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

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In the preceding number I have described a new genus of pipid toad immediately ancestral to *Pipa*. This genus, *Protopipa*, carries its eggs in dermal pockets on its back and its development is direct as in the case of *Pipa*. Is this similarity in life history further evidence that these genera are closely related? Is life history in the Salientia usually a very fluctuating process, or is it frequently sufficiently conservative to serve as an indicator of relationships? As a supplement to my description of *Protopipa* it has seemed advisable to briefly outline the evidence bearing on this problem.

This summary is especially pertinent at this time for Boulenger (1918, p. 62) has recently expressed himself very definitely in regard to one aspect of the subject (translation):

"While admitting the great importance of knowing larval stages, especially those which concern the elucidation of the affinities of degenerate types, I have always been of the opinion that the characters which they furnish can not guide us in our search for a natural classification of the anurous batrachians in either their great or small categories."

In my review of the classification of the anurous batrachians (Noble, 1922), the conclusions which I reached as to the phylogeny of the Salientia were based upon the osteology of adult material but received full confirmation from the myology. In the course of this study it came to my attention that several genera (*Eupemphix*, *Amphignathodon*, *Ceratobatrachus*, *Dendrobates*, etc.) had been in former classifications widely separated from their nearest relatives. I found that there was not only a close structural agreement between these genera and the genera from which they were immediately derived, but that in each case there was almost an exact agreement in life history, so far as known. This agreement was very striking for all these genera exhibited some "unusual mode" of development. Did not this life history data lend support to my classification? The similarity in most cases was as great as that between *Protopipa* and *Pipa*. A brief review of these life histories will make this matter clearer.

Dendrobates is structurally identical with *Phyllobates* except that it lacks maxillary teeth. These two genera are unique among frogs in that the male parent carries the young tadpoles adhering to his back until he finds a suitable pool in which to release them. Other frogs having no relation to these genera, such as *Hemisus* and *Sooglossus*, may permit the tadpoles to cling to their backs for a longer or shorter period, but the tadpoles are structurally unlike those of *Phyllobates* and they are not carried to the pools. In *Sooglossus*, which is most like *Phyllobates*, the tadpoles lack both internal gills and a spiracle.

Turning to another pair of genera, I indicated that the toothless *Pseudophryne* was evolved directly from *Crinia*. Here the life history data is a little more complicated. One species of *Crinia* lays its eggs on land (*lævis*), while another in the water (*signifera*); similarly, one species of *Pseudophryne* lays its eggs in the water, and two others, on land (*australis* and *bibronii*). The larvæ exhibit only rudimentary external gills at an early stage. Development proceeds to the limb-bud stage and remains stationary for months until a rain releases the tadpoles from their capsules. The details of egg-size, number, larval form, etc., are so close between *Crinia lævis* and *Pseudophryne australis* that Harrison (1922, p. 31) concludes:

"This fact affords additional indication that the genera *Crinia* and *Pseudophryne* are closely related, and should not be separated into different families."

Another pair of genera widely separated in former classifications solely because of a difference in dentition is the neotropical *Paludicola* and *Eupemphix*. *Paludicola fuscomaculata* lays its eggs in a foamy mass which floats on the surface of the water. The eggs are small, only 1 mm. in diameter (exclusive of capsules). Fernandez (1921) states that the alveolar structure of the foam is much more minute than in *Leptodactylus ocellatus*. The egg masses are always laid on the borders of lakes where they are frequently attached to water plants. Fernandez never found the egg masses guarded by parent frogs. The eggs are numerous (over a thousand), unpigmented, and very difficult to see in the white foam. The development of *P. fuscomaculata* has been described and the various stages figured by Bles (1907), affording us splendid data for comparison.

The life history of *Eupemphix* was first made known by Dr. J. P. Chapin while on the Princeton Panama Expedition. Mr. C. M. Breder, Jr., secured further data in regard to the same species, *E. pustulosus*, while a member of the Marsh Darien Expedition. A detailed report of the discoveries of these investigators will be made elsewhere. It may be

noted here that *E. pustulosus* deposits a foamy egg mass on the edge of small bodies of water. The mass floats lightly on the surface of the water unless stranded by receding waters. The eggs of *E. pustulosus* are practically identical to those of *P. fuscomaculata*, being only 1.4 mm. in diameter, unpigmented, and laid in large numbers. Development, however, is slower in the former species, and many details, which Budgett tells us are "blurred and as it were hurried over" in *P. fuscomaculata*, are accentuated in *E. pustulosus*. In both species the yolk is small, but obviously dense, for the embryo soon curves around it instead of incorporating it at once into the body as in our common frogs and toads. The adhesive organs which Bles found to arise separately in *Paludicola* differentiate in *Eupemphix* from a crescent as in less specialized frogs (*Scaphiopus*, etc.). The external gills which remain small in the first genus soon develop extraordinary proportions in the latter. These differences are only matters of degree due to the fact that *Paludicola* runs rapidly over the early stages. There is a remarkable agreement between the later and mature larvæ of *Paludicola* and *Eupemphix*. The mature larva of *P. fuscomaculata* has one less row of teeth than *E. pustulosus* but, according to Fernandez (1921), the larval teeth of *Paludicola cinerea* are arranged in exactly the same number of rows. When the whole life history of *Paludicola fuscomaculata* is compared with that of other South American frogs it is found to agree more closely with that of *Eupemphix pustulosus* than with any other species.

