THE INFLUENCE OF THYROXINE, EPINEPHRINE, AND X-RAYS ON METAMORPHOSIS OF SOME NEOTENOUS URODELES[1]

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Introduction

After investigation of the comparative anatomy of the aortic arches of neotenous urodeles in comparison with other urodeles (Baker, 1949), it was decided to attempt metamorphosis in these animals. Changes in the aortic arches probably would be among the first results of metamorphosis, particularly in animals with external gills. Alphonse and Baumann (1935) found that the modifications in the aortic arches of *Bufo vulgaris* caused the involution of the operculum in metamorphosis. The purpose of these experiments would be to examine the aortic arches of the artificially metamorphosed urodeles for comparison with the arotic arches of naturally metamorphosed urodeles.

As early as 1912, Gudernatsch found that the thyroid gland had a profound effect on metamorphosis of amphibian larvae. Thyroxine, the active constituent of the thyroid gland, was used in these experiments since the dosage can be more accurately determined. In some early investigative work Jensen (1916, 1930) reported some success in metamorphosing *Necturus* and *Proteus*. One adult *Necturus* was fed thyroid and injected with iodothyrine. He observed a resorption of one gill on one side and slight changes in pigmentation following which the animal died. In experiments on *Proteus* four animals 12-24 cm. in length were used. Some were fed thyroid and some were injected with thyroid substance. They attained a slight atrophy of the tail fin and gills but soon returned to normal. Huxley and Hogben (1922) fed two specimens of *Necturus* fresh ox thyroid triweekly for seven months. They reported that there were no appreciable changes in the gills except what could be attributed to vasomotor phenomenon. They found no exophthalmos which always accompanies metamorphosis in amphibia. Huxley (1925) again reported that neither *Necturus* nor *Proteus* could be metamorphosed by large doses of thyroid. Swingle (1922) reported that the perennibranchiate amphibians have small but perfectly formed thyroid glands. Thyroid glands of *Necturus* transplanted into *Rana clamata* caused hyperthyroidism. Although he fed *Necturus* large quantities of physiologically active thyroid and anterior lobe of the pituitary and simultaneously transplanted into them frog thyroids, after four months no signs of metamorphosis could be detected. Noble (1924)

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reported success in causing an atrophy of the gills in young *Siren* and *Pseudobranchus* in ten days by placing them in iodothyrine solutions of 0.05 percent. He did not consider this a metamorphosis. He reported no success in trying to metamorphose recently hatched or adult *Pseudobranchus*, young or old *Siren*, young *Necturus punctatum* or adult *Cryptobranchus* by iodothyrine or thyroxine solutions or by feeding urodele thyroids.

Gutman (1926) reported successful metamorphosis of *Necturus maculosus* by means of thyroxine-adrenalin treatment. He placed 57 mm. larvae in thyroxine solutions and added adrenalin 1:2000 which was renewed daily. After four weeks changes were noted in one specimen; two gills had disappeared and the remaining four lost filaments and were non-functional. Exophthalmos was very pronounced and skin was sloughing off. The animal died the next day with signs of dyspnea. In a following experiment six animals treated similarly showed reduction of gills with complete disappearance of the gills of one animal. Exophthalmos was very distinct, the head was blunt caudad, and specimens made continued attempts to breathe air. Death inevitably resulted. Microsections showed the transformations in the gills to be identical with those found in other species. During this time adrenalin and thyroxine alone had no effect, nor did the control animals change. Feeding and injection of thyroid gland and thyroid extracts failed to produce metamorphosis in *Proteus, Siren,* and *Amphiuma* (Sachs, 1930).

Figge (1928, 1930) used *Amblystoma tigrinum* in metamorphosis experiments to duplicate the condition found in *Necturus*. It was his hypothesis that absence of a spiral valve and the ventral portion of the sixth arch in *Necturus* caused failure to metamorphose. He believed there was a definite relationship between the oxygen content of the blood going to the gills and thyroid activity. In *Amblystoma* at metamorphosis the third and fourth arches lose their respiratory function and become the carotid and aortae respectively. The fifth arch is reduced. The dorsal portion of the sixth is reduced and anastomoses to the fifth to give a single vessel to the lungs, the pulmonary artery, which takes on all the respiratory activity. The spiral valve appears to separate the blood. As metamorphosis progresses the oxygen content of the blood to the gills is higher and that to the lungs is lower, which affects the development of the lungs and reduction of the gills. *Amblystoma* with aortic arches ligated to duplicate the condition found in *Necturus* failed to metamorphose although non-ligated *Amblystoma* metamorphosed. However Figge in 1934 found that ligated *Amblystoma* would metamorphose under different environmental conditions including low altitude, warmer temperatures, and high oxygen tension. Thus while absence of the sixth arch and spiral valve might inhibit metamorphosis, it would not prevent it. After complete removal of the lungs of an axolotl metamorphosis was accomplished by thyroid administration (Garber, 1930). There were cutaneous and pharyngeal arterial branches

