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AN OUTLINE OF THE RELATION OF ONTOGENY TO PHYLOGENY WITHIN THE AMPHIBIA. II.

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In the preceding number I have pointed out the value of life history in determining the relationships of many of the disputed genera of Salientia. We may go further than this in the urodeles and sketch an actual (even though fragmentary) phylogeny of life history, for in this group there are fewer genera to consider, their life histories are usually better known than in the Salientia, and only a few forms have suffered a sudden change in the yolk content of their eggs. To conclude this discussion of the relation of ontogeny to phylogeny within the Amphibia (see the two preceding papers, Amer. Mus. Novitates Nos. 164, 165), we may run rapidly over the progressive changes in life history found within the Caudata.

The most primitive urodeles existing today are included in the families Hynobiidæ and Cryptobranchidæ. Both of these practice external fertilization but, as the males of *Cryptobranchus* and *Hynobius* are provided with cloacal glands, we may assume that this condition has resulted from a secondary degeneration. Only one type of gland surrounds the cloacas of these genera, not two or three, as in other families. These glands are subject to many changes and even closely related species may differ in the presence or absence of one of the glands, the abdominal. The hynobiids form a very uniform group and their life histories are equally uniform. All species, so far as known, lay their eggs in two spindle-like sacs (Dunn, 1923). *Hynobius*, the least specialized genus of the family, has a life history very similar to that of *Ambystoma maculatum*. The eggs vary in size from 2.5 mm. to 3.2 mm. (exclusive of capsules). There are from 35 to 70 eggs within each sac. They are laid in quiet or slow-moving water. One end of the egg sac is usually attached, although rarely the sacs are found free on the bottom. The early larvæ so far as known, are all *Ambystoma*-like with a dorsal fin, balancers, and long, external gills. The legs develop slowly, the anterior pair in advance of the posterior ones. In short, there is nothing in the life history of *Hynobius* except the external fertilization and the spindle shape of the egg sacs to distinguish it from that of

the pond-breeding species of *Ambystoma*. A close comparison will show minute differences, some of which—such as the reported double balancers to *H. nœvius*—may require further explanation, but on the whole the details are astonishingly similar.

The mountain-brook genera of hynobiids, *Onychodactylus* and *Ranodon*, retain the spindle-like egg capsules. These genera have probably arisen independently from *Hynobius* but frequenting the same habitat they possess certain specializations which are common to practically all mountain-brook forms and cannot be used as characters indicating relationship. These “habitus” characters are (1) increase in egg-size and reduction in number, (2) loss of balancer, (3) restriction of dorsal fin to the tail and its reduction in width, (4) loss of digital elongation at an early stage, (5) reduction of gill rachis, the gill filaments appearing short and bushy, not branch-like. Modifications 2–5 seem directly correlated with life in swift water and may have been easily brought about by natural selection. It is difficult to account for the increase in egg-size in mountain-brook forms, especially as changes in yolk content have not occurred so haphazardly in the urodeles as in the Salientia.

The Cryptobranchidæ have arisen directly from the Hynobiidæ. The two genera which comprise this family are both “permanent larvæ” of some unknown hynobiid. *Cryptobranchus* in its open branchial clefts and greater number of branchial arches is more larval, i. e., has assumed fewer metamorphic changes than *Megalobatrachus*. The life history of these two genera as shown by Smith (1912) and others is practically identical. Their life histories do not differ radically from that of *Ranodon sibiricus*. Fertilization is external. The “slim and spindle-shaped” egg sacs of the latter species are here elongated until they form two cords. The outer egg capsule does not form a sac but merely a covering to the individual eggs and the gelatinous connection between eggs. The eggs, although large, are proportionately smaller (as compared with body length of female) than in *Ranodon*. They are also more numerous. A detailed comparison of the egg capsule and larvæ cannot be made because of our inadequate knowledge of the development of *Ranodon*. It should be noted, however, that *Cryptobranchus* larvæ have no body fin, no elongate digits at an early stage, and that their external gills are short. Most of these “swift-water adaptations” are found in the larva of *Ranodon*.

The Sirenidæ form the “most larval” group of all salamanders. Their relationships are unknown. The life history does not help us to determine these relationships for the eggs are very small and the re-

cently hatched larvæ are very similar to the adults. The horny mouth-parts of both larva and adult may perhaps be compared with the pre-dental sheath in *Ambystoma* and *Onychodactylus* larvæ. I have shown elsewhere (Noble, 1924b) that the "retrograde metamorphosis" of the Sirenidæ is in no sense an attempt to metamorphose.