The life histories of none of the other pairs of genera mentioned in my earlier paper as closely related (Noble, 1922, Table 2) have been so fully studied as the above. It may be pointed out, however, that *Gastrotheca* and *Amphignathodon*, the only two genera of frogs which develop a single dorsal pouch for the brooding of their eggs, I have grouped together in one family, and have assumed that *Gastrotheca* is directly ancestral to *Amphignathodon*.

If an identical mode of life history, provided this is a specialized or distinctive one, may be taken as an indication of relationship between two genera of Salientia, we might expect that the nearest relatives of any genus having an "unusual mode" of development would exhibit the same type of life history. This is found to hold true for the two large burrowing frogs of Australia, *Philocryphus flavoguttatus* and *Heleioporus albopunctatus*. Both lay their eggs on land in burrows. The eggs are of large size and covered with a frothy outer envelope. So far as known, the later development is very similar. This habit of beating the spawn into a froth crops out in unrelated families, but the details of

breeding and development are different in these unrelated families and similar within a natural group of genera. The classical frothmaker is *Rhacophorus*. The vast majority of the species of this genus lay their eggs out of water, and beat the egg masses with their hind legs into a foam. The tadpoles which soon leave the foamy "nest" agree in most of their larval characters. A few mountain species of *Rhacophorus* have succeeded in increasing the yolk content of their eggs. These large eggs are not beat into a foam, probably because of mechanical difficulties. This sudden increase in yolk content may seem detrimental to the theses expressed above. We shall see, however, that in the Amphibia yolk may be suddenly increased or decreased without altering certain details of life history. Thus, *Gastrotheca* may have large or small eggs, but all of its larvæ while within the pouch possess enormous bell-shaped gills which as we shall see below are peculiar to a natural group of forms. It would be interesting to know more of the development of *Rhacophorus reticulatus* and *R. everetti*. The first was reported long ago as laying large eggs which are guarded by the female. The second species was recently discovered by Mr. E. H. Taylor on Thumb Peak, Palawan, P. I., to lay large, unpigmented eggs. These measure 2.5 mm. when within the ovaries of a female 42 mm. head and body length, as I have determined by dissection.

Rhacophorus has for a long time been recognized as ancestral to several other ranid genera. Perhaps the closest of these derived groups is *Philautus*. The life history of *Philautus* has been found to agree entirely with that of *Rhacophorus*. The eggs of only two species of the genus have been previously described, but Mr. Clifford H. Pope has discovered two other species breeding in Hainan. The mode of life history of *Rhacophorus* and *Philautus* is distinctly different from that of all other Asiatic batrachians. The tadpoles of *Philautus* are well known to be very similar to those of *Rhacophorus*.

A second genus directly derived from *Rhacophorus* is the African *Chiromantis*. *C. rufescens* has long been known to make froth nests and sometimes, but not always, close to water (Noble, 1924a, p. 231). *Chiromantis xerampelina* apparently has breeding habits similar to *C. rufescens* (Hewitt, J. and Power, J. W., 1913). Mr. Arthur Loveridge assures me that *C. petersii* also builds foam nests but always over water. So far as known, the life history of *Chiromantis* agrees in all essential features with that of *Rhacophorus*.

This brief outline of the relation of life history to phylogeny in the Amphibia can include only a fraction of the genera in any detail. In

any genus the difference between the tadpoles of two species during the early larval stages is usually dependent on the stage of development reached before the hatching process is initiated. Such a difference is very conspicuous even in our local region where *Rana pipiens* hatches when only 4 mm. in length. It has no external gills and possesses the merest rudiment of a tail-bud (1 mm. long). These rudimentary larvæ do not react to tactile stimuli. *R. sylvatica* on the other hand has larger eggs. Its tadpoles measure about 7.5 mm. on hatching. The tail is 3.5 mm. in length and has a distinct fin. Gills are present. The tadpole reacts violently to tactile stimuli. There is abundant evidence that change in yolk size has occurred often and suddenly in the Salientia. It has, therefore, been difficult to distinguish in the early stages of some related species very much that is similar. The apparently more superficial characters such as method of oviposition, form of the egg capsules, structure of the mature larva, would seem to guide us more surely in our general comparisons. Of more importance still is the presence of specialized larval organs of similar character in two groups. I shall, therefore, lay stress upon these organs in this brief review.

