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FURTHER OBSERVATIONS ON THE LIFE-HISTORY OF THE NEWT, *TRITURUS VIRIDESCENS*

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In 1926 I pointed out that the newt *Triturus viridescens* Rafinesque does not always pass through a terrestrial red-eft stage as had been hitherto believed, since small aquatic newts collected on Long Island proved, on histological examination, to be sexually immature although metamorphosed. More recently Pope (1928) has discussed my conclusions which he says (p. 62) are "based upon local conditions on Long Island and do not apply to the greater part of the animal's range." The series of newts available to me was small and I was careful to emphasize that my data on the immature newt proved "merely that some sexually immature newts may be aquatic." Pope, in reviewing my paper, has raised a number of questions which it seems to me might be more profitably answered by considering the life-history of the newt in a mainland locality and thus avoid the objection that the material considered was physiologically even if not morphologically distinct from the material discussed by Pope. For this purpose I selected the Woods Hole region of Cape Cod, for during the past summer I enjoyed the privileges of investigator while at the Marine Biological Laboratory. My thanks are due to the Supply Department of the Laboratory in aiding me in collecting, to Mrs. L. Baker for technical assistance, and Mrs. E. M. Beutenmüller for the drawings made from my cleared preparations. The observations made at Woods Hole not only confirm but considerably extend the conclusions of my former paper.

THE WOODS HOLE NEWT

The newt in the Woods Hole region seems to show a preference for certain ponds. It was found abundantly in Whittemore's Pond, a small body of water between the sand-dunes about a quarter of a mile inland of Racing Beach, but was not found at all in a smaller pool in the woods opposite Endicott Lodge. The bottom of the latter pool was covered, during my investigation, with a thick layer of rotting leaves. Thirty larvæ of *Ambystoma maculatum* were collected here and a few tadpoles

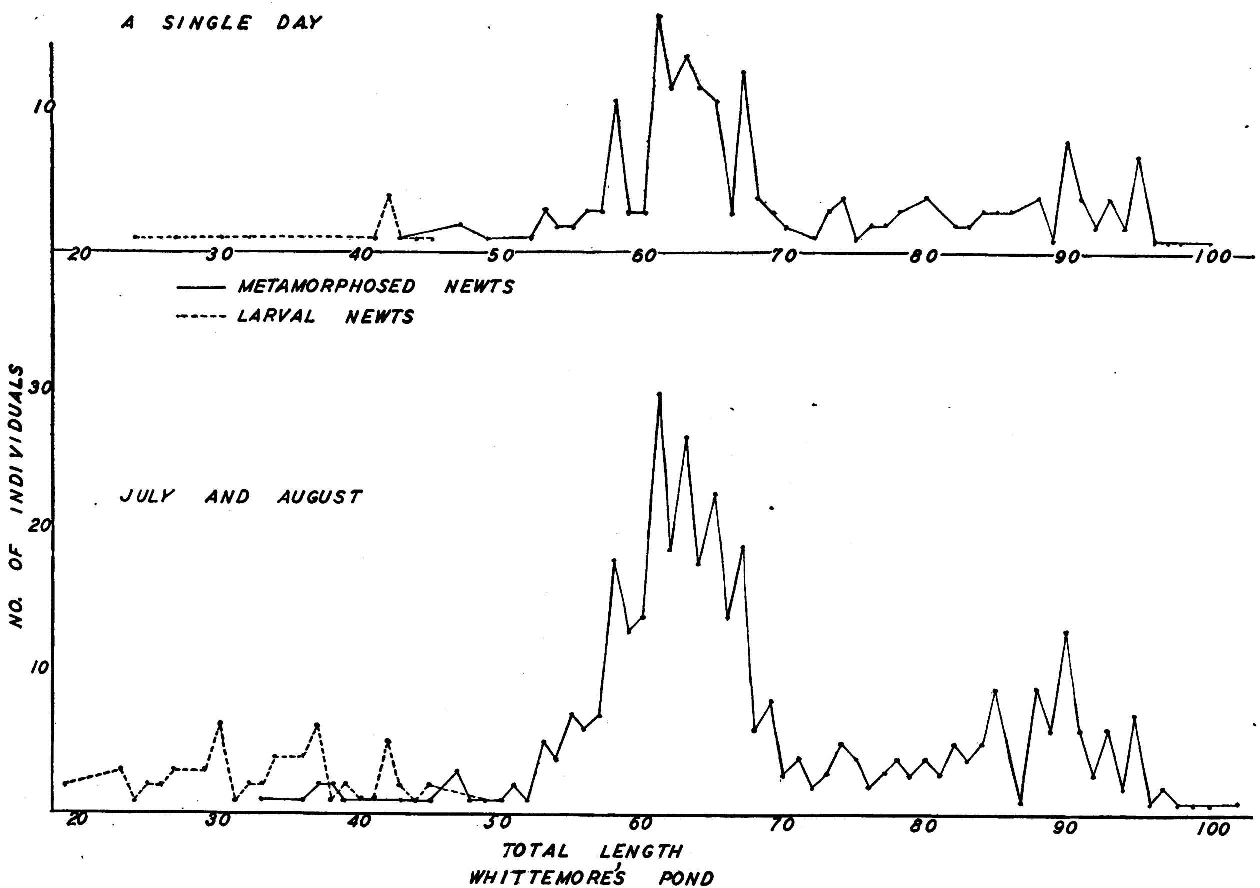

Fig. 1. Frequency graphs of larval and adult newts from a single pond in the Woods Hole region. One day's collection compared with the series obtained during July and August.

of *Hyla versicolor*. Weeks' Pond, near the main road from Woods Hole to Falmouth, was only twenty to thirty feet wide at the time of my observations but it contained newt larvæ as well as the larvæ of *A. maculatum, Hyla versicolor, H. crucifer* and *Rana clamitans.* Newts, both larval and adult, were found in two large ponds known to the Supply Department as the "Mashpee Ponds" and lying within the town of Mashpee near the Falmouth border. No newts were found in the several other ponds visited near Mashpee and Falmouth. Fish may be responsible for the absence of newts from some of the larger ponds but not from the Endicott Lodge pond. The species was abundant in the much smaller body of water on the Weeks' property. The only unusual feature of the Endicott Lodge pond was the thick deposit of decaying leaves which would tend to render the waters more acid.

