METAMORPHOSIS IN FROGS

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14.5 METAMORPHOSIS

Metamorphosis is the post embryonic transformation of a larva of an organism into a juvenile adult. The changes during this period of development are dramatic and rather rapid. The phenomenon of metamorphosis is well established in amphibians, specially anurans (tail less amphibians) e.g. frogs and toads. They show dramatic metamorphic changes during their development, affecting nearly all organ systems and major functions. Amphibians are the first class of vertebrates to show transition from aquatic to terrestrial mode of life. Therefore, the metamorphic changes are associated with the change in their habitat. A number of features distinguish metamorphic changes from early embryogenesis and other post embryonic changes. The signals that bring about metamorphic changes are usually hormonal unlike the short term signals during embryogenesis that are typically protein growth factors. The synthesis of these hormones is directed by the central nervous system in response to environmental cues and there is a complex feedback mechanism that controls their production as well.

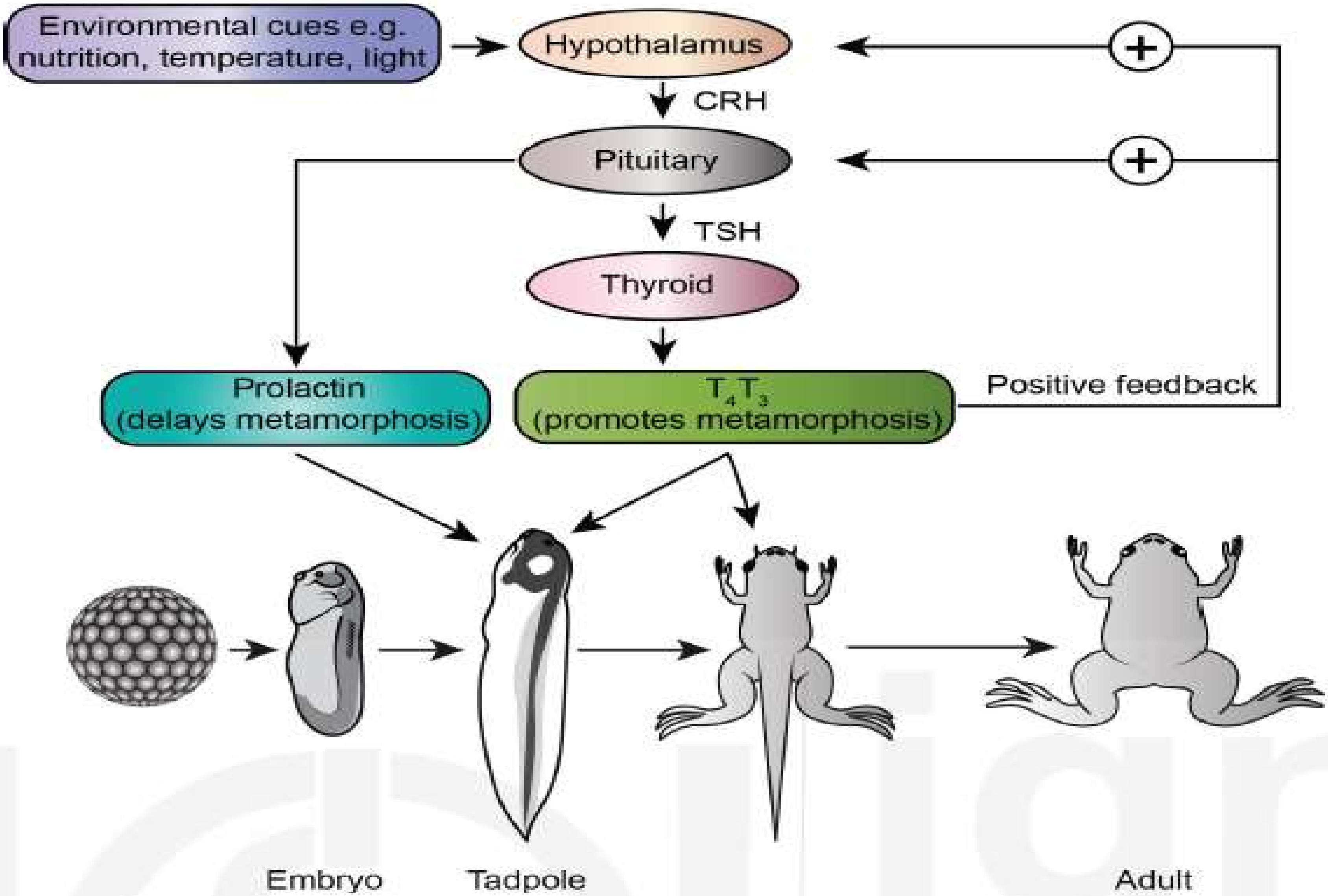


Fig.14.13: Environmental and nutrional cues cause the initiation of metamorphosis by secretion of corticotrophin stimulating hormone (CRH) from the larval hypothalamus which acts on the pituitary gland to release TSH. This in turn acts on the thyroid stimulating hormone (TSH) to release T4 and T3 that cause metamorphosis to happen. The thyroid hormones also act on the hypothalamus and pituitary to maintain the secretion of CRH and TSH.

Figure 14.13 shows metamorphosis in frog. You can see that the egg develops into a larvae which is strikingly different from the adult in morphology. Apart from the appearance there are other significant changes in the physiology and biochemistry in the larva. Larva of frog is called tadpole. It is free swimming, and possesses a tail. It has three pairs of external gills covered by operculum for respiration. Locomotion is brought about by tail and chordal fin. The alimentary canal is long and coiled to aid herbivorous mode of digestion. Brain of tadpole is quite small and simple. Heart is two chambered consisting of auricle and ventricle.

Three distinct stages of Metamorphosis:

Morphologically as seen in the Figure 14.13, the typical frog metamorphosis is divided into three stages.

1. Premetamorphosis – it is the first stage of metamorphosis when the tadpole has no limbs. This is the initial period of extensive growth but little developmental changes. Size of tadpole increases.

2. Prometamorphosis – during this stage developmental changes occur such as shortening of tail, gills becoming internal and growth of hind limbs take place.

Metamorphic climax – emergence of forelimbs marks the beginning of metamorphic climax. It is a brief period in which morphological changes occur very rapidly in quick succession including full limb growth and tail resorption.

14.5.1 Metamorphic Changes

The transformation of aquatic tailed tadpole larvae to a terrestrial adult frog involves major metamorphic changes. These can be classified as:

1. Ecological with respect to change in habitat.