Rana opisthodon lays eggs on land which develop directly into frogs. The chief peculiarity of the encapsuled larva is a row of transverse folds along each side of the abdomen. *Cornufer* is closely allied to *Rana opisthodon*, differing chiefly in the extent of webbing between the digits. *C. guentheri*, according to Mr. E. H. Taylor, lays large-yolked eggs on land as in the case of *R. opisthodon*. I find that the encapsuled froglets have abdominal folds in the same position as in that species. These folds have always been assumed to be respiratory structures in *R. opisthodon*. Sections of the folds of *Cornufer* reveal the fact that their chief peculiarity is that they are composed of an enormous number of minute, longitudinal ridges which in cross-section appear as villi. Capillaries are not found in these villousities and only a few insignificant blood vessels. A comparison of this tissue with gill tissue in other Amphibia, or even with such respiratory integument as is found in the pouch of the marsupial frog, in the brooding sac of *Pipa*, or on the villousities of the "hairy frog" (Noble, in press) will make it clear that these filaments in *Cornufer*, and by inference in *Rana opisthodon*, cannot function in respiration. I interpret them as due to the great folding of the somatopleure of the flanks which accompanies the rapid absorption and readjustment of the yolk in these frogs just before hatching.

It has been pointed out elsewhere (Noble, 1922, p. 20) that the toothed ("dyscophids") and the toothless brevicipitids arose from a

displasiocoelous stock which differed from the Ranidæ only in the expanded sacral diapophyses. Some toothless genera arose directly from toothed forms, but more often one toothless genus arose from another. One group of brevipitids in southeastern Asia is of especial interest for it illustrates almost diagrammatically the main stages in the reduction of the pectoral girdle from the primitive and complete *Rana*-like girdle to the highly modified girdle of *Microhyla*. This group includes the genera *Kalophrynus*, *Kaloula*, and *Microhyla*. *Kalophrynus* agrees most closely with the ancestral ranid stock. Omosternum, clavicles, procoracoids and coracoids are present. In *Kaloula*,¹ in spite of Boulenger's (1882) and Barbour's (1909) statements to the contrary, the omosternum and procoracoids are both present but reduced. The clavicles have disappeared. Finally in *Microhyla* this reduction has continued to the extreme condition. The omosternum, clavicles, and procoracoids are lost. How may we be sure that these genera are closely related when they exhibit such enormous differences in shoulder girdle? All three lay small, pigmented eggs in the water. This is not a distinctive feature for there are many genera of frogs which have secondarily diminished the yolk content of their eggs. The larvæ which hatch from the eggs are very peculiar and readily distinguished from all other tadpoles except a few to be discussed below. The external nares do not break through in these tadpoles until late in larval life. The olfactory chamber is protected from the contents of the buccal cavity by a tongue-shaped flap which projects forward. The tadpoles of these genera have no horny mandibles or larval teeth. The lower lip is rather extensible and assists the tadpoles in their surface feeding. The spiracle is median in the three genera. The tadpoles have a broad webbing to their toes which is reduced on metamorphosis.

One species of *Microhyla*, *M. achatina*, differs slightly from the "*Kalophrynus* type" in that the lower lip is more produced than in other species of the genus. In other genera, such as *Megalophrys*, *Phyllobates*, and *Phyllomedusa*, certain species exhibit unusually produced lips. The causes of this dimorphism of larval mouth-form within a genus are not known. They do not seem to have any phylogenetic or adaptational significance.

Is this distinctive tadpole, this "*Kalophrynus* type," found in any other batrachian? We might expect it to occur in the "dyscophid" ancestors of the *Kalophrynus-Microhyla* group if living today and also

¹In this connection I may add that *Cacopoides borealis* Barbour should be referred to *Kaloula* as it does not differ in either the structure of its pectoral girdle or its terminal phalanges from *Kaloula pulchra* or *K. verrucosa*. I have examined the type of Barbour's species.

in any brevicipitid genera allied to this group. This is exactly what we find on looking further into the life histories of Asiatic Salientia. The "dyscophid" *Calluella* has been described by Smith (1917, p. 270) as having the same peculiar tadpoles of *Kalophrynus*. The toothless *Cacopus* and *Glyphoglossus* have similar tadpoles. Further, the American *Gastrophryne* which structurally is very similar to *Microhyla* has the same type of tadpole, at least so far as known today (Wright and Wright, 1923).