In discussing the life-history of the newt, Pope (1928) takes exception to my statement that Long Island newts "do not require more than one season as a metamorphosed individual to reach sexual maturity," although he presents no data to show when he conceives newts reach maturity as distinguished from full size. I have dissected the gonads of a large series of the newts collected near Woods Hole and have found very large testes in fourteen newts from Whittemore's Pond collected from August 8 to August 29, and measuring 51.3 mm. to 64 mm. total length (28 to 32 head and body-length). As shown in figures 1 and 3 of a graph of the sizes of the total population collected from this pond at the same time, this size range covers the first mode of our graph of metamorphosed individuals. As the size at metamorphosis is known from a series of larvæ taken from Whittemore's Pond and metamorphosed in the laboratory to be approximately 32 mm. total length, there can be no interpretation other than that some Whittemore Pond newts, as some Long Islands newts, reach sexual maturity not later than one year after metamorphosis. The criteria of metamorphosis as used here include primarily the loss of body fin, the change of skin structure and color, and the transformation of the skull, exclusive of the hyobranchial apparatus.

The newts from the Mashpee ponds, as shown in graphs (Fig. 2 and 3), may reach a much larger size before metamorphosing (in the construction of all the graphs fractions have been increased or diminished to the nearest whole number). I have examined a series of fifteen larvæ measuring 56 mm. to 66 mm. total length which had greatly enlarged testes. In sections of the testis of one of these, measuring 61 mm. total length, and collected August 30, 1928, I found a large part of the tubules packed with

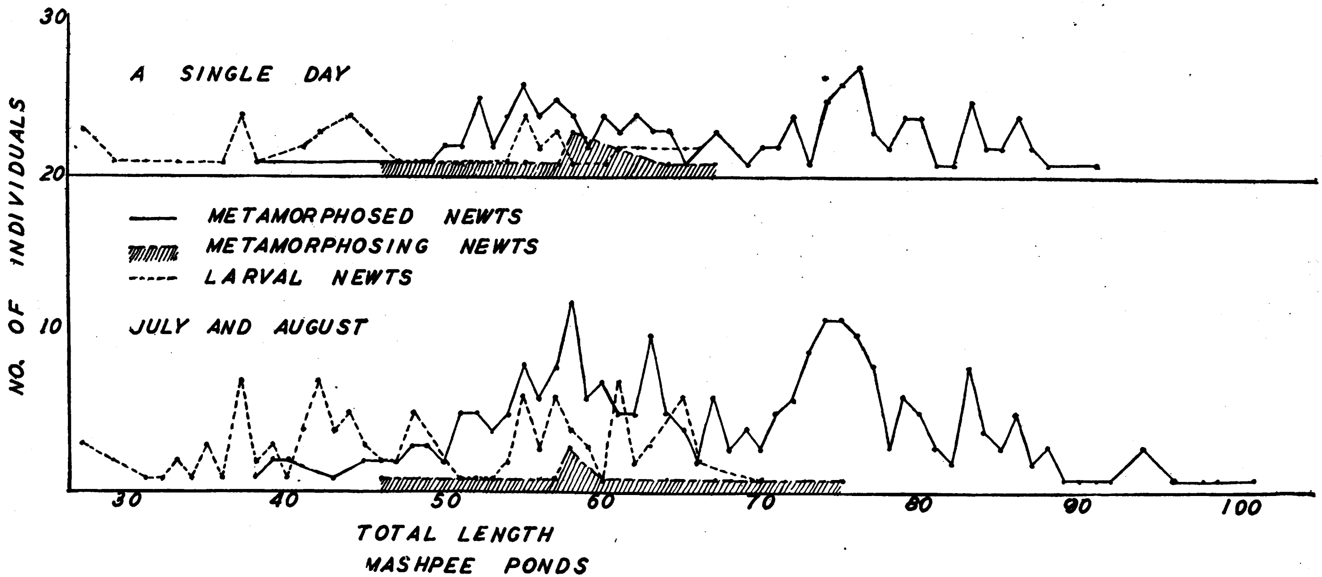

Fig. 2. Frequency graphs of larval, adult, and metamorphosing newts collected in two adjacent ponds in the Woods Hole region. The series collected in a single day compared with that collected during July and August.

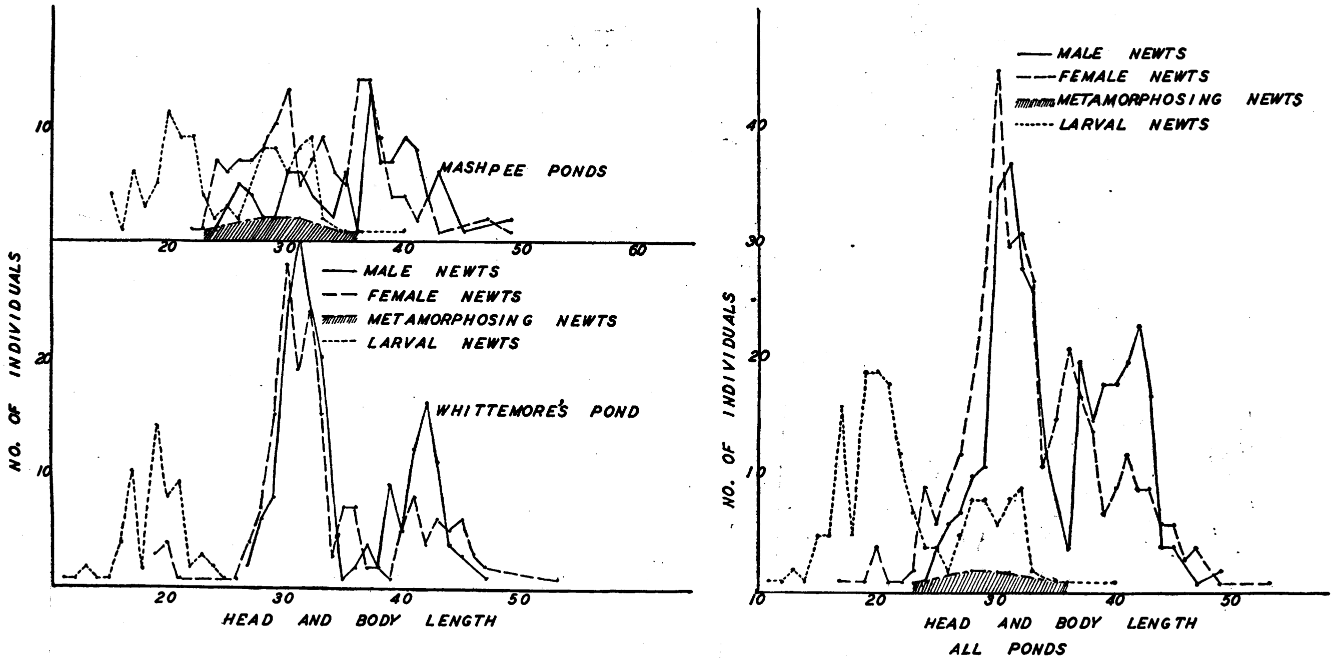

Fig. 3. Frequency graphs of newts from the Woods Hole region, head and body-lengths compared.

