatory adult life.

Ecological, Morphological, Physiological metamorphic changes in amphibians (Metamorphosis in about 46 days in Indian frogs)

Ecological change is transition from the aquatic to the terrestrial habitat. As a result there is change in the mode of locomotion, respiration, circulation and also in sensory system of the body. The larva changes from herbivore to carnivore. The change in locomotor pattern, respiratory structures and sensory system is due to the change in the physical properties of water and air.

Morphological change from larva to the adult is grouped separately as progressive, regressive and remodelling. These morphological changes are less marked in tailed amphibians or urodeles.

A) Regressive changes are:

- 1) Resorption of tail and tail fin by autolysis.
- 2) Resorption of gills, closure of gill cleft and disappearance of prebranchial cavity.
- 3) Horny lining of jaws is shed.
- 4) Shortening of cloacal tube.
- 5) Reduction of some larval blood vessels
- 6) Loss of lateral line system

B) Progressive changes are:

- 1) Development of limbs. Hindlimbs appear first then forelimbs.
- 2) Development of middle ear and tympanic membrane to respond to air vibrations.
- 3) Eyes protrude, eyelids develop, the eyes change from lateral to frontal position for binocular vision.
- 4) Development of lung.
- 5) Development of tongue and tongue muscles.
- 6) Replacement of cartilage skeleton with that of bony.

C) Remodelling:

- 1) Increase in epidermal thickness.
- 2) Development of multicellular mucous and serous glands. The formation of different colored patches on skin due to change in pigmentation.
- 3) Heart becomes three chambered with development of portal system.
- 4) More differentiation of brain.
- 5) Shortening of gut and repositioning of cloacal aperture.
- 6) Development of excretory system that is functional mesonephric kidneys.

- 7) Development of reproductive system.
- 8) Neural tissue undergoes remodelling where new neuronal pathways develop for the binocular vision in response to thyroid hormone. Neurons develop in tongue, jaw and in tail muscles.

Physiological Changes:

- 1) Change in eye pigment from larval porphyropsin to adult rhodopsin.
- 2) Change in affinity of haemoglobin to oxygen because dissolved oxygen content in water is less so larva needs to load more oxygen in the blood. Better unloading of oxygen by adult hemoglobin helps in quick supply of oxygen to tissues of the adult . The hemoglobin also shows Bohr's effect in adult..
- 3) Increase of enzymes necessary for the production of urea by the urea cycle in the liver as there is change from ammonotely to ureotely. Enzymes like carbamoyl phosphate synthase, ornithine carbamoyal transferase, argininosuccinate synthase and lyase increase (Fig.7.4).
- 4) There is increase in proteolytic enzymes (trypsin and pepsin) to handle the high protein diet. There is loss of some larval enzymes but formation of new enzymes.
- 5) There is shift of erythropoiesis from liver to bone marrow and spleen.
- 6) Degrowth occurs when feeding is suspended and it uses reserve food only.
- 7) Metamorphic changes in urodele amphibians are less dramatic which involve loss of external adult gills, tail fin, development of lungs, appearance of eye lids, ossification of skeleton, thickening of skin and development of skin glands.

Hormonal regulation of metamorphosis

The metamorphosis is under the hormonal control. It mainly results in activation of genomic set up of the larva to convert it to adult. The metamorphic changes are a result of interplay of hormones of thyroid, pituitary and hypothalamus (Fig7.3).

The works of Gudernatsch (1912), Allen (1916) and Adler (1914) have contributed long time back in unfolding the mystery of amphibian metamorphosis. The important role of thyroid was demonstrated by Gudernatsch (1912) when he fed frog tadpoles on dried powdered sheep extracts of thyroid. It resulted in precocious development to adult. The frog tadpoles remained as larvae when they were fed on other glands.