The Proteidæ are "more larval" than *Cryptobranchus* and "more adult" than *Siren*. It is generally agreed that they are not closely allied to any existing family. In the Sirenidæ the eggs and early larvæ of the two genera in the family are much alike and readily distinguished from all other larvæ. Similarly in the Proteidæ we find a close resemblance between eggs and larvæ of the two genera in the family. In both *Necturus* and *Proteus* the eggs are laid singly, attached to the undersurface of some object in still or slowly running water. The number of eggs varies, 66 being an average for *Necturus* and 50 for *Proteus*. Two well-defined capsules surround each egg in addition to a vitelline membrane of duplex origin. The eggs are large, 4 mm. being an average diameter for *Proteus* and 5.8 mm. for the larger *Necturus*. The egg capsules of *Necturus* are narrower than those of *Proteus*, but the form is the same. The larvæ of the two genera have the same shaped head, gills, and exhibit the same general proportions in their appendages. *Proteus* under adverse conditions (cold, starvation, etc.) may retain the larva within the oviducts until well formed. Neither oviducts nor larva are known to be especially modified for this intra-uterine development. The larva remains very similar to that of *Necturus*.

The Ambystomidæ exhibit the same modifications as the Hynobiidæ. Pond-breeders have small-yolked eggs and broad-finned dodging larvæ equipped with long digits and balancers. Mountain-brook forms such as *Rhyacotriton* and *Dicamptodon* have larvæ with restricted dorsal fins, shorter gills, and shorter limbs. A few species of *Ambystoma* (*A. opacum*, *A. annulatum*, and occasionally *A. maculatum*) lay their eggs on land and wait for the rains or rising waters to cover them. The eggs may develop slowly but the larvæ on escaping from the capsules take up their lives in the water and exhibit the broad fins and larval peculiarities characteristic of the other species of *Ambystoma*. No *Ambystoma* has succeeded in freeing itself from its aquatic larval life, nor from the *Ambystoma* larval "habitus."

The Salamandridæ are related to both hynobiids and ambystomids but probably arose from some pre-hynobiid stock. The eggs of the more primitive genera, *Tylototriton* and *Pleurodeles*, are very similar to those of *Ambystoma maculatum* and *A. tigrinum*. They are laid in ponds and the

larvæ which emerge are of the "pond-type,"—that is, they have the broad tail, dorsal fin, and long gills of *Ambystoma*. Certain salamandrids breed in mountain brooks and their larvæ have the mountain-brook "habitus." Perhaps the best known of these species is *Euproctus asper*. It attaches its eggs singly to the underside of stones in running water. They are unpigmented and of large size (4.5–5 mm.). The Salamandridæ are not so uniform a group as the Ambystomidæ. The relationships of *Salamandra* are not clear, but such features as the long ypsiloid apparatus would indicate that it might have been derived from pond-breeding ancestors. *Salamandra* is a mountain form and the large eggs of *S. maculosa* would suggest affinity to *Euproctus*. But the larva as it develops shows definite evidence of a "pond-type" ancestry. A balancer is present in both *S. atra* and *S. maculosa*, although, of course, rudimentary and non-functional (Wunderer, 1910a). This balancer we have found characteristic of "pond-type" larvæ, whether of *Hynobius*, *Ambystoma*, or *Triturus*. It is never found in any mountain-brook forms nor in genera such as *Hemidactylium* which have been derived from terrestrial or mountain-brook forms. The adult *Salamandra* shows no mountain-brook adaptations such as lunglessness or modified integument. Both anatomical and life history data point towards a pond-type ancestry for *Salamandra*.

Within the genus *Salamandra* we find what appears to be a considerable difference in life history. *S. atra* gives birth to metamorphosed young, while *S. maculosa* to larvæ in various stages of development. Wunderer (1910), impressed by the difference in egg-size between these two species and their consequent differences in development, is inclined to believe the two species not closely related. In the Salientia we have seen great differences in egg-size within the genus *Gastrotheca*. But the extreme larval specializations reoccurred in every species. In *Salamandra* there are two conspicuous specializations: the highly vasculated oviducts and the long filamentous gills of the larva. These features are found in both *S. atra* and *S. maculosa*.