that could hypertrophy to carry on respiration. Helff (1931) removed the lungs of tadpoles with resulting decreased metabolism but unhindered metamorphosis. Skin respiration could suffice. Ichikawa (1931) removed the sixth aortic and visceral arches of *Hynobius* larvae 45-50 mm. in length. Metamorphosis consequently took place. He stated that the small size of the animals enabled skin respiration to suffice with the aid of oxygen bubbled into the water. From the above data it seems safe to assume that the lack of the sixth arch would not greatly hinder *Necturus* from metamorphosing as auxilliary areas for respiration could be utilized.

An attempt was made to reduce the gills in neotenous newts, *Triturus viridescens,* by removal from water to force disuse of the gills and development of auxiliary respiration (Morgan and Sondheim, 1932). The animals were placed in jars cushioned with earth and moss. They were sprinkled sparingly with water on occasion but the water was never allowed to accumulate. Control animals were kept in water. A third group were kept on land and a fourth group in water. All the animals were fed, those newts on land by force. Twice weekly when they were fed the newts were placed in shallow water to observe the gills. The gills would appear greatly reduced and dried up but when placed in water they would expand and blood could be seen flowing through them. The newts in the moss huddled down, lost weight and breathed pharyngeally. The animals lived over seven months in this environment. No changes took place in the gills after transplanting anterior lobe of the pituitary into the animals. Animals receiving thyroid gland transplants from gill-less newts showed no changes in the gills in the 10-27 days that they survived. Allen (1929, 1938) reported that earlier experiments on *Necturus* fed with thyroid powder had resulted in failure.

The problem of why the permanently larval urodeles fail to metamorphose has received many different answers. Huxley and Hogben (1922) offered four possible explanations for the perennibranchiate state: (1) these animals never possessed genetic factors for typical adult Urodela, (2) defective thyroid cannot utilize iodine to make active iodine compounds, (3) endogenous factors for maintenance of the thyroid at functional activity are not operating properly, and (4) larval tissues concerned have collectively lost the ability to respond to the thyroid activator. Noble (1927) concluded there is no thyroid deficiency in Perennibranchiates; the fact that the tissues are not sensitized to the thyroid hormone is due to genetic factors. Blacher (1928) states simply that in urodele metamorphosis there is a "dead point," *i.e.,* when the amount of stimulation is not sufficient to complete the metamorphosis, and the latter has proceeded far enough, a condition of equilibrium is established, leading to a cessation of metamorphosis. Ingram (1929) has shown that in axolotls, animals whose tissues are sensitized to the thyroid hormone, inorganic iodine in sufficient quantities will metamorphose hypophysectomized and thyroidectomized animals.

Necturus has an active thyroid gland as shown by Grant (1930). Anterior lobe of the pituitary was transplanted to the peritoneal cavity of *Necturus* specimens averaging 45 mm. in length. The thyroid gland released colloid in a normal way. Grant concluded that the explanation of neoteny in *Necturus* may be due to factors other than the endocrine system. The thyroid gland of *Necturus* when transplanted into amphibians capable of response causes metamorphosis (Allen, 1938; Charipper and Corey, 1930; Swingle, 1922).

Spaul (1930) believed that the anterior lobe of the pituitary may function independently of the thyroid in metamorphosis. In urodeles he stated inhibitory influences gain and retain supremacy at some stage before complete metamorphosis and establish a permanent relationship and stability in the endocrine system as far as metamorphosis is concerned. The size and weight of the thyroid in relation to the size and weight of the body are not necessarily criteria of activity. Other investigators (Figge and Uhlenhuth, 1932) concluded that the anterior lobe of the pituitary gland excretes a specific thyroid activator and by it controls the activity of the thyroid gland. Thyroidectomized axolotls did not metamorphose after 30 injections of anterior lobe of the pituitary extract. Control animals metamorphosed after 6-8 injections. After many experiments with thyroxine on *Salamandra maculosa* Kuhn (1933) concluded that sensitivity to thyroxine decreases with increasing age. Thus it would probably be more profitable to conduct metamorphosis experiments on young larvae rather than adult animals.

It can readily be seen from the above data that varying results after thyroid administration to *Necturus* have been reported. Various explanations for neoteny in urodeles also have been offered.