Allen emphasized on the role of thyroid in metamorphosis when the tadpoles after undergoing thyroidectomy did not metamorphose but when fed on thyroid extracts or when immersed in thyroid extracts metamorphosed. Adler in (1914) proved that thyroid is activated by thyrotropin hormone from the pituitary. He observed that

- 1) When the early larvae are hypophysectomised (pituitary removed) there is no metamorphosis.
- 2) When the larvae are hypophysectomised and thyroidectomised again there was no metamorphosis.
- 3) When pituitary is implanted back or reimplanted the larva changes to adult.
- 4) If the pituitary is reimplanted at the later larval stage, there is no metamorphosis which shows that the initial trigger to the tadpole for metamorphosis is given by the pituitary hypothalamic axis. The pituitary secretes the hormone called Thyroid

Stimulating Hormone (TSH) under the influence of Thyrotropin Releasing Hormone from the neurosecretory cells of the hypothalamus. TSH stimulates the thyroid gland to release the Thyroxine. The endogenous clock of the animal and various environmental factors affect the neurosecretory cells of the hypothalamus for secretion. The anterior lobe of the pituitary secretes prolactin like hormone in the initial larval stages which helps the larva to maintain its larval structures. The concentration and effect of prolactin decreases once, the pituitary starts producing TSH. When prolactin levels are high, larva does not metamorphose.

The pace of metamorphic events depends on the concentration of thyroid hormone and also the reactivity of the different tissues. The tissues which respond to the low concentrations of TSH have low threshold and metamorphose early compared to the tissues which have high threshold. The hindlimbs appear earlier than the forelimbs due to low threshold response by them.

According to the changing levels of hormones, which is manifested as morphological changes in the larva, Etkin divided the metamorphosis into three phases as follows:

- **Pre metamorphosis:** which is a period of growth of larva: It acquires thyroid hormone synthesizing capacity but the level of thyroid hormone is negligible.
- **Prometamorphosis:** is the beginning of metamorphosis. As the growth continues, the brain and pituitary also differentiates and pituitary produces TSH, the level of which rises with increased development of larva. The hindlegs appear in the larva during this phase.
- **Metamorphic climax:** is the profound metamorphic change in the larva. The rapid **metamorphic climax** is the result of tenfold increase in the thyroid hormone concentration by the positive feed back mechanism. Each tissue responds differently to the different levels of the thyroid hormone and this response is programmed in the genome of larva. The metamorphic changes are evident first by the appearance of hindleg, then foreleg followed by resorption of tail. Very heavy doses of Thyroxine levels upset the normal sequence of events resulting in the death of larva. The coordinated hormonal interactions cause the completion of metamorphosis in proper sequence. Loss of tail occurs once the larva develops new locomotor appendages (Fig.7.2).

The thyroid follicle has thyroglobulin which is a large complex protein of molecular weight 675000. It is made of Triiodothyronine T^3 and Tetraiodothyronine. T^4 . Of the two compounds T^3 and T^4 , the T^3 is more potent which brings metamorphic changes at a much lower concentration than T^4 (Robinson *et al*, 1977)

Metamorphic response is organ specific also because if the tip of tail is transplanted in the trunk region, it undergoes atrophy but eye cup transplanted in the tail region is unaffected by the regressing tail tissue which shows that the information for the progressive and regressive change is inherent in the tissue itself. The regression of tail is cell's autonomous programmed death or **apoptosis**.

The ability to respond to the hormone by the target tissue is called **competence**. It is acquired by the tissue in course of the development of larva. The degeneration of tail is by various proteolytic enzymes like collagenase, cathepsin and proteinases, the synthesis of which depends on the thyroid hormone. The degeneration of tail though starts late but it is resorbed quickly. (Wasserburg, 1989).

The metamorphic changes are not only regulated by the hormones but are also guided by the development processes such as induction. If tadpole skin of tail region removed and transplanted to the trunk region, it does not regress but if the skin is removed with the underlying muscles, it regresses. The regression of skin is by the induction from the underlying tail musculature. Another example of induction is the development of the tympanic membrane which is formed by the induction of underlying tympanic cartilage but not by the direct action of the thyroid hormone.