The next family in our phylogenetic survey may be mentioned briefly. *Amphiuma* is a "permanent larva" derived from some unknown genus. It is important to note that its eggs and larvæ do not agree in detail with those of any other urodele. It may be added that its life history approaches nearer to that of the plethodontids than to the crypto-branchids and sirenids with which *Amphiuma* is frequently compared. *Amphiuma* possesses lungs and hence could not have been derived from any plethodontid. The similarity of life history between *Desmognathus*

fuscus and *Amphiuma* is due to parallelism in divergent stocks from a common, probably salamandrid, ancestry.

By far the best family of urodeles to follow through in this phylogenetic survey of life-history evolution is the Plethodontidæ. Wilder and Dunn (1920) have emphasized that the family probably arose in a mountain-brook habitat. The plethodontids arose from salamandrids, and in life history the most primitive genera of the family agree closely with *Euproctus*. *Gyrinophilus danielsi* has been found by Bishop (1924) to attach its eggs to the underside of stones in the water. *Pseudotriton montanus* has large, unpigmented eggs, but they are apparently laid among the leaves in running water and not attached to an overhanging rock. *Eurycea* conforms to *Gyrinophilus* in its egg-laying, although its derivative, *Manculus*, may scatter its eggs among dead leaves as in the case of *Pseudotriton*. Within the genus *Desmognathus* there occurs a gradual change from an aquatic to a terrestrial breeding habit. The primitive *Desmognathus quadra-maculatus* lays its eggs in the manner of *Eurycea*, although these eggs may be in or out of water. *Leurognathus marmorata* which has been directly evolved from *D. quadra-maculatus* was found by Pope (1924) to have identical breeding habits. *D. phoca* which is more terrestrial than *D. quadra-maculatus* lays its eggs in the manner of the latter but, so far as known, always out of water. The eggs of *D. fusca* differ from those of *D. phoca* in that they are laid in the form of a rosary and are not attached singly. In this series of species, *D. quadra-maculatus*, *D. phoca*, and *D. fuscus*, a gradual change occurs from a condition in which the eggs are laid singly on the underside of stones in the water, as in *Eurycea bislineata*, to a condition in which the eggs are laid in a single string (or stringy cluster) at a short distance from the water.

The larvæ of the various species of *Desmognathus* and *Leurognathus* are very similar as to body and gill form. The larvæ while within the egg capsules have long and filamentous gills. When they escape into the water these gills become shorter and form a brush on each side of the neck. There is never a short central ramus with a fringe of filaments as in the more primitive salamandrids. The current does not mold the gills of mountain-brook salamanders; it merely places a limit on their greatest extent in length.

Desmognathus is in some characters more primitive than *Plethodon* even though it is probably not directly ancestral to it. *Plethodon* is well known to pass its entire life on land. To the several species whose life history has been studied in detail, I may add *Plethodon vandykei*.

Mr. Phillips Putnam has sent me a cluster of eggs of this species which he found "fastened together in a grape-like mass and attached to the stone by a string of elastic material." The stone was in a damp situation and covered by moss. At this writing I shall not report in detail on these eggs nor attempt to make comparisons between the larvæ of *Plethodon* and related genera. Suffice it to say that *Autodax* and *Batrachoseps* which have been directly derived from *Plethodon* have the same life-history mode. The eggs are laid on land; development is direct. Certain differences in gill-form have been found in the different genera. These have been accounted for by Emmel (1924, p. 372) in an ingenious way.

One genus of plethodontids may receive special mention. *Hemidactylium*, although directly derived from *Plethodon*, passes a larval life in the water. Bishop (1919, p. 266) concludes: "The large number of eggs deposited, their intimate relation to sources of moisture and early absorption of the yolk, indicate recent adaptation to terrestrial life."

Is this the correct interpretation? Yolk-size differs in certain related species of salamandrids. Increase in egg-number usually accompanies a reduction in egg-size. Such a reduction in yolk-content must mean an early larval life outside the egg capsules. A close parallel occurs in *Gastrotheca*. The failure to develop "stag-horn" gills may mean only a precocial start towards gills adapted to the water. The gills of *Hemidactylium* are not like those of *Desmognathus* or *Eurycea*. They have some features in common with those of *Batrachoseps*. In short, the life cycle of *Hemidactylium* seems to have been forced on it by a reduction of the yolk. Such a yolk reduction has occurred many times in the Salientia. If a larva is poorly provided with yolk and its ancestors had no special larval modifications which may have been passed on to the derived forms, the relations of the latter are very difficult to determine on the basis of life history.