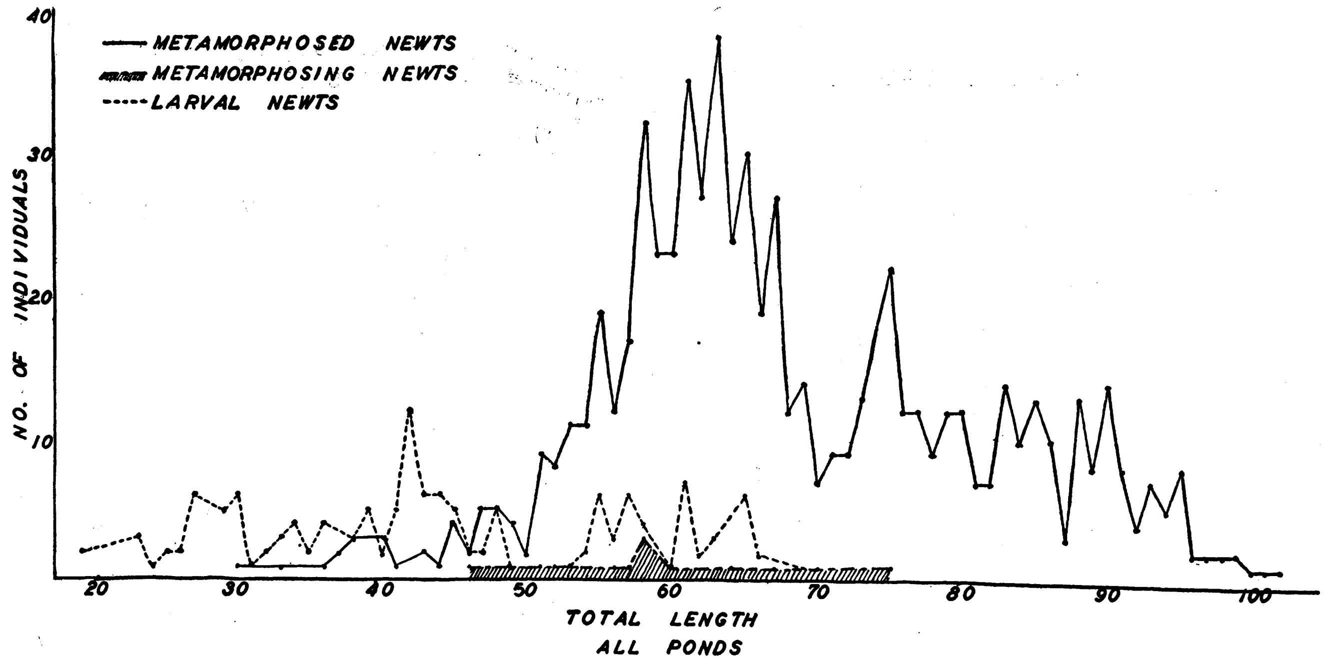

Fig. 4. Frequency graphs of newts from the Woods Hole region. The entire population collected in all ponds during July and August considered.

sperm. It is thus proved that some specimens of *Triturus viridescens* may reach sexual maturity while still larvæ.

Pope (1928) gives a lengthy discussion of the size at which newts metamorphose. He is unable to agree with me that Long Island newts probably metamorphose at different sizes and cites as evidence "a cold, spring fed pond in Manchester, Maine, where metamorphosis was delayed as much as two or three weeks, yet none of the larvæ grew any larger before metamorphosis than those in warm, shallow pools either in Maine or Pennsylvania." He adds, "Laboratory conditions do not seem to influence size either, for the larvæ raised from the egg metamorphosed at about the same size; from 28 to 34 mm." As shown in the graph (Fig. 2), I collected a series of metamorphosing newts in the Mashpee ponds. They ranged from 46 to 75 mm. total length. Further, I metamorphosed in the laboratory as early as July 27 three newt larvæ, from the same locality, measuring 45, 49 and 50.5 mm. respectively in total length. On the other hand, metamorphosed adults from Mashpee may range as low as 38 mm. total length. There is no doubt from the graph that some Mashpee newts in nature normally reach over 70 mm. total length before beginning metamorphosis. In contrast to this I found that larvæ from Whittemore's Pond and Weeks' Pond metamorphosed usually at a much smaller size. Of 380 metamorphosed newts from Whittemore's Pond, collected during July and August, the smallest was 37.5 mm. total length when taken in the field, while I collected larvæ as large as 50 mm. total length from the same locality. It appears, from the above, impossible to judge the years which have elapsed since metamorphosis on the basis of size alone, although Pope (1928) does not hesitate in reaching conclusions with such data.

At Woods Hole I studied over a thousand newts, 880 of which have been used in the construction of the graphs. All of these newts were collected in the water whether they were larvæ, immature metamorphosed individuals, or adults. One would conclude from field observations alone that the newt of the Woods Hole region never left the water for any extended period. But Pope (1928) states: "Various observers, from Monks (1880) down, have agreed that the larva becomes terrestrial upon metamorphosis. After a certain stage the metamorphic newt becomes helpless in the water and sometimes drowns unless given a chance to crawl out on land." This statement, if true, would not affect the conclusions I reached in the study of the Long Island newts for while I found that they passed "one spring and summer as dark reddish or yellowish forms in the water before reaching sexual maturity," I also found that "many of the ponds inhabited by newts either dry up entirely or become very low in the fall" and recently metamorphosed newts would have a short, enforced stay on land before the spring rains flooded their pools. However, I have tested Pope's contention by experiments on both Whittemore and Mashpee newts:

On July 11, I placed three larvæ from Mashpee in a jar with approximately a liter of water but without water-weed or floats. By the 27th all had metamorphosed and none during the process had floated for any period near the surface or showed any other symptoms of drowning. On July 17, I placed three others which had already begun to metamorphose in another jar without floats. By the 27th these had also metamorphosed in the water, without difficulty.