Molecular response to thyroid hormone

The various changes in the morphology and physiology of the larva depends on the concentration and response to thyroid hormone. The thyroid hormone causes the transcription activation of thyroid hormone receptor genes. Before metamorphosis, the mRNA of these receptors are present in low levels. With increase in the level of thyroid hormone, T3 receptors increase affecting the sensitivity as well as response of the target tissue or its competence. The metamorphic climax is the result of enhanced production and induction of T3 receptors that result in quick response by the target tissues. A negative thyroid hormone receptor blocks amphibian metamorphosis by retaining corepressor at target genes (Buchholz *et al.* 2003). Metamorphosis is an example of embryonic development where molecular biology, cell biology, physiology and development processes are integrated for the better understanding of the process.

Heterochrony : It is the phenomenon when the animal changes the relative time of rate of development of characters already present in its ancestors. The two main steps of developmental changes in the animal are (i) onset and offset of particular development process (ii) the rate at which the process operates. It is because of this we observe the paedomorphic / neotenic forms and can also understand progenesis. The above stated two factors may alter due to environmental, hormonal and genetic reasons. When the rate of somatic development is slow it results in neotenic forms and when gonadal development is fast it causes progenesis. The paedomorphosis/ neoteny, paedogenesis and progenesis are the types of heterochrony.

Paedomorphosis/Neoteny: Paedomorphosis (paedo means child and morphosis means form) is a phenomenon observed in tailed amphibians. There are certain tailed amphibians which retain the larval characters in the adult. There are two types of paedomorphosis (i) obligatory (ii) facultative. Some urodeles retain gills as the larval characters throughout their life for example Necturus. They are permanent larva as the developing tissues fail to respond to thyroid hormone. Facultative paedomorphosis is seen in urodeles like Ambystoma and Triturus. The larva metamorphose to adult if the environmental conditions change. An American axolotl Ambystoma metamorphose when the water dries up. The gonadal development is normal but the somatic development is delayed. It remains aquatic larva for along time and change to the adult when there is change in the environment. This kind of **paedomorphosis** is called **neoteny**. Neoteny is derived from a greek word, *Neoteineu* where Neo means 'young' and teineu means 'to extend'. It is a condition of retention of juvenile form due to the retardation of the body or somatic development relative to the gonadal development. It is also defined as the dissociation of time of morphological change from the maturation of germ cells due to environmental factors (high temperature, cold temperature, Iodine concentration etc.) or genetic factors or both. The incomplete metamorphosis is an advantage conferred on the urodeles that might perish if forced by loss of gills to abandon an aquatic environment when the terrestrial environment is unfriendly. It is called **partial metamorphosis** when it is delayed due to the temporary ecological or physiological changes with change of season. It is **intermediate** type as shown by axolotls (name given by natives

of Mexico as servants of water) when they undergo metamorphosis in a suitable environment. Necturus, Proteus and Siren show **total neoteny** when they remain larval throughout their life and treatment with the thyroxine hormone fails to induce them.

The cause for the neoteny is not properly understood but environmental factors affect metamorphosis like abundance of food, cold, low iodine etc. The drying of swamps, lack of food and rise in temperature in the surrounding water induce axolotls to metamorphose. The neotenic forms that retain gills permanently are called **perrenibranchiates** and those which shed their gills are called **caducibranchiates**.

The metamorphosis is regulated by the hypothalamus, pituitary and thyroid axis, if any of the steps on this axis are blocked, it results in failure of larva to reach the adult stage (Fig.7.5).

Ambystoma mexicanum does not metamorphose because pituitary gland fails to produce Thyroid Stimulating Hormone TSH; but when injected with TSH it metamorphose. Ambystoma tigrinum metamorphose in hot water as hypothalamus of this species could not produce TSH release factors at low temperatures.

Necturus, remains unresponsive to thyroid hormone as mRNA for thyroid hormone receptor is absent.

Direct development is seen in small frog of island of Puerto Rico that is Eleutherodactylus coqui. There is advantage of neoteny to the individual as it can exploit two different food resources but may sometimes result in lack of gene flow and reduced genetic diversity in the population.

Progenesis is a condition when the juvenile form retains the larval characters but the gonads develop faster and become sexually mature as in Ambystoma tigrinum and A. mexicanum. The red spotted salamander of United States, Notophthalmus viridescens, exhibits a very different pattern of metamorphosis where the larva undergoes morphological change that enables it to emerge from pond and assume a juvenile existence in advance to maturation of gonads in this state. They are called efts. Efts remain on land for one to three years before the onset of sexual maturity which is stimulated by the hormone prolactin. Later on the efts metamorphose, gonads mature and then they reproduce.