There is still an additional peculiarity which will probably be found throughout this entire group of genera. The egg capsules of *Kaloula* (Annandale, 1917) and of *Gastrophryne* (Wright and Wright, 1924) are flattened at one pole, and hence maintain an upright position in the water. This peculiar modification of the egg capsules is not found in any other Amphibia in the world. It would be interesting to know if *Calluella*, *Glyphoglossus*, *Microhyla*, and *Kalophrynus* did not have their egg capsules flattened at one end as in *Gastrophryne*. It would seem that we had in the Brevicipitidæ a splendid example of where identical larval (and possibly egg capsule) modifications stamp a group of genera as related in spite of their widely separated ranges and in spite of the fact that some of these genera have maxillary teeth, an omosternum, clavicles, and procoracoids, while others lack these structures entirely. We find, therefore, an agreement between the phylogeny of the Brevicipitidæ as I outlined it in 1922 and the evidence to be derived from homologous larval specializations throughout this family.

Many brevicipitids have large-yolked eggs and, while it is possible that some of these may have arisen suddenly from small-yolked species, just as we have seen in other families, it is also possible that a series of large-yolked species may be found which undergoes the same progressive modifications in the adults which are found in the *Kalophrynus-Microhyla* group. Thus, *Oreophryne verrucosa*, which has a nearly complete shoulder girdle, lays 10 to 20 large-yolked eggs attached to the substratum by a mucilaginous cord. Development is direct. *Hylophorbus* (= *Mantophryne*) has lost both clavicle and procoracoid (Méhely, 1901) and yet its life history seems to be nearly identical with that of *Oreophryne*. The fact that the eggs of *Hylophorbus biroi* were found under the surface of the water would apparently mean that these eggs were covered by a freshet. The life histories of all these large-yolked brevicipitids have been compared with that of *Eleutherodactylus*. The difference between the latter and the former genera has not been sufficiently stressed. The mucilaginous cord of *Hylophorbus robustus* is not

found in *Eleutherodactylus*. No egg teeth have been described in any brevicipitid. Other differences will doubtlessly be made known as further specimens are collected.

In my classification of 1922 I left one family of frogs, the Hylidæ, not clearly distinguished from its bufonid progenitors. It seemed that the one family gradually merged into the other. A reëxamination of all the intermediate genera available has brought out some interesting differences. The typical hylids are distinguished from the bufonids by the presence of an intercalary cartilage. In my review of the ranids of Africa (Noble, 1924a) I found this structure was present in a closely related group of genera and absent in all others. Similarly, in the East Indian and Oriental regions the genera with the intercalary cartilage are more closely related to one another than they are to any ranid without the cartilage or bone. In the African ranids mentioned the shape of the terminal phalanx was frequently variable. Within a closely related group of genera the primitive genus (*Chiromantis*) had dilated terminal phalanges. Two genera (*Leptopelis* and *Hylambates*) derived from this had claw-shaped phalanges, while the most specialized group (*Kassina*) had apparently secondarily developed dilated terminal phalanges again. All of these genera possessed the intercalary cartilage whether or not the terminal phalanges were claw- or T-shaped. In the Ranidæ the presence of an intercalary cartilage is more fundamental than the shape of the terminal phalanx.

Applying this same conception to the Hylidæ we may redefine this family in order that it may embrace two groups of border-line genera; namely, the *Hyloscirtus* group and *Centrolenella* and the allied *Centrolene*. In another paper I shall discuss these genera in more detail. For the present we may define this family as follows:

HYLIDÆ.—Characters of the Bufonidæ, but an intercalary cartilage or bone between the ultimate and penultimate phalanges of each digit. Sacral diapophyses usually dilated.

Under this arrangement the family is sharply divided into two groups of genera:

I.—*Hyloscirtus* group:

- (1) *Hyloscirtus*, (2) *Cerathyla*, (3) *Gastrotheca*, (4) *Amphignathodon*.

II.—*Hyla* group:

- (1) *Hyla*, (2) *Phyllomedusa*, (3) *Centrolene*, (4) *Centrolenella*, (5) *Pternohyla*, (6) *Tripurion*, (7) *Corythomantis*, (8) *Diaglena*, (9) *Lophyohyla*, (10) *Amphodus*.

The *Hyloscirtus* group is characterized by cylindrical or slightly dilated sacral diapophyses. The terminal phalanges may or may not be claw-shaped, but are never T-shaped. The genera in this group differ

radically from all other batrachians in that the females carry the eggs on their back either merely adhering to the unmodified integument or enclosed within a single sac. The larvæ as they develop are characterized by membranous or cup-shaped gills. These differ from genus to genus, the least specialized species having the more primitive type. *Hyloscirtus evansi* and *H. goeldii* possess two pairs of gill membranes. Mr. H. W. Parker has kindly sent me a sketch of the encapsuled larva of *H. goeldii* which I have compared with a series of larvæ removed from the capsules of a female *H. evansi* secured by Mr. H. Lang in British Guiana. *Hyloscirtus fuhrmanni* possesses only one pair of gills. This has resulted not from fusion of the two gills in *H. evansi* but from a loss of the posterior pair. Serial sections reveal only one enlarged aortic arch in *H. fuhrmanni* but two in *H. evansi*.