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Materials and Methods

The Urodeles studied are *Siren lacertina* from Florida, *Necturus maculosus* from Wisconsin, and *Amphiuma tridactylum* from the Mississippi Valley. The *Siren* varied from twenty to thirty inches, the *Necturus* from ten to twelve inches, and the *Amphiuma* from ten to thirty inches.

The thyroxine was administered to all animals in the form of intramuscular injections of one milligram. Efforts were made to always maintain a sterile injection technique. Apparently some animals died at the beginning of the experiments from infection introduced at the injection site as sores developed. After more precautions were taken no more animals died this way. It was found more difficult to keep the animals alive in summer than in winter. Some *Amphiuma* apparently died from trauma resulting from bites of other *Amphiuma*.

When animals were sacrificed and wherever possible when they died, the arterial system was injected with vinyl resin as described by Baker (1949).

Amphiuma

Six animals were included in this study. Thyroxine was administered weekly to four animals. One animal died after two weeks, one after three weeks, one after four weeks, and one after five weeks. Two small animals received one-half dose of thyroxine; one died after one week and the other after two weeks. No external evidences of metamorphosis could be detected in any of the animals. Vinyl resin injections of the arterial systems were made in all possible cases. Since the work was carried on in the summer, autolysis had progressed so far by the time some animals were discovered that injection was impossible. The vinyl resin injections of the thyroxine treated animals did not differ significantly from those of control animals.

Siren

Four animals were included in this study. They received from seven to nine doses of thyroxine over a period of several months. All the animals died and the arterial systems were injected with vinyl resin except in one case where autolysis was evident. These injections were compared to those of control animals but there were no significant differences. There were no external evidences of metamorphosis. It was found that the gills would appear for days to be closely drawn knobs against the head of the animal but upon use and/or movement the filaments could be seen as large as ever. This observation was true of both the control and experimental animals.

Necturus

Fifteen animals were used in this study. A group of five animals were given doses of thyroxine approximately weekly. They survived over a period of from six weeks to three months. These specimens were examined frequently for external evidences of metamorphosis. There was no exophthalmos, reduction of gills or tail fin, or unusual skin sloughing. A certain amount of skin sloughing is normal whenever the animals are dried out in handling or even if they remain in an aquarium (Dawson, 1920; Grant, 1930). The gills at times when the animals were quiescent would appear as very small knobs folded back against the body. Examining the animals frequently for several days might reveal no movement of the gills which were apparently greatly reduced. At the next examination, however, the animals would be rhythmically moving the external gills which were fully expanded into numerous branchiae, red with blood. As the animals died the circulatory system of each one was injected with vinyl acetate and compared with control injections. No significant changes were observed.

A group of twelve *Necturus* were used in a further experiment. The animals were anesthetized before each injection in a 0.1 percent solution of chloretone until they wouldn't move when handled (Figge, 1954). After the thyroxine injection they were revived in running water. Eight animals received thyroxine, one received sterile saline solution, one was anesthetized only, and the other two were kept as control animals. After approximately weekly injections over a period of six months no external evidences of metamorphosis could be detected. They had a similar appearance to the group of five *Necturus* described above. At the end of this time three of the group of eight animals were subjected to x-ray radiation once a week for three weeks in addition to the thyroxine injections. The technique used was similar to that used by McCord and Marinus (1918). The animals were exposed for four minutes at a distance of twelve inches from the anode with a spark gap of five inches and a current of five milliamperes. A period of one week was allowed to elapse before the animals were sacrificed and the circulatory systems injected with vinyl resin. There were no external evidences of metamorphosis. The vinyl resin injections showed no evidences of metamorphosis when compared with control injections. One difference was noted. In untreated *Necturus* the external carotid artery arises from the first efferent arch then passes anteriorly by the first afferent artery and anastomoses with it (Baker, 1949). The presence of this carotid anastomosis or gill by-pass was also observed by Darnell (1949). The carotid anastomosis is a definite larval feature. In one vinyl resin replica of a thyroxine and x-ray treated *Necturus* this carotid anastomosis was absent on both sides.

Discussion

Some successful attempts to metamorphose the neotenous urodeles have been reported but none of these investigators showed the internal effects of metamorphosis on the circulatory system. The aortic arches probably would be first to show the effects of thyroxine administration. Since metamorphosis involves a change from gill respiration to lung respiration usually, the circulatory system must alter so that the change-over can occur. Other larval features that are absent in completely metamorphosed forms are the ductus Botalli, the ductus caroticus, and the branchial arteries. The carotid anastomosis is enlarged in metamorphosed amphibians to supply completely the external carotid because the original connection between the external carotid and the first efferent arch is lost. All these changes could be expected to appear if metamorphosis could be accomplished. Alphonse and Baumann (1935) reported that in *Bufo vulgaris* thyroxine administration speeds up the normal processes of metamorphosis and causes the premature metamorphosis of the vascular system far beyond other tissues. It was felt that the technique of injecting the circulatory system with vinyl resin (Baker, 1949) could be used to advantage in detecting even slight degrees of metamorphosis in neoten-

ous urodeles after thyroxine administration. However, the original purpose was not attained as no evidences of metamorphosis in any experimental animals were discovered.