On August 8, several larvæ collected at Weeks' Pond were placed in a glass aquarium with approximately the same amount of water and by the 23d one of these had metamorphosed without making any attempt to leave the water.

On August 26, twenty-one of the larvæ collected at Whittemore's Pond metamorphosed in the small wooden tubs of several liters capacity where they were being kept in the dark. Only two of these were seen to be paddling near the surface in the manner common to many metamorphosing salamanders. This exception to the above results may be accounted for by assuming an overcrowding in the tub.

On August 31, one larva from Weeks' Pond, and a series from Mashpee and Whittemore ponds metamorphosed without any deaths and yet none left the aquaria or were seen floating near the surface.

These observations show conclusively that newts collected in the Woods Hole region may successfully metamorphose in the water without any extensive floating period and without the assistance of floats.

The chief point of Pope's recent paper (1928) is the reiteration of his belief that the red, land stage is not omitted from the life-history of any individuals of *Triturus viridescens*, even of those on Long Island which I showed to have a post-metamorphic life in the water before reaching sexual maturity. This subject may therefore be considered in some detail. Pope states: "there is much negative evidence from Gage (1891) down to show that intermediate sizes are not to be found in the water." An examination of the size graphs of the 880 newts from the ponds of the Woods Hole area, collected during July and August, 1928, will show positive evidence that all the intermediate sizes occur in the water during these months. Further, except for newts which live in temporary ponds, there is some positive evidence that the greater part of the newt population never leaves the ponds at any time of the year. This evidence is the presence of gill-rudiments and frequently gill-slits and larval branchial apparatus in metamorphosed newts. Of 249 metamorphosed newts collected in the Mashpee ponds only 13 lack gills or gill-rudiments and no less than 96 have the gill-slits fully open. Many breeding adults of both sexes have the gills fully developed although usually one or more is missing, apparently due to their having been bitten off. Adult newts having rudimentary gill-stubs almost invariably have the opercular fold fused to the throat and the gill-slits more or less closed. Of 380 metamorphosed newts collected in Whittemore's Pond only 3 small individuals were found with the gill-slits fully open. The great majority had the gill-slits closed but retained rudimentary gills, while 45 lacked all evidence of gills. Thus the Mashpee newts not only tend to reach a larger size before metamorphosing as shown above, but they tend to retain gill-slits, opercular fold, and well-developed gills. Further, gills or gill-rudiments are present in 95 per cent as contrasted with 88 per cent in the Whittemore newts.

It would seem certain that all newts with open gill-slits never passed an extensive period on land, while it would appear probable that none with gill-rudiments had enjoyed a terrestrial stage. I have tested this proposition by a number of experiments.

On July 11, seven recently metamorphosed newts with prominent gill-rudiments collected in Mashpee ponds and averaging 54.5 mm. total length were placed in a glass jar with dirt and damp moss but no free water. Seven others were put in a jar of the same size and about a liter of water added. By August 8 all trace of gill-rudiments had been lost from the first series while none had been lost from the second.

On July 17, five recently metamorphosed newts from the same place and about the size of the above were placed in a jar of the same size half full of wet sphagnum. Three of these had gill-rudiments. By August 8 all had lost the gill-rudiments.

On August 23, four large adults ranging from 74.5 to 94 mm. total length and averaging 82 mm. were placed in a glass jar with dry dirt and a little water added. These newts had the gill-clefts wide open, the opercular fold free and distinct gill-rudiments present. A control series, eleven others, were kept in water. ByAugust 31 it was necessary to discontinue the experiment but at this time three of the four had the gill-clefts closed and the fourth, which retained the largest gill-rudiments, had the clefts partly fused. In all four the gill-rudiments had become reduced.

These experiments demonstrate that terrestrial life causes a reduction of the gill-stubs and a fusion of the gill-clefts in metamorphosed newts. As enforced aquatic life never caused the redevelopment of the gill-stubs in any of the newts, I conclude that none of the adults having open gill-clefts or prominent gill-rudiments ever passed through a terrestrial stage in their life-history.

Nevertheless, it is probable that some newts in the Woods Hole region may undergo terrestrial migrations in the fall. Weeks' Pond was rapidly drying up by the end of August and Whittemore's Pond was low. It is highly probable that newts would hibernate among the aquatic vegetation at the bottom of the latter pond but Weeks' Pond had little vegetation and if any water remained during the winter it would freeze to the bottom. Thus it would seem possible that newts, to survive, would leave Weeks' Pond in the fall to hibernate under logs in the adjacent wood. On August 8 I found seven newt larvæ in this little pond but not a single adult in spite of a thorough scooping. No fish occur in this pond. I can think of no reason for the absence of adults other than that they left the pond as the water became low. No newts were seen by me on land although parts of several days were spent in turning over logs near the various ponds.

It is, therefore, possible that a few newts in the Woods Hole region undergo terrestrial migrations, but the great majority pass their entire life-cycle in the water. This raises the question of what happens to the red-eft stage in the ontogeny of these newts. In this connection the following observations are of interest.

(a) A series of newts was collected at Mashpee, July 9. On the same day several of these shed their skins indicating the beginning of metamorphosis. One metamorphosing individual measures 56.3 mm. total length (27.5 head and body-length) while two larvæ measure 52 and 57 mm. respectively in total length (24.7 and 18.5 head and body-length). In the same series there are fully metamorphosed (except for branchial region) adults measuring only 39, 43, and 46.5 mm. total length and many others ranging to a maximum of 97.7 mm. total length. None of the recently metamorphosed newts are reddish but a few are yellower than the others. Metamorphosis is marked by a change in coloration. The small larva is uniformly greenish gray, faintly stippled with a dark tone except for the immediate vicinity of the lateral-line organs, which is generally unpigmented. A series of indistinct dark spots is scattered over the body and is best developed on the tail. Metamorphosis induces an increase in number and size of the larger dark spots, particularly those on the body. It causes the appearance of yellow spots which later become vermilion and affects a darkening and a marked increase in the opacity of the integument. The larger larvæ assume some of the coloration of metamorphosis, for the skin is much browner, more spotted, and more opaque than that of smaller larvæ. Recently metamorphosed newts vary from brownish or yellowish to greenish.