The external gills of *Gastrotheca* and *Cerathyla* are apparently identical and different from those of *H. evansi* in that the two membranes of each side are united into a single cup. I have found that in *Gastrotheca monticola* the gills on each side fuse at a very early stage, and soon form a cup which has been described and figured many times. It should be noticed that the genera of the *Hyloscirtus* group which have the least specialized gills are also the least specialized when adult. The fused-gilled or typical bell-gilled genera either have dorsal sacs in the female or excessive bony growths partly in the shape of teeth (in one case true teeth). Here again we find larval and adult specialization going hand in hand. Surely encapsuled larvæ of *Cerathyla* could live with gill membranes similar to those of *H. evansi*, but they nevertheless have the more specialized type of gills. It is impossible to say at this time from what genus of bufonids or hylids *H. evansi* may have been evolved. Starting with *Hyloscirtus*, we find that the more specialized genera derived from it have the more specialized larval organs.

The second group of hylids never have large eggs or membranous gills. Some, however, have specialized breeding habits which may be compared phylogenetically as in the case of the *Hyloscirtus* group. The least specialized genus of the second group is *Hyla*. Most species of this genus lay their eggs in water and the tadpoles which develop may be either of the "pollywog type," that is, round-bodied without body fin, or they may be of the "sunfish type,"—swimming larvæ with a broad body fin. There is a close correlation between the current rate and the body form of these tadpoles; and in the case of pond larvæ, between body form and swimming movements. All tropical species of *Hyla* undergo part of their development in the water.

Turning to the more specialized genera we find that Boulenger (1882) in his "Catalogue" considered that two species of *Hyla* having a vertical pupil might well be relegated to a distinct genus, *Nyctimantis*. But Stejneger, realizing that this vertical pupil probably arose independently in the New Guinean and South American species, erected a new generic name, *Nyctimystes* for the New Guinean species. I have found that in Santo Domingo the pupil of the tadpole of *Hyla vasta* is vertical and diamond-shaped. The pupil of the adult is four angled but not diamond-shaped. When dilated the two longer sides of the pupil extend far forward, giving an acute anterior angle and making the main axis a horizontal one, but when the pupil is contracted these anterior sides draw so close to the posterior ones that the pupil is a vertical slit. Should we, therefore, describe the pupil of *H. vasta* as horizontal or vertical? It cannot be argued that the dead specimen of *H. vasta* would have a contracted pupil and hence the species should be referred to *Nyctimantis*. Preserved specimens of *Hyla* may have either a contracted or an expanded pupil.

It is interesting to see what light life history sheds on this problem. The life history of *Nyctimantis* and *Nyctimystes* is unknown, but if *H. vasta* agrees closely in life history with some species of *Hyla* we have evidence of relationship. *H. vasta* is so enormous that we would compare it first with some of the large species of *Hyla*. *H. vasta* lays its eggs in small rocky basins near the edge of mountain streams in Santo Domingo. These basins which may possibly be scooped out by the parent frog are filled with water by seepage from the stream. The tadpoles have small external gills. After six days they wriggle out of water through the damp spaces between the rocks and soon reach the main mountain pool. Here they grow into thick-tailed, large-mouthed tadpoles having no back fin. The mature larva in its adhesive mouth and slim body-form is well adapted to life in a mountain stream.

The basin breeding of *H. vasta* suggests the breeding habits of *Hyla faber* as made known by Goeldi. Unfortunately, Goeldi's observations were never confirmed and we know nothing about the details of nest building, or the development of the larvæ other than the few general statements Goeldi published. On the other hand, the closely related species, *Hyla rosenbergi*, was found by Mr. C. M. Breder, Jr., to build mud-nests similar to those of *H. faber*, but if Goeldi's account is correct, the part played by the sexes in the nest building is different in the two species. In the case of *H. rosenbergi* the male does all the nest building. This was not determined by direct observation but by the discovery

that when the nests are being built only the males are in or near them. The nests are made in the forest along drying pools, close enough to the edge of these rain water or stream pools to be filled by seepage from the main body of water. Occasionally they are constructed exactly as in the case of *H. faber* in shallow water and the walls of the circular basins or nests built up above the surface of the water. On one occasion a rock crevice was utilized for a nest and a dam was thrown up across the outer end converting the crevice into a basin. A comparison between this nest and that of *H. vasta* is obvious. The eggs of *H. rosenbergi* and of *H. vasta* are pigmented; the former float in a single layer, the latter are stuck in clumps to the rocks in the bottom of the basin (at least just before hatching). The recently hatched larvæ of the two species are both dark but not identical in form. The chief difference seems to be in the development of external gills. Shortly after hatching they are enormous in *H. rosenbergi* and are apparently utilized by the larvæ to keep their hold on the surface film exactly as in the case of *Leptodactylus ocellatus* larvæ, according to Fernandez (1921). Attached to the surface film these gills must function to the fullest extent. *H. vasta* never develops large external gills, nor do the early larvæ ever rise to the surface of their rock-lined nests. In another paper I shall show that this difference in external gills seems to be correlated with different temperatures in the nests of the two species, and also with a difference of stagnation in the waters. For our present purpose it is of interest to note that the breeding habits of *H. vasta* and *H. rosenbergi* are not unlike.