2. Morphological with respect to change in morphology.
3. Physiological / Biochemical with respect to change in different bodily functions.

Ecological Changes:

The habitat of the tadpole larvae is fresh water whereas adult frog is land dwelling. Tadpole is herbivorous. Its horny beak and teeth help in rasping away the plant tissues. Frog is carnivorous feeding on insects and worms.

Morphological changes:

The morphological changes during metamorphosis are of three types; a) regressive changes, b) progressive changes and c) remodeling of existing structures in larvae.

a) Regressive changes: The organs or structures necessary during larval life, but redundant in adult are gradually reduced and ultimately disappear in adults. Resorption of the long tail, chordal fin, external gills and ventral suckers take place. The gill clefts are closed. Peribranchial cavities are lost. Horny teeth and horny lining of jaw are shed. The cloacal tube gets reduced. Lateral line of the larva disappears. Aortic arches get modified due to reduced branchial arteries.

b) Progressive changes: Some organs develop and become functional only during and after metamorphosis. These involve the development and differentiation of fore limbs and hind limbs; the middle ear from the first pharyngeal pouch, tympanic cartilage and tympanic membrane; and hyoid apparatus from the pharyngeal arch to support the tongue which develops from floor of the mouth. The eyes protrude on the dorsal surface of the head developing eyelids and nictitating membranes.

c) Remodeling of existing larval structures: Some structures which function both in larval and adult form but undergo remodeling during metamorphosis. These involve basically skin, intestine and brain. The skin thickens and becomes multilayered with moucus and serous glands so that it remains moist. The skin acquires a characteristic color and pattern of pigmentation. The outer layer becomes keratinized. The long and coiled intestine shortens. Mesonephric kidney develops from pronephric kidney. Heart becomes three chambered from the earlier two chambered heart. Liver and pancreas become functional. Brain gets highly differentiated.

Biochemical / Physiological changes:

Along with morphological changes, certain biochemical / physiological changes take place during metamorphosis as explained below:

a) Tadpole larva is ammonotelic, excreting nitrogenous waste as ammonia which can be easily disposed off by diffusion in the aquatic medium. After metamorphosis, adult frog becomes ureotelic, excreting urea. This change occurs when the liver starts producing appropriate enzymes for the urea cycle.

b) The larval eye pigment porphyropsin is replaced by rhodopsin.

c) The respiratory pigment, larval haemoglobin is replaced by adult haemoglobin having more oxygen carrying capacity.

d) The site of erythropoiesis changes from liver to bone marrow and spleen.

e) Various digestive enzymes and hydrolytic enzymes are secreted.

f) Amoeboid macrophages by phagocytosis bring about autolysis of larval organs like gills and tails etc.

g) Shrinkage of body occurs because of suspended feeding and loss of some body parts like tails and gills. As a result degrowth (reduction in body mass) occurs. Head and trunk become small in adult.