The neoteny and progenesis are the important mechanisms resulting in mutations. Neoteny delays the physiological and sexual maturity in the individual but progenesis stops the development of organism before achieving adulthood. This may sometimes lead to the evolution by bringing mutations so that the species may become independent of environmental stresses. The ability of larva to reproduce is called paedogenesis.

Insect metamorphosis: Phylum insecta is the largest invertebrate phyla. Insect body is divisible into head, thorax and abdomen with three pairs of legs. The wings may be present or absent. They are accordingly classified as **pterygota** or **apterygota**.

The development of wings may be external (exopterygota) or internal endopterygota). Because of the different morphology in large group of insects, different patterns of metamorphosis are recognized. The larva may change to adult by simple growth and remodeling, or it may be accompanied by the extensive morphological changes by losing many larval characters.

The insects are covered by an exoskeleton of hard cuticle. As the insect larva grows it sheds its old cuticle in order to accommodate the increasing size of the larva. This shedding of the old cuticle and replacement by the new one is called **molting**. Accordingly, the development in insects is accompanied by series of molts. The interval between two successive molts is called **stadium**, and the form that the insect assumes as a result of the molts is called **instar**.

All the insects undergo several molts before transforming to adult stage which is called **imago**.

The number of molts may vary in each species and is predetermined for that species. The insect larva after each molt not only undergoes changes in its cuticle covering but also in its internal organization.

Types of insect metamorphosis: Insect metamorphosis is broadly classified into three types:-

- 1) **Ametabolous:** It is a type of metamorphosis seen in primitive insects as apterygotes, (silver fish, springtails etc) where the young ones that hatch from the egg are similar to adult or imago but differ only in size, maturity of reproductive organs and external genitalia. They molt several times resulting in increase in size of the larva.
- 2) **Hemimetabolous:** Some exopterygote insects undergo gradual or incomplete metamorphosis and are called hemimetabolous. The young one of the terrestrial exopterygotes (cockroaches, cicadas) have the larval stage called **nymph** where it is similar to adult except for the size and development of wings and maturity of gonads. The wings develop externally as budlike outgrowths in the early instars and then increase in size in the adults. The aquatic exopterygotes pass through the larval stage called **naiads** which have larval structures for the aquatic life like tracheal gills.
- 3) **Holometabolous:** The endopterygota insects like beetles, bees, moths and butterflies undergo complete metamorphosis or are holometabolous. The insect passes through the stages of egg, larva (caterpillar), pupa and adult or (imago) (Fig.7.6). Each of the stage lives in different surroundings and eats food different from the adult for example the caterpillar larva of butterfly is wingless and eats leaves whereas adult feeds on nectar from the flowers. The mosquito larva is aquatic and feeds on algae but the adult sucks the blood of man. The larvae are usually voracious feeders. The last larval molt is an inactive dormant larval state called **pupa**. The pupa is enclosed in a case or **puparium** secreted by the labial glands of larva. The pupa does not move or feed when enclosed in the pupal case. During the pupal stage, all the larval structures are broken down and are used as the raw material in the development of adult. Thus, there is histolyses (breakdown of tissues) and histogenesis that is formation of new structures. The pupa undergoes the final molt to form the adult capable of reproduction.

In the holometabolous insects, there is development of imaginal discs which are the rudiments of future organs of the adult, such as mouth parts, wings, antennae, walking legs and internal organs etc. During the pupal stage, they grow in size and differentiate to form adult structures which remain collapsed or folded in the pupa and unfold when pupa metamorphose to adult. The last molt, is called **imaginal molt** and later on the insects develop exoskeleton of chitin on it. The chitinous exoskeleton of larva, pupa and adult is composed of different layers with various patterns of bristles and hairy projections.