It is possible that *H. vasta* is not closely allied to *H. rosenbergi* but to some other basin-breeding species. In this connection it may be noted that the breeding habits of *H. resinificatrix* probably do not differ radically from these other basin breeders. Dr. Lorenz Müller writes me (translation):

"Above all may I state that the report which Goeldi has made on the breeding habits of *Hyla resinificatrix* rests upon a great error. The frog does not build its nest with gum but uses the nest of certain American bees."

From this life-history data it would not seem advisable to separate *Hyla vasta* from other basin-breeding species of the genus merely because its pupil when contracted is vertical. There is another group of hylids closely allied to *Hyla* which is separated from the genus chiefly because of its vertical pupil. It is placed in the genus *Phyllomedusa*. In this genus I include *Agalychnis* for there seems to be every degree of intergradation between species with opposable inner fingers and toes and

those without such types of appendages. The species included in the genus are all green in life, usually brightly variegated with other colors on the sides and rarely spotted above. All of the species, so far as known, lay their eggs on leaves above the water. The less specialized *P. spurrelli* lays its pigmentless eggs on the upper surfaces of leaves which curl around the egg mass (Boulenger, 1913). The more specialized *P. hypochondrialis* and *P. sawagii* curl the leaves over the egg cluster to form the nests which have been so fully described by Budgett (1899) and Agar (1909).

Very recently Dunn (1924) has found that the larvæ of *Hyla uranochroa* have a red iris similar to those of most species of the genus *Phyllomedusa*. This species when adult is brilliant green and has every appearance of a *Phyllomedusa* other than its horizontal pupil. Dunn found eggs attached to leaves over the stream which he attributed to this species. The form of the nest was similar to that of *Phyllomedusa*. Dunn concludes (p. 3):

"It would seem that *Hyla uranochroa* might well be an approach towards the two more specialized genera in eye color and in habits, while in form of pupil and character of hand still a technical *Hyla*."

The hand characters mentioned by Dunn do not hold throughout the genus as one may convince oneself by comparing *Phyllomedusa callidryas* with *Hyla pulchrrilineata* or *H. andersonii*. It would, therefore, seem that one group of *Hyla* species has specialized in a red iris, a bright green color, and in laying its eggs out of water on leaves over the stream. The more primitive species of this group we still retain in *Hyla* because of the horizontal pupil. The more specialized forms add to the color modifications a hand and foot modification especially adapted for gripping branches. These forms beat the egg masses into a foam and fold leaves over it to better protect it. No detailed comparisons between the early larvæ of the more specialized and more primitive species have been made but we may expect a certain similarity. It may be noticed, however, that the later larvæ are of different "adaptive types." The tadpole of *H. uranochroa* is of a mountain-brook type even though its mouth is not greatly modified for holding on to rocks. Most species of *Phyllomedusa* are broad-finned pond-types similar to the tadpole of *Hyla versicolor*. Further, Lutz (1924) has recently described among these pond-type larvæ one species that has its mouth produced into a funnel to assist it in surface feeding. Here, then, within an obvious natural group of species we find the mature tadpoles adapted to mountain stream, to pond, or to plankton feeding. The mode of life history, however, has remained constant throughout the group.

One of the difficulties in the new definition of the Hylidæ proposed above was that the family would embrace *Centrolene* and *Centrolenella* which at first sight do not seem related to *Hyla* for they possess T-shaped terminal phalanges. Does the life-history data help us in this matter? The life history of neither *Centrolene* nor *Centrolenella* is known, but Mr. C. M. Breder, Jr., made some observations in Panama on the breeding of another tree-frog which may be of assistance to us. This tree-frog I cannot distinguish from *Hylella parabambæ* as described by Boulenger. It agrees externally with the less specialized species of *Phyllomedusa*, except that its pupil is horizontal and its iris is silvery. In life the iris was silver and covered with a network of dark lines. The absence of vomerine teeth is a feature of no consequence. I have discussed elsewhere (Noble, 1924a, p. 186) the many exceptions to the use of the presence or absence of vomerine teeth as a generic or even a specific character in the Salientia. It would seem superficially that *H. parabambæ* was a species of *Phyllomedusa* which had retained the iris and pupil of a *Hyla*.