Some important metamorphic changes seen in frog are summarized in Table:

System	Larva	Adult
Locomotory	Aquatic; tail fins	Terrestrial; tailless tetrapod
Respiratory	Gills, skin, lungs; larval hemoglobins	Skin, lungs; adult hemoglobins
Circulatory	Aortic arches; aorta; anterior, posterior and common jugular veins	Carotid arch; systemic arch; cardinal veins
Nutritional	Herbivorous; long spiral gut; intestinal symbionts; small mouth, horny jaws, labial teeth.	Carnivorous; short gut; proteases, large mouth with long tongue.
Nervous	Lack of nictitating membrane; porphyropsin, lateral line system, Mauthner neurons	Development of ocular muscles, nictitating membrane, tympanic membrane; rhodopsin; lateral line system lost, Mauthner neurons degenerate
Excretory	Largely ammonia, some urea (amoniotellic)	Largely urea; high activity of enzymes of ornithine-urea cycle (urotelic)
Integument	Thin, bilayered epidermis with thin dermis; no mucous or granular glands.	Stratified squamous epidermis with adult keratins; well-developed dermis contains mucous and granular glands secreting antimicrobial peptides

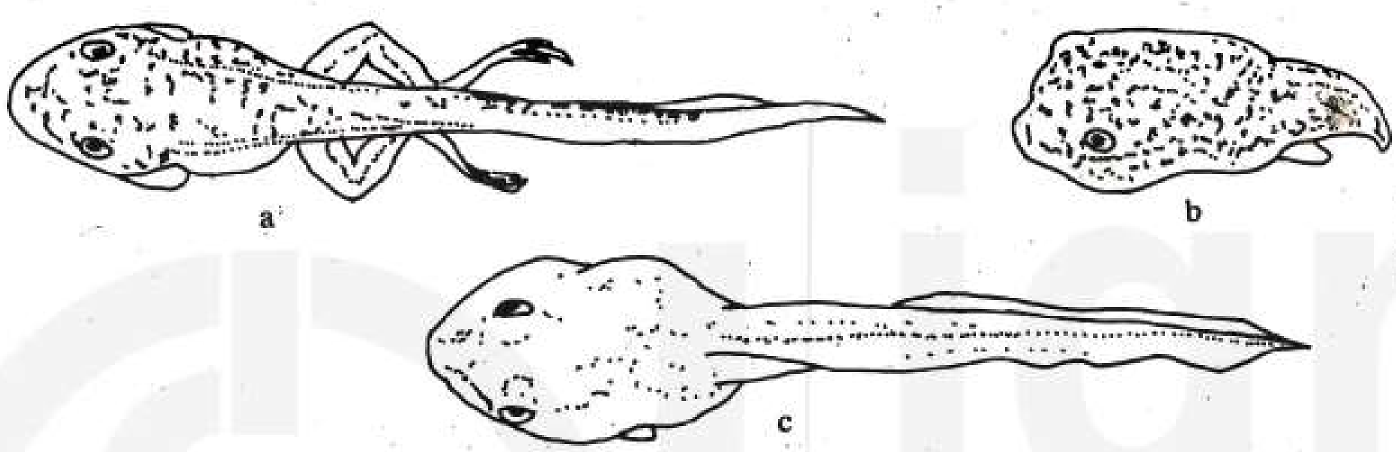
14.5.2 Hormonal Regulation

In amphibians, nutritional status and environmental cues such as, light and temperature, cause the neurosecretory cells of the hypothalamus to release **corticotrophin- releasing hormone (CRH)**. This hormone acts on the pituitary gland to release **thyroid stimulating hormone** (**TSH**) which in turn causes the release of thyroid hormones. This action of corticotrophin releasing hormone is peculiar to non-mammalian vertebrates and occurs in *Xenopus* only at the tadpole stage. In the adult frogs the release of thyroid stimulating hormone is due to **thyrotropin stimulating hormone**. The principal hormones which regulate metamorphosis in frog are **thyroid hormones** (TH) secreted by the thyroid gland (see Box 14.1). **Prolactin** and thyrotropic hormones released from the pituitary along with thyroxin from thyroid gland regulate metamorphic events in a sequential and coordinated manner (see Fig. 14.13).