(*b*) In a series of newts collected at Mashpee, July 16, there is one metamorphosing individual 75 mm. total length (36 mm. head and body-length). The larvæ measure from 48 to 61 mm. total length (28.5 to 39.5 mm. head and body-length). Some of the recently metamorphosed individuals measuring 69 to 72.5 mm. total length are distinctly reddish but others of the same size are brownish to brownish green. There is no difference of color between the coloration of the latter and that of newts over 90 mm. in total length.

(*c*) The larvæ collected July 11 and metamorphosed July 27 in the laboratory remained brownish and did not take on a reddish or orange hue. Of those larvæ collected July 17 and metamorphosed July 27 three took on a decided orange tone and one remained brownish. The metamorphosed individuals were kept in a separate terrarium and by August 31 none showed any further change in their coloration.

(*d*) The recently metamorphosed newts reported above as being placed in a dry terrarium turned dark chocolate-brown and developed rough skins; those placed in wet moss turned dark brown, slightly tinged with greenish. The controls remained brownish green. Thus, forced land-life caused a darkening and a browning of the skin but it did not induce the appearance of a reddish color.

(*e*) On August 21, eleven larvæ ranging from 60 to 65.5 mm. total length were collected at Mashpee, besides seven metamorphosing individuals of 46 to 66.3 mm. total length (22.5 to 31 mm. head and body-length). Several of these showed a decided reddish tone while others were merely brownish. Larvæ collected the same date ranged as small as 27 mm. total length (14.5 mm. head and body-length).

On August 26, twenty-one larvæ from Whittemore's Pond were metamorphosed in the laboratory without one showing any reddish or orange tone. Six more metamorphosed the 29th and a large number not included in the graphs on the 30th. None of these showed any reddish tones.

(*f*) A series of 14 newts from Whittemore's Pond were metamorphosed in the laboratory and kept in a terrarium at the American Museum in good health until the time of writing this note (February 1). One well-fed individual has become reddish brown but none a vermilion such as the color of a typical red eft. A control series has been kept in tanks well supplied with water-weed; these are paler and greener than the terrarium series.

From the above data it is clear that the newts of the Woods Hole region, unlike the Long Island newts, usually lack a reddish or orange color-phase in their ontogeny. Some newts from the Mashpee ponds exhibited a distinct suggestion of this color-phase but the Whittemore newts which metamorphose at a smaller size usually gave no evidence of passing through a reddish phase. Thus it appears that a terrestrial stage and a bright reddish color-stage, which usually coincide in Appalachian newts, are both lacking in Woods Hole newts, although a suggestion of the latter may occur in a few newts before metamorphosis and be continued for some months thereafter.

It has been demonstrated above that there is no terrestrial stage in the life-history of the Woods Hole newt and the stage will very probably be found to be omitted from the life-cycle of other newts living on the coastal plain. I have never found a typical red eft, and by this I mean the vermilion terrestrial form, on Long Island nor have any of the various naturalists who live there brought me one alive. However, Dr. S. C. Bishop, Mr. G. Engelhardt, and Mr. W. J. Shoonmaker collected a reddish immature newt 57 mm. in total length, on October 16, 1925, on the Hudson Estate, Syosset, at a distance from water. This is the place where November 8, 1921, I caught brownish newts under logs near water and considered them to be hibernating (Noble, 1926, p. 11). I have compared the first-mentioned newt with an individual which I collected as a larva at Mashpee and kept for a month after metamorphosis in a dry terrarium. There is no significant difference in size, dorsal coloration, or rugosity of skin in these two specimens. The ventral tone is slightly yellower in the Long Island specimen but this, as has been pointed out previously (Noble, 1926, p. 6), is a characteristic of aquatic Long Island newts. The specimen which was considered by its discoverers to be a red eft is in all probability an immature reddish newt beginning its hibernation on land. At least this specimen can not be taken as evidence that the red-eft stage occurs on Long Island. Newts, as I previously stated, may winter on land or in the water but the immatures never become vermilion or remain on land more than the one winter.

NEOTENY AND THE PROBLEM OF METAMORPHOSIS

The above observations are of interest in their bearing on the problem of metamorphosis. I have reported above the first instance of true neoteny in *Triturus viridescens*. Newts collected from the same pond have their metamorphic processes so delayed that frequently they fail to complete the transformation of all their structures. True neoteny or sexual maturity in the larval individual has been reported for various European newts: *Triturus alpestris*, Wichand (1906), Zeller (1899); *T. tæniatus*, Zeller (1899); *T. cristatus*, Ebner (1877), Kuhn (1925); and *T. vulgaris*, Bœttger and Schwarz (1928). Wichand (1906) described a case in *T. vulgaris* similar to the large Mashpee newts where all the external characters of the adult were developed but the gills were retained. By far the greater number of European naturalists have not distinguished in their writings between complete and partial failure to metamorphose. This is unfortunate, for the two phenomena, while unquestionably genetically related, should be clearly distinguished.

True neoteny is well known in many urodeles other than newts. The most familiar example is the axolotl. Here we must distinguish between the various races. In the Mexican race raised extensively in Europe the neoteny is hereditary while in the western races of *A. tigrinum* neoteny is in some forms at least environmental, produced by the direct effect of the cold (Uhlenhuth, 1921). The latter would seem to be the cause of neoteny in some specimens of *Salamandra salamandra* (Germershausen, 1910), and possibly the cause of neoteny in *Dicamptodon ensatus*, although I know of no experiments which definitely establish the point. It is apparently also the cause of neoteny in *Hynobiuslich enatus* (Sasaki, 1924), for this species, when reared in small temporary pools, metamorphoses the first year, when in cold lakes it reproduces as a larva. Cold would also seem to be the factor preventing metamorphosis in various newts living at high altitudes, as for example, in *Triturus alpestris* (Wichand, 1906). The mountain species, *Triturus wolterstorffi*, to judge from Boulenger's (1905) account, undergoes a partial metamorphosis similar to some Mashpee newts. On the other hand it has been well established that neoteny may occur sporadically among newts and other salamandrids living in warmer waters at low altitudes. The case reported by Van Swinderen (1924) in *Triturus tæniatus* was apparently very similar to that of the Mashpee newts, for the greater number of adults collected from a particular bog were neotenic. Van Swinderen describes them with gills present and with gill-slits open but does not state if the remainder of the characters were similar to those of a metamorphosed individual. Van Swinderen bred a neotenic female with a metamorphosed male and obtained 30 young, half of which were neotenic. The experiment, although incomplete, further suggests that newts localized in particular ponds may not metamorphose because of certain genetic factors. Van Swinderen makes it clear that his neotenic newts were maintained in good health.