The life history of *H. parabambæ* would support this conclusion. Breder found two clusters of eggs on the undersurfaces of leaves overhanging the water at a place where *H. parabambæ* was the only frog calling. These eggs were unpigmented, 2 mm. in diameter (without capsules). The first bunch of eggs were hatching and only nine larvæ were left within the capsules. There were thirty-seven eggs in the second cluster. These were well supplied with clear jelly which enclosed the eggs in a single mass measuring 25×22×10 mm. The developing tadpole showed a great similarity to that of *Phyllomedusa hypochondrialis* at a similar stage. Each has a long, narrow tail and a small, rounded yolk well marked off from the rest of the tadpole's body. The gill filaments in each are long and tenuous. In breeding site, eggs, larvæ, and apparently development, *H. parabambæ* agrees fairly well with the more primitive species of *Phyllomedusa*.

An examination of the skeleton of a specimen of *H. parabambæ* has shown that this species should be referred to *Centrolenella* even though the digital dilations are not truncated as in the type species of the genus. The terminal phalanges are T-shaped and there is no omosternum. In external features the species agrees with the uranochroa group of *Hyla* (except for iris color); in internal characters it agrees with *Centrolenella*. This would suggest that *Centrolenella* and *Centrolene* have sprung from *Hyla*, and that the new definition of the Hylidæ given above is better than the old one, for it embraces all genera of a natural group of tree frogs.

The Hylidæ arose directly from some group of toothed bufonids. The life histories of only a small proportion of the bufonid genera are known. A few of the best known may be mentioned here. Some years ago Wandolleck (1907) described a little Brazilian frog as *Hylodes petropolitanus*. The life history of the various West Indian species of *Hylodes* (= *Eleutherodactylus*) was well known to be very different from that which Wandolleck described for this species. Thanks to the kindness of the Director of the Dresden Museum, there is now in the collections of the American Museum one of the adults, one of the larvæ, and two of the eggs which Wandolleck described. I was struck at once by the great superficial resemblance between the frog and another species of much larger size living in the same region. The latter species I have shown (Noble, 1917) cannot be referred to *Hylodes* because of its rounded terminal phalanges in the adult. I have called it a species of *Borborocætes*, following the suggestion of Boulenger. It is still a matter for investigation whether this species is congeneric with the various species of *Borborocætes* found along the Pacific coast of South America. The little *Hylodes petropolitanus* I find on dissection to be osteologically nearly identical with *Borborocætes miliaris*. Whatever genus the latter species is placed in must include the former as well. Both live side by side in the vicinity of Petropolis, Brazil. Their life histories are unique among Salientia and practically identical one with the other. The eggs are laid near mossy brooks. The tadpoles which have a peculiar flattened form scoot over the trickles which cover the rocks. No other tadpoles have exactly the same form as these. Once more we see that in forms having a specialized life history, related forms exhibit the same peculiarities.

It is well known that the genus *Eleutherodactylus* is characterized by direct development. The only reported case of an *Eleutherodactylus* having indirect development other than the one just discussed is much more difficult to dispose of than that. In the 'Check List of North American Amphibians and Reptiles' (Stejneger and Barbour, 1923) there appear only two species of the genus recorded from the United States. One, *E. ricordii*, is known from the unpublished work of Dunn in Cuba and Deckert in Florida to have direct development, while the other, *E. latrans* of Texas, is reported by Strecker (1910) to pass through a tadpole stage in the water. *E. latrans* has never been carefully dissected to determine if it is a true *Eleutherodactylus*. Its toes (to judge from photographs) are narrow, apparently not broader than those of *Borborocætes*. It would, therefore, seem likely that it may be found to have

the terminal phalanges similar to *Borborocætes*. The status of *E. latrans* cannot be determined without further data.

I have recently secured the eggs of five species of *Eleutherodactylus* in Santo Domingo. Development was in all cases direct. It is usually assumed that in *Eleutherodactylus* there are no external gills present at any stage of development, and that gill clefts are never formed. This assumption is based on the careful work of Sampson on the development of a Jamaican species. In two Santo Domingan species, *E. abbotti* and *E. flavescens*, the same conditions prevail as I have determined by a study of several nearly complete developmental series of these species. In the very much larger *E. inoptatus* of the same region there are functional gills present for several days before the tail becomes fully thinned and expanded. These gills have a peculiar form. No filaments are present, but a single folded sheet of tissue to each gill. This sheet has the form of a handkerchief held in the middle and allowed to fall in loose folds. As such gills are unique in the Amphibia we may call them "handkerchief gills" to distinguish them from "bell gills" or other types of external gills in the Salientia. There are two pairs of such gills present in *E. inoptatus*, the anterior pair much larger than the posterior, but neither reaching a very large size. How may we account for these gills of *E. inoptatus* when other members of the genus lack them? *E. inoptatus* is a much larger species. It is possible that it requires a greater oxygen supply than the latter species and that its gills are retained to supply this need. It is also possible that the greater number of eggs in a single mass would cut down the respiratory surface available to each. *E. inoptatus* is the only species of the genus known to lay its eggs in holes in the banks near streams. Such situations are very moist and not well aerated. There is no reason for assuming that *E. inoptatus* is more primitive than other members of the genus. The presence of these small gills during the early stages of development does not change the mode of life history. In egg-capsule form, direct development, tail form of the larva, and egg tooth on the upper lip over the premaxillary symphysis, *E. inoptatus* agrees with other species of the genus.