Only two investigators (Jensen, 1916, 1920; Gutman, 1926) reported any success in metamorphosing *Necturus*. They both described a reduction or resorption of gills with a disappearance of gills in one animal. A similar appearance of reduced gills was described by Morgan and Sondheim (1932) in *Triturus* which were kept out of water in moss-filled jars. When the animals were placed in water the gills would expand and were functional. In the experimental work reported here the same observation was made of periods of apparent gill reduction followed by gill expansion. This was true of experimental and control animals. Since this is true, it would seem that the amount of gill reduction is a subjective observation. More objective evidence of metamorphosis such as changes in the aortic arches would be in order. To date no one has recorded such evidence.

The failure of *Necturus* to metamorphose can hardly be explained by the absence of the sixth arch and the spiral valve since Figge (1934) found that *Amblystoma* with the gills ligated to reproduce the condition found in *Necturus* would metamorphose under certain environmental conditions. The removal of the lungs of axolotls and tadpoles and the sixth arch of toad larvae with subsequent metamorphosis (Garber, 1930; Helff, 1931; Ichikawa, 1931) further substantiates this viewpoint. Since *Necturus* has an active and potent thyroid gland (Allen, 1938; Charipper and Corey, 1930; Grant, 1930; and Swingle, 1922), it is not a malfunction of the thyroid that causes neoteny. Grant (1930) concluded that the failure of *Necturus* to metamorphose is caused by some factor outside the endocrine system. Since Ingram (1929) has shown that inorganic iodine will cause metamorphosis in hypophysectomized and thyroidectomized axolotls, it would appear that the endocrine system is not at fault in *Necturus*.

Two other possible explanations for neoteny in Urodeles are: (1) the animals never possessed the genetic factors for typical amphibian development and (2) the larval tissues concerned have collectively lost the ability to respond to the thyroid activator. (Huxley and Hogben, 1922). It was noted by Kuhn (1933) that sensitivity to thyroxine decreases with increasing age. It might be more profitable to conduct experiments on young larvae if such forms were available.

The vinyl replicas of the arterial systems of thyroxine treated *Amphiuma* and *Siren* did not differ significantly from those of control animals. In *Necturus* treated with thyroxine over a period of months and with x-rays for a period of weeks the usual anastomoses between the first afferent artery and the external carotid artery were lacking. This is definitely not evidence of metamorphosis because the anastomoses should be enlarged so the blood could by-pass the gills. Baker (1949) pointed out that in the development of all am-

phibia the external carotid arises from the first efferent arch and subsequently anastomoses with the first afferent artery. As the state of metamorphosis increases the number of vessels in the carotid anastomosis decreases until only one remains. In *Siren* there are eight to ten vessels, *Necturus* has two to three, and *Amphiuma* one to two. This order indicates the degree of metamorphosis of each of the urodeles determined by structural features unrelated to the aortic arches. In completely metamorphosed animals the carotid anastomosis becomes the carotid gland and the external carotid arises from the median side of the gland after completely losing the earlier connection with the first efferent arch. Thus the lack of the carotid anastomosis would be regarded as a retrogression rather than metamorphosis.

Summary

Although some success has been reported in metamorphosing *Necturus*, no objective evidence such as changes in the aortic arches has been presented. It was the purpose of this study to procure such evidence but the animals showed no evidence of metamorphosis. The failure of *Necturus* to metamorphose is not due to the lack of the sixth arch and spiral valve. The thyroid gland of *Necturus* is active and potent and neoteny is not due to its malfunction.

Two possible explanations of neoteny in Urodeles are: (1) the animals never possessed the genetic factors for typical amphibian development, and (2) the larval tissues have collectively lost their ability to respond to the thyroid activator.

The vinyl resin injections of thyroxine treated *Amphiuma* and *Siren* showed no significant differences from control injections. The vinyl resin injection of thyroxiine and x-ray treated *Necturus* indicated a lack of the usual carotid anastomosis between the external carotid artery and the first afferent artery. This condition would be regarded as a retrogression instead of metamorphosis. The degree of metamorphosis in these Urodeles is illustrated by the degree of development of the carotid anastomosis.

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(Continued from page 31)

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