If metamorphosis in some races of axolotl and in some localized groups of Old World newts is prevented by a hereditary cause, what might be the nature of this factor? It is well known that metamorphosis is induced by the secretion of the thyroid gland. Kuhn (1925) claimed that the thyroid of a neotenous *Triturus cristatus* showed various abnormal features but Duchosal and Junet (1927) failed to find any significant differences between the thyroid of a neotenous *T. alpestris* and that of a metamorphosed individual. Both observers may be correct, for in one case neoteny may be due to an abnormality of the thyroid and in another to the fact that an environmental or a genetic factor has prevented the release of the colloid from the thyroid follicles. Both Uhlenhuth (1921) and Swingle (1922) have stressed this releasing factor in their writings. Experiments in recent years have emphasized the close functional relationship between the anterior lobe of the pituitary and the thyroid. Hereditary neoteny may be due to changes in the thyroid or in mechanisms controlling the function of the thyroid. In the case of the Mashpee newts no attempt has been made at this time to determine whether the effect is environmental or genetic. But if the latter should prove to be the correct explanation it would lend support to the suggestion that the loss of the red-eft stage was also due to genetic factors.

There is another aspect of the problem of metamorphosis on which the present study has a direct bearing. I have indicated that authors have frequently failed to indicate whether they were considering sexually

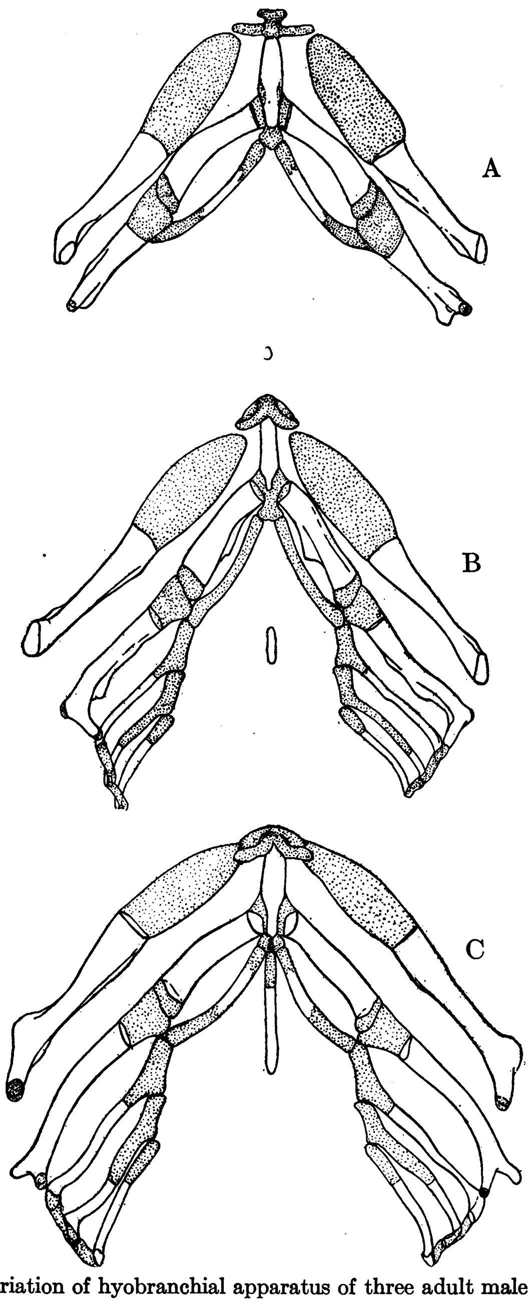

Fig. 5. Variation of hyobranchial apparatus of three adult male newts collected at Mashpee ponds, August 21, 1928. ×10.

(*a*) The gill-clefts closed and the gills reduced to stubs.
(*b*) The gill-clefts open but the opercular fold partly fused. Gill-rudiments present.
(*c*) Gill-clefts open and opercular fold free. Gill rudiments present.

Bone in outline, cartilage stippled.

mature larvæ or partly metamorphosed individuals. This raises the question: Does the delayed metamorphosis of the Mashpee newts shed any light on the nature of neoteny in the perennibranchs? An examination of the branchial apparatus of a series of adult male newts collected the same day in a Mashpee pond has revealed a great variation in the extent of transformation of this apparatus (Fig. 5*a–c*). Further, there is a close correlation with the extent of fusion of the opercular fold and closure of the gill-slits with the degree of metamorphic change attained by the branchial apparatus. On the other hand the degree of transformation has no relation to the extent of ossification of the hyobranchial apparatus. Thus, I find the hyobranchial apparatus in a series of recently metamorphosed newts from Whittemore's Pond is entirely cartilaginous while in the adults with gill-slits open, collected at Mashpee, some ossification occurs in each of the four pairs of epibranchials, as well as in other parts of the apparatus.

It is noteworthy that in practically all of the large adult male newts from Mashpee the skull has completed its metamorphic changes. The only exception I have found in a series of ten skulls is that one retained the coronoids in the lower jaw (Fig. 6) although these were fused to the dentaries. Thus the Mashpee newts eventually metamorphose completely except that some retain gills and open gill-slits. In those with

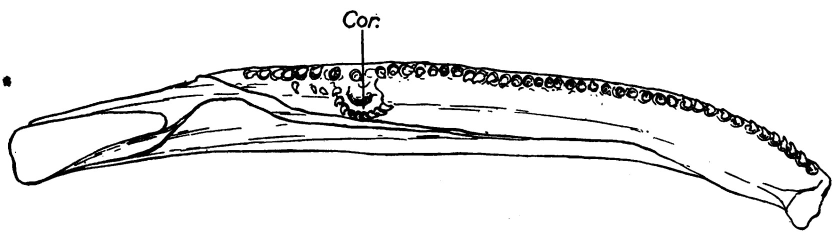

Fig. 6. Oblique view from above of the left half of the lower jaw of an adult female newt showing the retention of the coronoid. The gill-clefts were closed in this individual. ×20.