There remains to be mentioned only three highly specialized plethodontids. These, *Hydromantes*, *Ædipus*, and *Ædipina*, are terrestrial and apparently closely related. All three give birth to their young alive. Anatomically these genera have much in common with *Plethodon*. They may have arisen directly from *Plethodon*, although *Ædipus* shows certain features in common with *Eurycea*. It is interesting to note that the only viviparous plethodontids are closely related and were possibly derived from forms laying large-yolked eggs on land. Life history is not the plastic, changeable process usually supposed. Life history is a much better indicator of relationship than usually conceded.

Life history is not, however, progressively modified the more specialized an adult may become. Occasionally larval specialization will

occur before the adult modification has arisen, as, for example, in the case of *Hyla uranochroa* or *Rana opisthodon*. Rarely, a single natural genus may show two types of life history, both its own or more characteristic one and another one found in a derived genus. There is no reason why we should expect that life history when it changes from one to another type should do so exactly at that point in our phylogenetic tree where one genus branches from another. Life history affords even in these cases evidence of relationship.

In drawing this sketch to a conclusion it may be well to view the whole subject for a moment from a distance. Exactly what is the relation of ontogeny to phylogeny in the Amphibia? Is there any evidence of ontogeny repeating phylogeny? What happens to the life history as the adults are modified? We have seen above that the modus of life history and especially the larval type remains in most of these cases unchanged. This general rule was found to maintain for many pairs of genera such as *Paludicola* and *Eupemphix*, *Phyllobates* and *Dendrobates*, *Kalophrynus* and *Microhyla*, etc. The adults of one genus of each of these pairs are modified beyond the condition shown by the others; but the life history, fortunately highly specialized, remains the same in each pair as evidence of their relationship.

The ancestry of the Salientia, in spite of our great advances in palæontology, has remained a matter of conjecture. I have recently shown (Noble, 1924a) that the most primitive of living frogs, the Liopelmidæ, are very similar to the urodeles in their vertebræ, musculature, vascular system, etc. It has been maintained for many years that the urodeles arose from the branchiosaurs. If we compare the adult liopelmids with the branchiosaurs we must admit that they approach nearer to the latter in skull structure and pectoral girdle than do the urodeles. In general body form, the many ribs and the less specialized limbs, the urodeles are more branchiosaur-like than the liopelmids. There is, therefore, some reason for assuming that the Salientia arose from a phyllospondylous stock if not actually from the same group which gave rise to the urodeles.

If we compare the less specialized frog tadpoles with the urodele larvæ we shall find that they agree in general body and tail form, in the presence of external gills and an adhesive organ (the urodele balancer), and in many internal structures. Some urodele larvæ have horny mouth-parts, but no tadpoles show a precocial development of the teeth. The branchiosaur larvæ did not differ strikingly from the larvæ of either frog or urodele. It is safe to assume that the ancestors of both of the latter passed through a larval stage in the water.

It is now fairly well established that the Amphibia arose from crossopterygians and probably from some generalized rhipidistian of Devonian or Silurian times. The larva of the living *Polypterus* has been frequently compared with the urodele larva. It possesses external gills, adhesive organs and diphyccercal tail. The vertebrate stem which gave rise to the tetrapod line was probably characterized by a *Polypterus*-like tadpole during part of the Palæozoic. This tadpole stage has been passed on with slight modification to modern Amphibia. There is throughout this whole line no evidence of ontogeny repeating phylogeny. No amphibian shows any vestiges of adult crossopterygian structure during its ontogeny. During all this enormous period of time while genetic factors have molded the germ plasm, originally crossopterygian, into the great array of labyrinthodonts, branchiosaurs, microsaur, urodeles, cæcilians and frogs of which we have a record, the tadpole stage has been retained as the scaffolding around which these adult structures have been built. Occasionally in this enormous series forms have avoided an early life in the water by greatly increasing their yolk content. But nearly as often the yolk has secondarily been lost and the old tadpole habitus has been brought forth to give the poorly endowed larva a start in life.

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