The thyroid hormones exist as thyroglobulin in the thyroid follicles. These large proteins consists of tri-iodothyronine (T 3) containing three iodine atoms attached to tyrosine and tetra – iodothyronine (T 4) containing four iodine atoms attached to tyrosine. T 3 and T 4 are released during metamorphosis from the thyroid gland. T 4 is the precursor while T 3 is the active form of hormone. T 3 causes metamorphosis in thyroidectomized tadpoles in much lower concentration than T 4. Hypothalamus receives the exogenous signals such as temperature, light and nutrition etc. to release neurosecretory hormones. Pituitary also secretes another hormone, prolactin which is antagonistic to T 3. It inhibits metamorphosis and promotes growth in the larva. The action of prolactin is suppressed by dopamine produced by hypothalamus. Hypothalamus is the controlling centre for maintaining a balance between thyroid hormones and prolactin. During premetamorphosis, prometamorphosis and metamorphic climax the concentration of thyroid hormones circulating in blood vary, resulting in metamorphic changes.

Box 14.1

The role of thyroid hormone in metamorphosis was first demonstrated by Gudernatsch in 1912. He discovered that the tadpole when fed with powdered sheep thyroid glands, metamorphosed prematurely. Allen in 1916 showed that when thyroidectomy (removal of thyroid gland) was done on early tadpoles, the larvae failed to metamorphose and grew into giant tadpoles. If these tadpoles were fed dried powdered thyroid gland or immersed in iodine solution, they underwent metamorphosis. Subsequent studies by E.W.Etkin (1968) demonstrated the important role played by various hormones during metamorphosis. In the diagrams given below (a) shows normal metamorphic stage; (b) shows a tadpole exposed to thyroxin in the earlier stage undergoes premature metamorphosis and (c) shows the effect of removal of thyroid or pituitary gland which results in inhibition of metamorphosis



During premetamorphosis thyroid gland is still developing therefore, the **TH/Prolactin ratio is very low**. Prolactin secreted by pituitary gland stimulates growth of larval body. As hypothalamus develops in premetamorphosis, it produces CRH which causes rise in the level of TSH. As a response to this, T 3 and T 4 begin to rise causing premetamorphic changes. It also exerts positive feed back effect on the pituitary. As pituitary develops further, it causes increased flow of CRH between hypothalamus and pituitary. Hypothalamus releases prolactin inhibitor, causing increase in T 3 and T 4 and decrease in the level of prolactin. **In prometamorphosis, TH / prolactin ratio is intermediate.** When the level of T 3 and T 4 reaches the threshold, rapid metamorphic changes take place. *At this stage, TH/Prolactin ratio becomes very high*. High concentration of T 3 and T 4 exert a negative feed back on thyroid and hypothalamus causing decrease in CRH. Consequently thyroid gland partially degenerates.

Conversion of T 4 to its more active form T 3 takes place in the target tissue by the enzyme De – Iodinase II. Thyroid hormone acts on target cells by crossing the plasma membrane and interacting with thyroid receptors (TRs). T 3 binds to the nuclear thyroid receptors which has higher affinity than T 4. There are two types of thyroid hormone receptors; namely **TRα** and **TRβ**. Expression of thyroid receptors is under developmental control. Studies on *Xenopus* have shown the presence of TRα in all the tissues even before development of thyroid gland in the organism. The level of TRβ in the target tissue increased with high level of thyroid hormone as metamorphosis progresses. The thyroid receptors activate gene expression during metamorphosis in the presence of TH. **In prometamorphic** tadpoles, the receptors are unliganed and so gene expression is repressed in the absence of TH to prevent metamorphosis, thus ensuring proper tadpole growth period. However, in the presence of TH, transcription is activated. At **metamorphic climax** the level of TR β reaches maximum due to which, rapid metamorphic changes take place.

In summary, metamorphosis in frog is regulated hormonally in a sequential manner as follows:

1. The thyroid gland secretes hormone thyroxin, T 4 into the blood.
2. T 4 reaches the target tissue and is converted to by enzyme Deiodinase II T 3 which is a more active form of the hormone.
3. T 3 binds to the nuclear thyroid hormone receptors. T 3 has a higher affinity to bind to thyroid receptors (TRs) than T4.
4. T 3-TR complex binds with retinoid receptor forming a complex which activates transcription of genes responsible for metamorphic changes.