Cor. =Coronoid.

slits open and opercular fold free the branchial apparatus of the larva is retained while those which have undergone some fusion in fold exhibit some metamorphic change in the hyobranchial apparatus. Has the fact that the hyobranchial apparatus is the last part of the skeleton to undergo metamorphosis any general significance?

There is considerable difference of opinion in the literature as to the extent of metamorphic change which the various perennibranchs exhibit, and it may be of interest to see what bearing the delayed metamorphosis of the Mashpee newts has on this subject. If we consider only the most obvious changes of ontogeny, namely, the development of limbs, of maxillary bones, the loss of gills and reduction of branchial apparatus, etc., we might consider *Siren* a form which has ceased to differentiate beyond a very early stage of larval life. *Proteus* and *Necturus* would be forms which had reached a later stage of urodele ontogeny, *Cryptobranchus* one which had begun its metamorphosis, and *Megalobatrachus* and *Amphiuma* forms which, like some Mashpee newts, had nearly completed their metamorphosis.

A closer examination of the development of the perennibranchs will reveal that none of them run through a series of developmental stages identical in detail with those of caducibranchs. In all cases the growth or differentiation of certain parts is either speeded up or else eliminated entirely, making it difficult to compare the various stages in forms which are permanent larvæ with those which metamorphose. This state of affairs may be considered more closely.

The morphology of metamorphosis in urodeles has been considered recently in great detail by Wilder (1925) who states: "H. H. Wilder (1891) showed the similarity of *Siren* to *Siredon* (axolotl) and designated *Siren* as a degenerate larval form. With the more extended recognition of stages of development involved in the present discussion, I should classify *Siren* as a degenerate late metamorphic or transition form. The recently reported case of an example of *Siren* in which gills were wanting (Viosca, 1924) is corroborative of this view."

The loss of the gills has nothing to do with metamorphosis in *Siren* as I showed by experiment (Noble, 1924) but may be readily induced by keeping the animals in irritating fluids. Further, Blatchley (1899) had previously found *Siren* on land with the gills fully reduced. Irritating media or exposure to air induce a reduction of the gills but do not affect the branchial skeleton or other parts of the animal's organization.

On the other hand, *Siren* is distinctly a larva in its jaws (maxillaries lacking, dentigerous coronoids, and horny dentary plates present), its lidless eyes without lacrymal ducts, its hyobranchial apparatus, its hæmal arches incomplete ventrally, and its limbs—the hind pair never developing. Further, its glandless cloaca might be considered a larval feature. What, then, are its late metamorphic characters which Wilder stresses? Wilder does not state, but by comparison with the earlier literature and with the long list of criteria of metamorphosis given for *Eurycea bislineata* we may conclude that there are a number of modifications in *Siren* which require further explanation.

EAR OSSICLES.—Reed (1920) states that "the complete absence of the columella in *Siren* points to an extended period of terrestrial existence further back in its phylogeny." It is probable that the most primitive urodeles were largely terrestrial, but has this any bearing on the loss of the columella of *Siren?* I have found from the study of a series of cleared specimens of *Siren* that the operculum begins to ossify when the animal is only 55 mm. in total length. At this time the squamosal is approximately seven times the greatest length of the operculum away from the latter structure. In *Necturus* and *Typhlotriton* larvæ of about the same stage the distance between squamosal and operculum is approximately equal to the length of the latter. It would seem that the lengthening and narrowing of the snout in *Siren* had carried forward the squamosal, and the columella never formed, since it could not function without enormously increasing its length. I have not seen any change suggestive of metamorphosis in the otic apparatus of *Siren.*

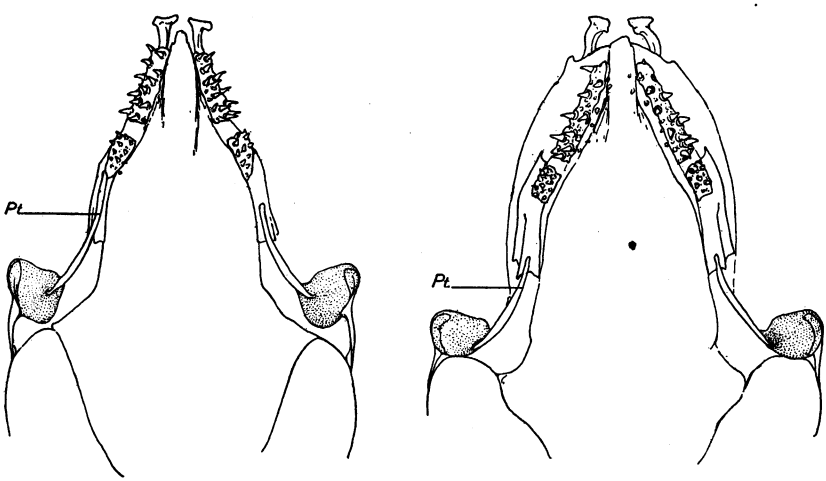

Fig. 7. The splitting of the palato-quadrate bar in *Siren lacertina*, a change which resembles metamorphosis in part but which is probably due to the disharmonic growth of the head. Ventral aspect of the palate region. × 30

(*a*) Individual, 42 mm. total length, showing the break on the left but not on the right side.
(*b*) Individual, 51 mm. total length, the pterygoid elements having already begun to degenerate.
Pt = Pterygoid.

PTERYGOID.—One of the most conspicuous changes of metamorphosis in urodeles is the splitting of the pterygo-palatine bar into two main parts. (Compare Wilder, 1925, Plate VIII, fig. 6, and Wintrebert, 1922, Fig. 37, with my Fig. 7.) Subsequently the bony pterygoid may be lost or considerably altered in form. A similar phenomena occurs in *Siren* between the 55 and 60 mm. stage. And subsequently the bony remnant of the pterygoid is lost as a distinct element. But the palatine element of the bar fails to continue the usual changes seen during metamorphosis in other salamanders.

Hence, here again we may consider this change as due to disproportionate growth of adjacent areas rather than to a thyroid activity. No metamorphic change of eyes, gills, branchial arches, or any other part of the animal occurs at this time, which is further evidence that the change is not to be considered one of metamorphosis.