Molting cycle Metamorphosis in insects can be called a special form of molting which means periodic shedding of cuticle. Accompanied by growth of larva, the cuticle is secreted by the epidermis of the insect. In between the two molts, the cells of the epidermis are quiescent, more or less flat and the epithelial layer is very thin. Before each molt, they become activated, detach themselves from the cuticle and enter a period of rapid growth and proliferation. The epidermis is also thrown into folds where the body parts increase in size so that these folds expand when the insect emerges out.

The old cuticle is digested by the secretions of the molting gland (Hepburn, 1985) and when it is reduced to a thin shell it is ruptured at the back of head and thorax and the insect crawls out of it. Thus, the growth of insects takes place in cycles in which the mitosis and cellular growth alternates with the deposition of new cuticle and the shedding of the old one. This cycle is called **molting cycle**.

Diapause There are number of external factors which are important for the initial trigger of the metamorphosis for example in blood sucking Rhodinus, intake of food is an important factor. In some insects, the pupa may continue to remain in the quiescent state with the reduced rate of metabolism. This arrested state is called **diapause**. In the Platysamia, the exposure to cold is essential to complete the development of pupa to adult. Precocious breaking of diapause may occur if the pupa is exposed to cold for at least two weeks for 3⁰ - 5⁰ C. The temporary cooling activates the vital processes in the pupa and it molts when the latter is brought to the warm environment. In insects, other factors as humidity, density, starvation etc may have some role in initiating the metamorphosis. In those insects, where molting is determined entirely by the internal processes, the extrinsic factors have no role in giving stimulus to molting.

Hormonal regulation of insect metamorphosis

Like amphibian metamorphosis, insect metamorphosis is also under the hormonal control (Fig.7.7). The secretions and the stimulations from **brain, corpora cardiaca, corpora allata, prothoracic gland** have important role in insect metamorphosis. The neurosecretory cells of brain secrete Brain Hormone (BH) (Gilbert and Goodman 1981, Granger and Bollenbacher, 1981). Brain hormone (BH) is released in response to neural, hormonal or environmental factors. The hormone after being released from the brain passes along the axons of these cells into the storage and release organs called corpora cardiaca located in the posterior side of brain. The corpora cardiaca releases activity hormone called **prothoracotropic hormone (PTTH)** which acts on the prothoracic gland causing it to secrete **molting hormone or ecdysone**. Attached to the posterior side of corpora cardiaca are present corpora allata which secrete **Juvenile hormone or neotenin** (Wigglesworth, 1934) that maintains the larval characters, determines degree of differentiation and decides whether it will be a larval molt or adult molt. The secretory cells of corpora allata are active during larval molts. It prevents metamorphosis of larva to the adult. In the last larval molt, that is imaginal molt, the signal from brain to the corpora allata inhibits the gland from producing Juvenile hormone and there in increase in the ability of the animal to degrade existing JH (Safranek and Williams, 1989). Once the JH levels drop, the release of PTTH is stimulated from the brain (Rountree and Bollenbacher, 1986). PTTH stimulates the prothoracic gland to secrete ecdysone which is not an active hormone but a prohormone and is converted in the fat body to active hormone 20-hydroxy ecdysone. Each molt is a result of increase of 20-hydroxy ecdysone. By the increase in ecdysone, pupa specific proteins due to transcription of pupa specific genes are produced (Riddiford, 1982, Nijhout, 1994).

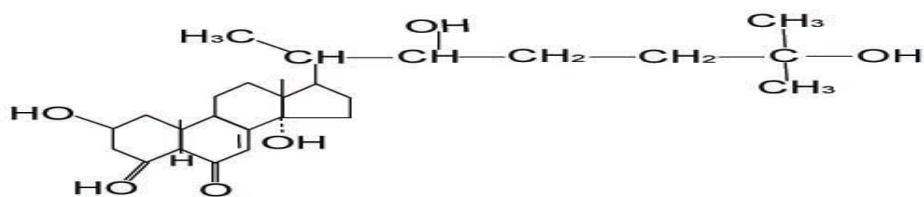
Earlier studies show that the levels of JH determine the type of molt whether larval, pupal or adult. However, it is more complicated process because the sensitivity or response of target cells to the Juvenile Hormone varies. If JH is present during the JH sensitive period, the larval state is maintained but if the JH is absent during this period then the tissue will progress to next development state. The JH sensitive period is the result of autonomous state of the cells (Nijhout, 1994). When the larva converts to pupa, the epidermis is sensitive to the JH but not the imaginal discs, as a result epidermis changes to pupal epidermis. In the last,

imaginal molt when the pupa transforms to the adult, JH is absent as a result imaginal discs differentiate to the adult structures.