Before concluding this discussion of *Eleutherodactylus*, reference should be made to some recent observations of Dunn, soon to be published. In the paper above referred to (Noble, 1922) I stated that a group of firmisternal or semifirmisternal Salientia found in the neotropics must have arisen from the Bufonidæ and had no relation to either the Ranidæ or Brevicipitidæ with which these genera had formerly been grouped. I ventured to state that one of these brachycephalids, *Sminthil-*

lus, was an *Eleutherodactylus* which had lost its vomerine teeth and partially fused two halves of its shoulder girdle in the midline. Dunn, at the suggestion of Dr. Barbour, has studied the life history of *Sminthillus* and has found that it lays its eggs on land. These are large, very few in number, and probably develop directly into frogs. The data which Dunn secured would tend to show that the life history of *Sminthillus* was identical with that of *Eleutherodactylus* except that the female laid fewer eggs. As a general rule the smaller the frog within a genus, the fewer eggs it lays. I found in Santo Domingo that the large *E. inoptatus* laid approximately twice as many eggs as the small *E. abbotti* and *E. flavescens*. Hence it is possible that the small number of eggs in *Sminthillus* may be correlated with its remarkable small size.

In continuing this hasty sketch of the Salientia we may glance briefly at the Pelobatidæ. *Pelobates* is osteologically more specialized than *Scaphiopus*. Although Boulenger (1899) has emphasized the close relationship of these genera, Stejneger and Barbour (1923) still place them in different families. The life histories of these two genera are extraordinarily similar. I have studied the life history of *S. holbrookii* and have compared it with Boulenger's account (1897) of *P. fusca*. Both species breed in temporary pools after rains. The egg mass is rope-like and attached to water weeds. Two egg capsules (in addition to the vitelline membrane) are present in spite of Boulenger's (1897) and Wright and Wright's (1924) statements to the contrary. The larvæ hatch early and have a very similar form. The tooth rows of the mature larvæ are very similar. Some differences appear in the number of bunches in which the egg rope is laid. The gills of *Scaphiopus holbrookii* are more pronounced at an early stage than those of *P. fusca*. There are slight differences in body form between these early larvæ. The differences between the method of egg-laying, the egg mass, the egg capsules, the early larvæ and the mature tadpoles of *Scaphiopus* and *Pelobates* are much less than between similar features of two closely related species of *Rana*.

I have suggested elsewhere (Noble, 1924) that the Pelobatidæ may have arisen from the Liopelmidæ and that the Discoglossidæ represent another branch from this primitive batrachian stock. I pointed out that the liopelmids have many *Urodele* features such as amphicœlous vertebræ, a single coraco-scapula (in addition to the coracoid), two post cardinals, etc. It is of great interest, therefore, to find that *Ascapheus* apparently has no voice but has a copulatory mechanism very similar to that of the salamanders. In the male a ring of enlarged cloacal glands is formed

well inside the orifice in the "tail." A cluster of horny spines is found inside the cloaca just posterior to the enlarged glands. When the "tail" is turgid with blood the cloaca is slightly everted until the spines are exposed. This mechanism suggests that the tail is pressed against the cloaca of the female in copulation (as the cloaca of certain salamanders). Breeding specimens readily extend their "tails" forward under the body until in the position to perform such an operation. My sections of the urinogenital organs of the breeding female reveal great masses of spermatozoa in the lumen of the oviducts and particularly in the glands along the posterior part of the oviducts. Sections of the oviducts of females taken after their eggs had been laid show many of the glands of the posterior part of the oviduct still filled with spermatozoa. These microscopic pictures recall at once the spermatheca of the female *Ambystoma*. It is possible that this similarity is due to mere convergence, for the *Urodele* spermathecae lie in the cloaca, while those of *Ascaphus* in the oviducts. I shall discuss this problem in more detail in a paper now in preparation.

In the above discussion I have made no attempt to trace through the progressive modifications in life history which have accompanied the phylogenesis of the Salientia. I have merely called attention to certain pairs or groups of genera which anatomical evidence would indicate as related. I have shown that the genera within each of these groups have nearly always the same mode of life history. This similarity is very striking when the life history is a distinctive or very specialized one.

LITERATURE

The literature cited above is included in the bibliography at the close of the next number (Novitates, No. 166).