JACOBSON'S ORGAN.—Another peculiarity of the adult *Siren* which might suggest that the species was well on the road to metamorphosis is its extraordinarily developed Jacobson's Organ. Wilder (1891) compared the Jacobson's Organ in *Siren* with that in the axolotl. As it is well developed in the latter the presence of a Jacobson's Organ is no criterion of metamorphosis. What might its hypertrophy signify? *Siren*, in spite of its long body, is not a burrowing but an aquatic form. Bruner (1914) pointed out that the external nares of *Siren* were valveless and this alone would preclude extensive burrowing operations. Gothard (as quoted by Werner, 1912) has shown in the laboratory that the species is primarily aquatic. But Blatchley (1899) and Viosca (1924) have noted in the field that the animal may live on land. The Jacobson's Organ is generally believed to have developed in the first tetrapods in correlation with land-life and it is possible that its hypertrophy in *Siren* may have developed in connection with special feeding habits in or out of water. As Jacobson's Organ develops before metamorphosis in many salamanders its presence in *Siren* is of interest but has no bearing on the present problem.

SKIN.—Endocrinologists who have studied the metamorphosis of Amphibia usually consider the first shedding of the skin in large pieces as proof that metamorphosis has begun. As pointed out many times, this shedding is usually accompanied by definite changes in the structure of the epidermis. The most conspicuous change in urodeles is a loss of the large Leydig cells. Other changes include the cornification of the superficial layers of the epidermis, the increase in thickness of the epidermis, the increase in the number of glands, etc. The changes in the epidermis differ with the species but most investigators have settled on the shedding of the skin as one of the most convenient criteria of metamorphosis and the loss of the Leydig cells has been considered proof that metamorphosis has occurred (Opacki, 1926).

Turning to the perennibranchs and derotremes we find that these criteria would define several forms as having metamorphosed. Wilder (1925) states that *Cryptobranchus*, *Amphiuma* and *Siren* "have a characteristically adult type of glandular skin with a remarkably well-developed *stratum corneum*, and with no Leydig cells, while in other respects the first two at least exhibit a fully adult, though somewhat degenerate structure. *Siren* alone with its retention of larval gills suggests the possibility of a form which has reached the late metamorphic stage with failure to transform and has secondarily become degenerate in structure."

As I have not made a histological study of the skin of perennibranchs or derotremes at different stages, I am unable to state when this apparent metamorphosis of the skin occurs. At the present moment the skin alone, of all the structures of *Siren*, seems to have undergone a complete metamorphosis.

Wilder (*loc. cit.*) speaks of *Cryptobranchus* and *Amphiuma* as exhibiting a "fully adult" structure. This would not apply to the branchial arches which are more larval than adult. Nor would it apply to the eye region. The lack of lids and lacrymal duct is a larval feature although Plate (1924, p. 309) attempts to correlate these losses with a degeneration of the eyes instead of with the more obvious feature of failure to metamorphose. The anterior position of the vomerine teeth is a larval character especially in *Cryptobranchus*.

The loss of gills in *Cryptobranchus* at a certain stage of development has been considered evidence of metamorphosis and the fusion of the opercular folds to the underlying integument would certainly come under this head. *Megalobatrachus* undergoes a partial metamorphosis of its branchial apparatus (Fukuda, 1928). If every perennibranch began as *Megalobatrachus*, with a typical larval hyobranchial apparatus, we could state to what extent each species is metamorphosed, for we could utilize as a scale of reference the degree of change in this apparatus. I have examined young *Amphiuma* within the egg-capsule, as well as older individuals, and have found that the second ceratobranchial is lacking in all. In *Necturus*, shortly after hatching, I have found the branchial arches to have the same reduced number and general form as the adult. It seemed in both these cases as if not enough branchial arch-forming material had been present when the arches were laid down, for certainly these reductions were in no sense a metamorphosis. Again, the development of the maxillæ in *Eurycea bislineata* is considered one of the criteria of metamorphosis by Wilder (1925), but these structures are present in old axolotls which no endocrinologist has ever considered to be metamorphosed. Further, in *Amphiuma* the development of the maxillæ is not correlated with any definite metamorphic change. In brief, metamorphosis is a series of changes proceeding at different rates and at different times in different species. For purposes of description it is necessary to consider one or more characters as the more important criteria. As *Megalobatrachus* undergoes more metamorphic changes than any other perennibranch or derotreme it may well be considered the standard of reference. In this species the changes in the hyobranchial apparatus seem to mark the climax of metamorphosis. We may describe *Megalobatrachus* as an enormous hynobiid salamander which has well begun but not quite completed its metamorphosis. Referring the Mashpee newts to the same standard it is found that they have run ahead of *Megalobatrachus* in the eye, lacrymal, and vomerine changes while many have fallen behind in the branchial changes. Comparing *Siren* to the standard it would be classified as a little developed larva which has hypertrophied its Jacobson's Organ and reduced its pterygoid while developing certain peculiarities such as the ossified coracoids, elongate body, and reduced ear ossicles. It may have evolved from hynobiids but the relationship is not close.

The Mashpee newts are of interest for they show how variable one of the best criteria of metamorphosis, namely, the degree of change in the hyobranchial skeleton, may be in some cases. Further, they show to what a great extent apparent metamorphic changes in the branchial region may be affected by the environment.

CONCLUSIONS

(1) The newt of the Woods Hole region passes through no terrestrial red-eft stage but usually lives throughout life in the water. Since temporary pools may be inhabited by newts some migration may occur. During July and August all growth-stages above that of the early larva are found in the water.

(2) Some male newts reach sexual maturity one year after metamorphosis.

(3) A typical larva from a Mashpee pond was found to contain fully formed spermatozoa. This is the first report of true neoteny in *Triturus viridescens*.

(4) Many newts in the Woods Hole region fail to complete metamorphosis but retain open gill-clefts, a more or less larval branchial apparatus and gills partly or fully developed. Partial neoteny is more pronounced in the Mashpee than in other ponds.

(5) The subjection of the incompletely metamorphosed newts to terrestrial conditions causes a fusion of the gill-clefts and a reduction of the gill-stubs.

(6) Perennibranchs and derotremes are not urodeles which have ceased differentiation at definite ontogenetic levels. Some of their structures, such as the skin, may have metamorphosed while others, such as the jaws, may have remained those of a larva. Certain larval structures may never appear during ontogeny, while others undergo changes which are not metamorphic.

(7) *Siren* is a form which has ceased to differentiate most of its structures beyond the stage characteristic of an early larva.

(8) Metamorphosis is a series of changes proceeding at different rates and at different times in different species.

(9) The degree of change in the hyobranchial skeleton affords one of the best criteria of metamorphosis.

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