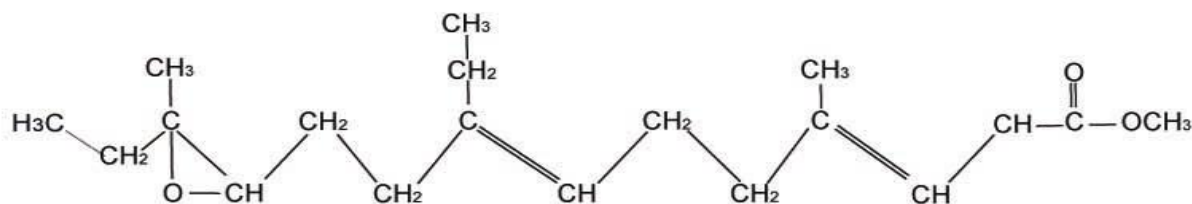
In order to hatch or come out of its chitinous shell, the larva moves under the influence of eclosion hormone from brain which activates ecdysis triggering hormone giving signals to the abdominal ganglia of each segment to allow the larva to move and shed its old cuticle (Zitnan et al, 1996)

Thus, the insect metamorphosis is an interplay of different hormones which may have direct or indirect effect on the target tissues.

Structure of Juvenile and molting hormone: The PTTH is a peptide hormone with the molecular weight of 40,000D. Ecdysone or molting hormone is a steroid hormone. It is converted by haeme containing oxidase in the mitochondria to active form called 20 - hydroxyecdysone. Juvenile hormone is also a steroid or a derivative of terpene group .



Chemical structures of ecdysone which is a steroid hormone



Chemical structure of juvenile hormone

Molecular Biology of Molting hormone The molting results in characteristic puffing pattern in the polytene chromosomes of insects (Ashburner and Berondes, 1978). The chromosome puffs represent areas where the DNA is actively transcribed and puffing pattern keeps on changing in the different larval forms. The puffing is induced by the binding of hydroxy - ecdysone to the specific genes on the chromosomes. The different changes in tissues are recognised due to the different response to the molting hormone specially during the late larval stages. Some of the tissues undergo regressive change and cell death, others reorganise and remodel whereas imaginal discs divide and differentiate to adult structures. There are different receptors in the tissues for the hormone ecdysone which activate variety of genes (EcR, BR-C, E74B). These genes are activated by different levels of ecdysone (Thomas et al, 1993, Stone and Thummel, 1993). The characteristic change in larval forms is thus an expression of different set of genes which are activated or inactivated at different periods of development history of the insect.

In the end, we summarise and list some of the important points of the development event , **metamorphosis**. :-

- Metamorphosis is the dramatic change in the morphology, anatomy and physiology of the animal.

- It is regulated by the intrinsic and extrinsic factors.
- The intrinsic factors regulating metamorphosis are different hormones which may have direct or indirect effect on the target tissue.
- Thyroid hormone has direct effect on the target tissue (amphibia).
- Metamorphic changes are regionally specific.
- Metamorphic changes are under the influence of inductive interactions.
- Insect metamorphosis is accompanied by the shedding of exoskeleton and it is called molting.
- Different molting patterns are observed in the insects.
- Molting is caused by hormone 20- hydroxy ecdysone
- Metamorphosis is an important development event from larva to adult, so if due to intrinsic or extrinsic factors its steps are disturbed, it results in heterochrony, paedomorphosis, neoteny and progenesis in the vertebrates.
- Metamorphosis is very important for those animals where food and other habits of adult are unsuitable for the developing young. It brings easy dispersal of sessile species such as Herdmania. The echinoderm larvae are produced to acquire sufficient food available on the surface of sea water. Metamorphic changes bring the adaptive changes in the adult so that they live and reproduce successfully in their permanent environment.

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